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New species of *Orygotherium* (Palaeomerycidae, Ruminantia) from the Early and Late Miocene of Eurasia

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(With 2 text-figures and 2 plates)

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Abstract

The Late Miocene Kohfidisch and Götzendorf faunas (Austria) provided new finds of a highly specialized enigmatic ruminant *Orygotherium*, previously known from the early Middle Miocene of Central Europe and Early Miocene of Eastern Siberia (Russia). In addition to the single species *O. escheri,* two new species are described: *O. heinzi* from the Kohfidisch fauna (MN11) and *O. tagaiensis* from the Tagai fauna (MN3) of the Olhon Island (Lake Baikal). The relationships and ecology of *Orygotherium* are discussed and its placing in the Palaeomerycidae is suggested.

Introduction

Orygotherium was a rather rare Miocene ruminant, represented by a restricted number of specimens from Central Europe and Eastern Siberia. Hitherto, only a single species *O. escheri* was attributed to the genus, the systematic position of which long remained uncertain (RÖSSNER & MÖRS 2001). The study of the Late Miocene Kohfidisch fauna from the southern Burgenland and the Götzendorf fauna from the Vienna Basin (Lower Austria) produced new finds of *Orygotherium.* Data from Kohfidisch stimulated the revision of the genus and considerably enriched the knowledge of its evolution and relationships.

The genus and species *Orygotherium escheri* were founded by von MEYER (1838) on the basis of some cheek teeth from Käpfnach (Switzerland). Later on, the upper and lower jaws of *O. escheri* were also described from Göriach (Austria) (HOFMANN 1893; THENIUS 1950a, b). In addition to these finds, an upper third molar (M3) was recently discovered in Hambach (Germany) (RÖSSNER & MÖRS 2001). All these specimens are associated with lignitic deposits corresponding to the Mammal Zone MN5 (RÖSSNER & MÖRS 2001). In Eastern Siberia, dental and postcranial remains of *Orygotherium* were found in the Early Miocene of Tagai on the Olhon Island (Lake Baikal) (VISLOBOKOVA 1994). These remains, originally described as *O*. aff. *escheri* (VISLOBOKOVA 1994), are referred here to a new species, *O. tagaiensis*. RÖSSNER & MÖRS (2001) doubted the Early Miocene age of the Tagai fauna but *Brachyodus intermedius* certainly indicates MN3 (VISLOBOKOVA 1994; MADE 1999).

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The new material from Austria essentially extends the stratigraphical range of *Orygotherium*. The Götzendorf fauna refers to the Early Vallesian and is correlated to the end of MN9 (DAXNER-HÖCK 2001). The Kohfidisch fauna first was thought to be of Early Turolian (MN11) age (BACHMAYER & WILSON 1970), later on the fauna was referred to the Late Vallesian (MN 10) (de BRUIJN et al. 1992, RÖGL & DAXNER-HÖCK 1996, DAXNER-HÖCK 1996, 2001), but according to recent data the Early Turolian (MN 11) age is confirmed (DAXNER-HÖCK 2003). *Orygotherium* from Kohfidish is described here as *O. heinzi*, n.sp. and that from Götzendorf as *Orygotherium* sp.

The terminology of tooth crown elements is mainly adopted from GENTRY et al. (1999). The MN boundary ages are according to HARZHAUSER et al. (2003).

Abbreviations: AW - anterior width; L - length; PW - posterior width; W - width; H - height. Institutions: NHMW - Natural History Museum in Vienna; PIMUZ - Palaontologisches Institute und Museum Zürich, Switzerland; PIN - Paleontological Institute of the Russian Academy of Sciences in Moscow.

Systematic paleontology

Suborder Ruminantia

Superfamily Giraffoidea

Family Palaeomerycidae

Orygotherium von MEYER, 1838

Orygotherium: von MEYER 1838: 413; 1839: 4; SCHLOSSER 1887: 296; STEHLIN 1914: 192; 1919: 151; THENIUS 1950a: 112; 1950b: 230-235, Abb. 2, 3; VISLOBOKOVA 1994: 186-188, pl. 2, figs 1-14; RÖSSNER & MÖRS 2001: 591-593.
Palaeomeryx: HOFMANN 1893: 65, Taf. XIII, Fig. 5, Taf. XV, Fig. 3.
Lagomeryx: PIA & SICKENBERG 1934: N 2091, 2116, 2132.
Micromeryx: MCKENNA & BELL 1997: 422.

T y p e s p e c i e s : *Orygotherium escheri* von MEYER, 1838

D i a g n o s i s: Small-sized. Molars brachyodont, with significantly enlarged basal and additional elements (cingula, styles, stylids and folds). M3 smaller than M2. Pillar of paracone strong, forming an elongated, anteriorly directed fold. Parastyle and mesostyle large, extending far labially. Anterior cingulum very strong and crest-like. On M3, metaconule smaller than protocone. Lower p1 apparently absent. Lower molar with strong, almost parallel *Palaeomeryx* fold, ectostylid and posterior cingulid. Posterior cingulid pocket-like. Metastylid present but unconnected with protoconid-entoconid crest. On m3, third lobe large, two-cuspid. Emended after THENIUS (1950b) and (RÖSSNER & MÖRS 2001).

R e m a r k s: *Orygotherium* was regarded as a synonym of *Palaeomeryx* (HOFMANN 1893) or some cervid genera (PIA & SICKENBERG 1934; MCKENNA & BELL 1997). However, many scientists consider the genus to be valid. *Orygotherium* differs from *Palaeomeryx* and other palaeomerycids in smaller size, a peculiar shape of the paracone pillar on the upper molars and in the more developed basal elements both on the upper and lower molars.

Orygotherium escheri von MEYER, 1838

Orygotherium escheri: von MEYER 1838: 413, 1839: 4; SCHLOSSER 1887: 296; STEHLIN 1914: 192, 1919, 151; THENIUS 1950a: 2-6, 1950b: 230; GENTRY et al. 1999: 230, 254; RÖSSNER & MÖRS 2001: 591-593 (pars.)
Palaeomeryx escheri: HOFMANN 1893: 65.
Lagomeryx escheri: PIA & SICKENBERG 1934: 248-253.

L e c t o t y p e: Right maxilla with M1-M3; Coll. PIMUZ A/V 0370 (RÖSSNER & MÖRS 2001, figs. 1B, D, E).

P a r a l e c t o t y p e: Right mandible with p2-m3; Coll. PIMUZ A/V 0369 (RÖSSNER & MÖRS 2001, figs. 1 A, C).

T y p e l o c a l i t y: Käpfnach, Canton of Zürich, Switzerland.

T y p e l e v e l: Brown coal, Lower Upper Freschwater Molasse (see RÖSSNER & MÖRS 2001).

O t h e r l o c a l i t i e s: Göriach, Austria; Hambach 6C, Germany.

A g e: Early Middle Miocene, Late Orleanian, MN 5.

D i a g n o s i s: On M3, metaconule enlarged, pillar of metacone absent or weak, neocrista weak. Premolar row elongated. On p3, metaconid weakly projected lingually. On lower molars, fold of entoconid absent (or weak). On m3, third lobe not very elongated.

M e a s u r e m e n t s and d e s c r i p t i o n: see THENIUS (1950b) and RÖSSNER & MÖRS (2001).

Orygotherium tagaiensis **sp. nov.**
(Plate 1, Figs. 1-3, Plate 2, Fig. 1)

Orygotherium aff. *escheri*: VISLOBOKOVA 1994: 186-188, figs. 6-12, pl. 2, figs. 1-14;
Orygotherium escheri: RÖSSNER & MÖRS 2001: 521.

D e r i v a t i o n o m i n i s: The species is named after the Tagai locality.

H o l o t y p e: Right mandible with p2-m1; Coll. PIN 4338/61 (VISLOBOKOVA 1994, pl. 2, fig. 8).

P a r a t y p e s: Right M3; Coll. PIN 4338/57 (VISLOBOKOVA 1994, pl. 2, fig. 2); right mandible with m1-m3; Coll. PIN 4338/59 (VISLOBOKOVA 1994, pl. 2, fig. 4).

T y p e l o c a l i t y: Tagai, the Tagai Bay of the Olhon Island in the Lake Baikal (Russia).

T y p e l e v e l: Khalagai Formation, lacustriane calcareous green clay (see VISLOBOKOVA 1994).

A g e: Early Miocene, Early Orleanian, MN 3.

D i a g n o s i s: Larger than *O. escheri* but with lower crowned cheek teeth. On upper molars the fold of paracone relatively short; metaconule very small; neocrista and pillar of metacone undeveloped. Premolar row elongated. On p3 and p4, metaconid slightly projected lingually. On lower molars, fold of entoconid absent or weak. On m3, third lobe is relatively small.

D i f f e r e n t i a l d i a g n o s i s: *O. tagaiensis* is more primitive than *O. escheri* in the more brachyodont molar crowns, a shorter fold of the paracone, a less developed M3 metaconule, absence of the M3 pillar of metacone and neocrista and the absence of the neocrista and the pillar of the metacone.

M a t e r i a l: In addition to holotype, left P2, Coll. PIN 4338/56; right M1, Coll. PIN 4338/63; two M2, Coll. PIN 4338/58, right, 4338/65; four M3, right, Coll. PIN 4338/57, PIN 4338/62, Coll. PIN 4338/64, Coll. PIN 4338/66; four m1, right, Coll. PIN 4338/71, right Coll. PIN 4338/72, right, Coll. PIN 4338/73, left, Coll. PIN 4338/79, two m2, Coll. PIN 4338/75, left, Coll. PIN 4338/76; two m3, right, Coll. PIN 4338/60, left, Coll. PIN 4338/69; fragments of the lower jaw with p3-p4, left, Coll. PIN 4338/67; m1-m2, left, Coll. PIN 4338/68; m1-m3, right, Coll. PIN 4338/59; and 24 fragmentary and complete limb-bones (listed in VISLOBOKOVA 1994).

M e a s u r e m e n t s (in mm): M3 (Coll. PIN 4338/57): L = 12, W = 13, AW = 12.2, PW = 9.3, H = 7.2.

		p2	p3	p4	m1	m2	m3			m1	m2	m3
Holotype	L	6.7	8.5	9.3	10.5			Coll. PIN	L	11.2	11.8	13+
	W	3.3	4.5	5.6	7.5			4338/59	W	7.6	8.0	7.8
	H	3.3	4.4	5.5	6+				AW	6.7	7.5	7.8
									PW	7.6	8.0	7.3
									H	5.9	7.0	7.0

The index of hypsodonty (H/W) of unworn teeth (Coll. PIN 4338/59) is 0.53 on m1 and 0.59 on m2. The index of premolar row length (p2-p4/m1-m3) is ap. 0.62. The other measurements of teeth and limb bones are given in VISLOBOKOVA (1994) and RÖSSNER & MÖRS (2001).

D e s c r i p t i o n: A short description of teeth and limb bones (except for phalanges I) was given in VISLOBOKOVA (1994). Some more data on the structure of teeth, astragalus, metatarsus and phalanges will be given below.

Teeth: The P2 is narrow, with a small hypocone slightly displaced backward. The parastyle is thin. The praeprotocrista is extremely short and pronounced only at the base of the crown. The posthypocrista reaches the postparacrista. The fossette is elongated and very narrow.

The upper molar crowns are very low, narrowing towards the occlusal surface and enlarged buccally. The M3 crown strongly narrows backward due to a very weakly developed metaconule (= the hypocone in GENTRY et al. 1999). The paracone fold is directed anterolabially. The fold is weak in the upper part of the crown and lengthens towards the crown mid-height. The labial wall of the metacone is concave and without the pillar. The mesostyle strengthens towards the crown base. The metastyle is weak and thin, slightly bent anteriorly on M3. On unworn M3, the anterior and posterior fossettes are open. On worn teeth, only the former is enclosed anteriorly. The neocrista is undeveloped. The praehypocrista and posthypocrista diverge at an obtuse angle. The spur at the posthypocrista is extremely weak and almost indistinguishable. The anterior and lingual cingula are strong and fused. The posterior cingulum is well developed on M1 and M2 and absent on M3. The entostyle is flattened.

The p2 is very small, with weakly bifurcated protoconulid and short wings of the hypoconid and entoconid. On p3, these elements are more pronounced. On p2 and p3, the metaconid is undeveloped, and the postprotocrisid is directed backward. The p4 is weakly molarized: the metaconid is just slightly extended posteriorly.

On lower molars the metaconid pillar forms a short fold directed posteriorly. In most samples the fold of the entoconid is absent. The outer crescents are weakly pointed. The posterior cingulid is pocket-like and approximately parallel to a slightly flattened ectostylid, while both are placed somewhat oblique to the longitudional axis of the tooth. A strong *Palaeomeryx* fold is almost parallel to that axis. The m3 third lobe possesses well-developed entoconulid and hypoconulid. On unworn teeth, the former is higher than the latter. The anterior fossette is enclosed. The postprotocristid is long but not fusing with the metastylid and the anterior fossette is open posterolingually. The praehypocristid is relatively short and low.

Limb bones: The astragalus is typical of ruminants and similar in many features to that of *Palaeomeryx* but smaller. The bone is weakly elongated, with a high lateral crest and a somewhat lower medial crest in the proximal trochlea and with a rather low distal trochlea. The sustentacular facet for the calcaneum preserves a strong curvature resembling the semicylindrical shape of this trochlea in ancient tragulines; however, this facet is more flattened proximally. Its lateral border is somewhart elevated and slightly rounded. A shallow median sulcus is placed closer to the medial edge of the sustentacular facet. The facet for the lateral process of the naviculocuboid and the cuboid fossa are in a very low position. The cuboid fossa is deep and forms a well-developed incisura at the posterolateral border of the bone. The astragalocalcaneal facet is absent. A relatively low distal trochlea possesses a well-pronounced ridge, oblique relative to a longitudinal axis of the trochlea. The sulcus on the distal trochlea is placed closer to its medial border.

The metatarsus possessed an enclosed anterior longitudinal groove at a markedly low level. The distal trochleae are low, with the weakly developed central trochlear crests on their dorsal surfaces and very prominent trochlear crests on their distal and palmar surfaces.

The first and second phalanges are elongated and slender, with the proximal articular surfaces slightly expanded anteroposteriorly and with low distal trochleae. The proximal articular surface of the first phalanx is similar in morphology to that in giraffids. The surface is low in the anteromedial part and strongly elevated posteromedially and especially posterolaterally; the median groove is extremely shallow anteriorly and deep in its posterior half; the lateral part of the articular surface is much narrower than its medial part. In the second phalanx, the postarticular plateau (typical of cervids) is absent.

The third phalanx of the fore-limb is low and elongated, with a slightly convex dorsal edge and a narrow sole slightly expanded backward. A few destroyed anterior end of the phalanx was narrowing but apparently not pointed.The articular surface is weakly inclined and large. A small, almost triangular facet under the articular surface is situated very close to the sole. The horizontal posterior extension of the articular surface (typical of bovoids) is absent.

Orygotherium heinzi sp. nov.

(Fig. 1-2, Plate 2, Figs. 2-8)

D e r i v a t i o n o m i n i s: The species is named in honor of Dr. Heinz KOLLMANN, Director of the Department of Geology and Paleontology, Natural History Museum in Vienna.

T y p e l o c a l i t y: Kohfidisch (Ko-I, Ko-III), Burgenland, Austria.

H o l o t y p e: Left mandible with p2-m3, Coll. NHMW2004z0051/0001.

P a r a t y pe (from sample Ko-III): Right M1, Coll. NHMW2004z0051/0002; right m2, Coll. NHMW2004z0051/0006.

T y p e l e v e l: Cave and fissure fillings.

A g e: Late Miocene, Pannonian, Early Turolian, MN 11.

D i a g n o s i s: Larger than *O. escheri,* with higher molar crown. On M3, fold of paracone long, metaconule large, neocrista and pillar of metacone developed. Premolar row shortened. On p3 and p4, metaconid strongly projected lingually. On lower molars, fold of entoconid present. On m3, third lobe enlarged and elongated; entoconulid enlarged, with strong lingual cingulid.

D i f f e r e n t i a l d i a g n o s i s: *O.heinzi* is more advanced than *O. escheri* in higher molar crowns; the more developed M3 metaconule, a stronger pillar of the metacone, shorter premolars with a stronger projected lingually metaconid, a well-developed entoconid fold and a longer m3 with an enlarged third lobe.

M a t e r i a l: In addition to holotype and paratypes, the following samples:

Ko-I: left M3, Coll. NHMW2004z0051/0003;

Ko-III: partial left M1, Coll. NHMW2004z0051/0005; left M1, Coll. NHMW2004z0051/0004; left m1, Coll. NHMW2004z0051/0008; left m2, Coll. NHMW2004z0051/0007; right m2, right and left m 3, Coll. NHMW2004z0051/0006, Ko-III, 1965; right m3, Coll. NHMW2004z0051/0009.

M e a s u r e m e n t s (in mm):

	M1	M3	m1	m2	m3	Holotype	p2	p3	p4	m1	m2	m3
L	11.2-11.4	12.0	11.2	11.5-11.8	15.8-16.3		6.8	8.3	8.5	11.5	10.9	12+
W	12.4-13.0	13.3	7.5	7.8	7.7-8.0		3.5	4.7	5.6	7.2	7.6	7.8
H	8.0-8.5	7.5	6.8	7.5	7.0-7.5		3.8	4.8	5.8	6.5	7.5	6.5

L p2-p4 = 21.8, L m1-m3 = ap. 37.0, p2-m3 = ap. 58.5, p2-p4/m1-m3 = 0.589. The index of hypsodonty (H/L) of weakly worn teeth is equal to 0.61 in m1 and 0.65 in m2.

D e s c r i p t i o n: On the upper molars, the pillar of the metacone is developed, the entostyle is weak, flattened and parallel to the lingual edge of the crown. The anterior cingulum is less pronounced than that in *O. escheri* and decreases from M1 to M3. Towards the occlusal surface, the styles become thinner and the fold less deep. Because of that they are not very strong in unworn teeth. The paracone fold is elongated and pressed stronger to the praeparacrista than that in *O. escheri*. The anterior and lingual cingula are rather strong. The mesostyle and parastyle are inclined anteriorly and buccally. The parastyle is enlarged linguobuccally. On M3 (Coll. NHMW2004z0051/0003), the neocrista is present; the anterior cingulum is very weak.

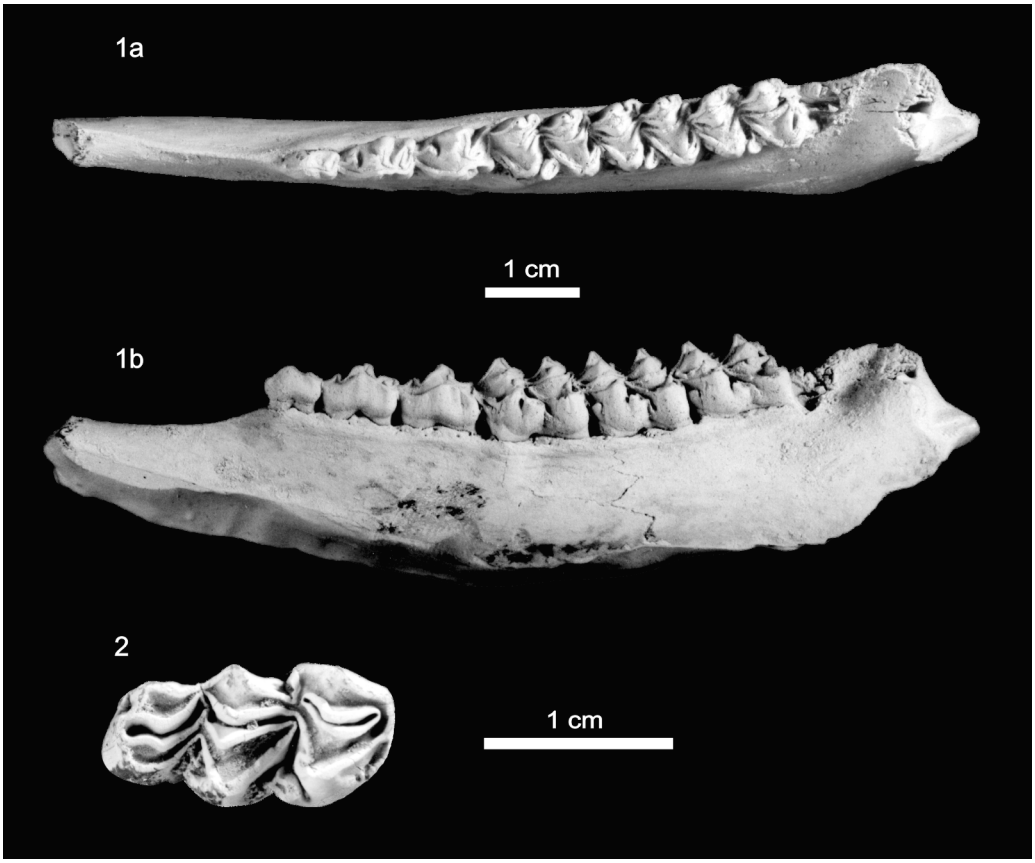

Fig. 1, 2: *Orygotherium heinzi* sp. nov. (1) Holotype: Left mandible with p2-m3, occlusal; Kohfidisch; Coll. NHMW2004z0051/0001; x 1.25. (2) Right m3, occlusal; Kohfidisch (Ko-III); Coll. NHMW2004z0051/0009; x 2.5

Lower premolars are relatively shorter and more molarized than those in *O.escheri*. They have a more developed metaconid strongly projected labially: the p3 and p4 crowns are widest in the middle. The posterior wings of the entoconid and hypoconid are elongated and the posterior valley is enclosed.

The m1 is somewhat smaller, lower and narrower than m2. A weakly worn m2 crown is relatively high. The anterior outer crescent is less narrow than that in *O. escheri*. The *Palaeomeryx* fold, a flattened ectostylid and the posterior cingulid are strong, almost parallel and oblique relative to the longitudional axis of the crown. The metastylid is considerably enlarged towards the crown base. The postentocristid possesses an additional well-developed cuspid. The pillars of the metaconid and entoconid are strong and fold-like. The first fossette is enclosed anterolingually, the second fossette is open anteriorly and posteriorly. On m3, the lingual stylids are better developed than those in *O.esheri*: the metastylid, stylids at the postenocristid are very well pronounced; the third lobe is very enlarged and is just a little smaller than the second lobe; an enlarged entoconulid is surrounded by a strong lingual cingulid.

***Orygotherium* sp.**
(Plate 2, Fig. 9, 10a-c)

L o c a l i t y and l e v e l: Götzendorf, Vienna Basin, Austria; flood sediments.

A g e: Late Miocene, Pannonian, Early Vallesian, MN 9.

M a t e r i a l: Partial left M3, Coll. NHMW2004z0052/0001 and right m2, Coll. Mus. Mannersdorf.

D e s c r i p t i o n and r e m a r k s: The teeth differ from those from Kohfidisch in considerably larger size and some features not allowing to refer them to *O. heinzi*. M3 differs from that of *O. heinzi* in a more developed fold of the paracone and a weaker and thinner parastyle. The worn m2 possesses a more elongated entoconid fold than in *O. heinzi.*

Phylogeny

There was no consensus on the relationships of *Orygotherium*. Apart from HOFMANN (1893), THENIUS (1950a, b) was the first who referred *Orygotherium* to the Palaeomerycinae. Nowadays, the genus is usually placed in the Cervoidea: as Cervoidea incertae sedis (GENTRY et al. 1999; RÖSSNER & MÖRS 2001) or even as a synonym of *Micromeryx* in the Moschidae (MCKENNA & BELL 1997). However, *Orygotherium* differs considerably from *Micromeryx,* moschids and cervids in the teeth and limb bones structure and shows more similarities with palaeomerycines.

Palaeomerycines are intermediate in morphology between cervids and giraffids and are regarded as cervoids (JANIS & SCOTT 1987; DURANTHON et al.1995; MCKENNA & BELL 1997; GENTRY et al. 1999 and others), as giraffoids (GINSBURG & HEINTZ 1966; QIU al.1985 and others) or as bovoids (together with Giraffidae) (GINSBURG 1985b). The group possessed many characters in common with cervoids (the *Palaeomeryx* fold, a distally bridged metatarsal gully, etc.), but differed from them in the presence of the occipital appendages and supraoccipital ossicones (dermal in origin) typical of giraffids. Palaeomerycines had relatively low crowned molars with well-developed basal and additional elements (cingula, folds, pillars) and were long-legged (GENTRY et al. 1999). These palaeomerycine dental and metatarsal features as well as elongated autopodium are equally present in *Orygotherium.*

Besides *Orygotherium,* palaeomerycines include five genera: *Palaeomeryx*, Early-Late Miocene (MN3b-MN9), Europe, Middle Miocene (MN 5-6), Asia; *Ampelomeryx*, Early Miocene (MN4), Spain and France*; Oriomeryx*, Early Miocene (MN2-MN3), Europe; *Triceromeryx*, early Middle Miocene (MN5), Spain; *Tauromeryx*, early Middle Miocene (MN5), Spain (GINSBURG 1985a; ASTIBIA 1987; DURANTHON et al. 1995; MCKENNA & BELL 1997; ASTIBIA et al. 1998; GENTRY et al. 1999). Data on *Orygotherium*, smallest among them, essentially extended the occurrence of palaeomerycids in Eurasia. Within palaeomerycines, *Orygotherium* shows the most resemblance with *Palaeomeryx* (in particular, in the shape of the paracone rib on upper molars, the absence of link between the metastylid and the protoconid-entoconid crest on lower molars, etc.).

Orygotherium appears to be an abberant palaeomerycid. It inhabited the suitable biotopes from the Early Orleanian to Early Turolian (MN3-MN11). Similar to other

palaeomerycids, *Orygotherium* has inherited some traguloid evolutionary trends as well as possessed some pecoran features shared with cervids and giraffids. In some characters *Orygotherium* surpassed two last groups, resembling some advanced traguloids (e.g., *Pseudogelocus* and *Paragelocus*) by the very strong cingula and shapes of the pillar of the paracone and ectostylid.

There are traced three different evolutionary stages of the genus: *O. tagaiensis* (MN 3, 20-18 Ma), *O. escheri* (MN 5, 16.8-14.9 Ma) and *O. heinzi* (MN 11, 8.7-8 Ma). The main evolutionary changes were the following: (1) slight increase of selenodonty and crown height; (2) enlargement of the M3 metaconule; (3) shortening of premolar row length; (4) increase of p4 width due to a more strong lingual projection of the metaconid; (5) enlargement and increase in number of additional and basal elements (the paracone fold became longer, the neocrista and the metacone pillar developed, the fold of the entoconid became stronger), and (6) enlargement of the third lobe in m3.

Palaeoecology

Orygotherium was undoubtedly a forest inhabitant. The evolutionary complication of its teeth reflects the increasing adaptation for feeding on foliages.

RÖSSNER & MÖRS (2001: 594) supposed that *Orygotherium* could live in swampy habitats and probably was semi-aquatic: the additional molar crests were regarded by these researchers as elements using for fibrous foods "which most likely may have been swamp vegetation due the depositional environment". Their opinion was based on the *Orygotherium* occurrence in the lignitic deposits in Käpfnach and Göriach and on the abundance of the tragulid *Dorcatherium gintianum* in Hambach (RÖSSNER & MÖRS 2001). Following KÖHLER (1993), RÖSSNER & MÖRS (2001) believe that *Dorcatherium* is an indicator for paludal habitats, beeing close in its ecology to a recent water chevrotains *Hyaemoschus aquaticus* from Africa. However, the water chevrotain is not a true semi-aquatic species but a terrestrial inhabitant living not far from the water; it favours the forest and enters the water only when there is in danger (WALKER's Mammals 1991).

Data from Hambach, Olhon, Kohfidisch and Götzendorf showed that the spectrum of deposits with *Orygotherium* remains were rather diverse and that *Orygotherium* apparently was not solely a marshy animal. Being a forest inhabitant, *Orygotherium* probably could live in various woodlands. In the Tagai fauna, it coexisted with other browsers (*Amphitragulus*, *Stephanocemas* and *Palaeomeryx*) predominated over the grazers (*Lagomeryx*), according to palynological data, the forests alternated with more open woodlands (LOGACHEV et al. 1964; VISLOBOKOVA 1994). Kohfidisch, besides *Orygotherium* remains, yeldies remains of many other forest animals (*Ictitherium*, *Hippotherium primigenium* (BACHMAYER & ZAPFE 1969; BERNOR et al. 1990, 1993; FRANZEN & STORCH 1999), cervids *Procapreolus*, *Euprox*, *Cervavitus*, etc., the bovid *Miotragocerus* as well as some bovids typical of more open woodlands (*Tragoportax gaudryi*, ?*Nisidorcas*, *Palaeoryx*, *Protoryx* and *Gazella*).

According to KÖHLER (1993), the preferred habitats of palaeomerycids were boggy forests. But it seems more probable that *Orygotherium* lived near the water on relatively wet grounds and could browse on soft foliages in forested places, bushwoods as well as in boggy forests.

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References

ASTIBIA, H. (1987): First data on the presence of Palaeomerycidae (Artiodactyla, Mammalia) in the European Upper Miocene. – Geobios, **20**/6: 833-836. – Lyon.

—— , MORALES, J. & MOYA-SOLA, S. (1998): *Tauromeryx*, a new genus of Palaeomerycidae (Artiodactyla, Mammalia) from the Miocene of Taeazona de Aragón (Ebro Basin, Aragón, Spain). – Bulletin de Société géologique de France, **169**/4 : 471-477. – Paris.

BACHMAYER, F. & WILSON, R.W. (1970): Die Fauna der altpliozänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). Small Mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch Fissures of Burgenland, Austria. – Ann. Naturhist. Mus., **74**: 533-587. – Wien.

—— & ZAPFE, H. (1969): Die Fauna der altpliozänene Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). – Ann. Naturhistor. Mus. Wien, **73**: 123-139. – Wien.

BERNOR, R.L., KOVAR-EDER, J., SUC, J.-P. & TOBIEN, H. (1990): Systematic, stratigraphic, and paleoenvironmental contexts of first-appearing Hipparion in the Vienna Basin, Austria. – Journal of Vertebrate Paleontology, **8**/4: 427-452. – Lawrence.

—— , MITTMANN, H.-W. & RÖGL, F. (1993): Systematics and Chronology of the Götzendorf "*Hipparion*" (Late Miocene, Pannonian F, Vienna Basin). – Ann. Naturhistor. Mus. Wien, **95**/A: 101-120. – Wien.

BRUIJN, H. de, DAAMS, R., DAXNER-HÖCK, G., FAHLBUSCH, V., GINSBURG, L., MEIN, P. & MORALES, J. (1992): Report of the RCMNS working group on fossil mammals, Reisenburg 1990. – Newslletters Stratigr., **26** /2-3: 65-118. – Berlin, Stuttgart.

DAXNER-HÖCK, G. (1996): Faunenewandel im Obermiozäan und Korrelation der MN-"Zonen" mit den Biozonen des Pannons der Zentralen Paratethys. – Beiträge zur Paläontologie **21**: 1-9. – Wien.

—— (2001): Early and Late Miocene correlation (Central Paratethys). – Ber. Inst. Geol. Palaont. K.-F.-Univ. Graz. **4**: 28-33. – Graz.

—— (2003): Palaeoenvironmental history of the Vallesian and Early Turolian reflected by vertebrate assemblages in the Vienna and Pannonian Basins. – EEDEN – Environments and Ecosystem Dynamics of the Eurasian Neogene. Birth of the New World. Stara Lesna, Slovakia, November 12-16: 38-39. – Univerzita Komenskeho Bratislava.

DURANTHON, F., MOYA-SOLA, S., ASTIBIA, H. & KÖHLER, M. (1995): *Ampelomeryx ginsburgi* nov. gen., nov. sp. (Artiodactyla, Cervoidea) et la famille des Palaeomerycidae. – Compt. rend. Acad. sci., (Sér. IIa) **321**: 339-346. – Paris.

FRANZEN, J.L. & STORCH, G. (1999): Late Miocene mammals from Central Europe. – In: AGUSTI, J., ROOK, L. & ANDREWS, P. (editors): The evolution of Neogene Terrestrial Ecosystems in Europe: pp. 164-190. – Cambridge University Press.

GENTRY, A.W., RÖSSNER, G.E. & HEIZMANN, E.P.J. (1999): Suborder Ruminantia. – In: RÖSSNER, G.E. & HEISSIG, K. (editors): The Miocene Land Mammals of Europe: pp. 225-258. – München (Verlag Dr. Friedrich Pfeil).

GINSBURG, L. (1985a): Systématique et évolution du genre *Palaeomeryx* (Artiodactyla, Giraffoidea) en Europe. – Compt. rend. Acad. sci., (Sér. II) **301**/14: 1075-1078. – Paris.

—— (1985b): Essai de phylogénie des Eupecora (Ruminantia, Artiodactyla, Mammalia). – Compt. rend. Acad. sci., (Sér. II) **301**/17: 1255-1257. – Paris.

—— & HEINTZ, E. (1966): Sur les affinitiés du genre *Palaeomeryx* (Ruminant du Miocene européen). – Compt. rend. Acad. sci., (D) **262**/9: 979-982. – Paris.

HARZHAUSER, M., DAXNER-HÖCK, G., BOON-KRISTKOIZ,E., CORIC, S., A, MANDIC, O., MIKLAS-TEMPFER, P., ROETZEL, R., RÖGL, F., SCHULTZ, O., SPEZZAFERRI, S., ZIEGLER, R. & ZORN, I. (2003): Paleoecology and biostratigraphy of the section Mühlbach (Gaindorf Formation, lower Middle Miocene, Lower Badenian, Austria). – Ann. Naturhist. Mus., (A) **104**: 323-334. – Wien.

HOFMANN, A. (1893): Die Fauna von Göriach. – Abh. kaiserl.-königl. geolog. Reichsanstalt, **15**/6: 1-87. – Wien.

JANIS, C.M. & SCOTT, K.M. (1987): The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. – Am. Mus. Novitates, **2893**: 1-85. – New York.

KÖHLER, M. (1993): Skeleton and habitat of recent and fossil ruminants. – Münchner Geowiss. Abh., (A) **25**: 1-88. – München.

LOGACHEV, N., LOMONOSOVA, T. & KLIMANOVA, V. (1964): The Cenozoic deposits of the Irkutsk Amphithetre. – 195 p. – Moscow (Science). (In Russian).

MADE, J. van der. (1989): Superfamily Hippopotamoidea. – In: RÖSSNER, G.E. & HEISSIG, K. (editors): The Miocene Land Mammals of Europe: pp. 203-208. – München (Verlag Dr. Friedrich Pfeil).

MCKENNA, M.C. & BELL, S.K. (1997): Classification of mammals above the species level. – 631 p. – New York (Columbia University Press).

MEYER, H. von. (1838): Mittheilungen an Professor Bronn gerichtet. – Neues Jarbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1838: 413-418.

—— (1939): Die fossilen Säugethiere, Reptilien und Vogel aus den Molasse Gebilten der Schweiz. – Neues Jarbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1839: 1-9.

PIA, J. & SICKENBERG, O. (1934): Katalog der in den Österreichischen Sammlungen befindlichen Säugetierreste des Jungtertiärs Österreichs und der Randgebiete. – Denkschrift Naturhist. Mus. Wien, **4**: 1-544. – Wien.

QIU ZHANXIANG, YAN DEFA, JIA HANG & SUN BO (1995): Preliminary Observations on the newly foun skeletons of *Palaeomeryx* from Shanwang, Shandong. – Vertebrata PalAsiatica, **23**/3: 173-195.

RÖGL, F. & DAXNER-HÖCK, G. (1996): Late Miocene Paratethys Correlations. – In: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (editors): The Evolution of Western Eurasian Neogene Mammal Faunas: pp. 47-55. – New York (John Wiley & Sons).

RÖSSNER, G.E. & MÖRS, T. (2001): A new record of the enigmatic Eurasian Miocene ruminant artiodactyl *Orygotherium*. – Journal of Vertebrate Paleontology, **21**/3: 591-595. – Lawrence.

SCHLOSSER, M. (1887): Paläontologische Notizen. – Morphologisches Jahrbuch, **12**: 287-298.

STEHLIN, H.G. (1914): Übersicht über die Säugetiere der Schweizerischen Molassformation ihre Fundorte und ihre stratigraphische Verbreitung. – Verhandlungen der Naturforschenden Gesellschaft Basel, **25:** 179-202. – Basel.

—— (1919): Verzeichnis der Säugetierfunde in der schweizerischen Molasse. - In: Heim, A. (editor): Geologie der Schweiz. – 704 p. – Leipzig (Tauchnitz Verlag).

THENIUS, E. (1950a): Die Cerviden und Lagomeryciden des steirischen Tertiärs. – Österreichische Akademie der Wissenschaften, Sitzung der Mathematisch-naturwiss. Klasse vom 9 März 1950: 1-7. – Wien.

—— (1950b): Die tertiären Lagomeryciden und Cerviden der Steiermark Beiträge zur Kenntnis der Säugetierreste des Steirischen Tertiärs. – Sitzungsbericht der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwiss. Klasse I, **159**: 219-254. – Wien.

VISLOBOKOVA, I. (1994): The Lower Miocene artiodactyls of Tagai Bay, Olhon Island, Lake Baikal (Russia). – Palaeovertebrata, **23**/1-4: 177-197. – Montpellier.

WALKER's Mammals of the World. II. – In: NOWAK, R.M. (editor). – 1629 p. – Baltimor and London (The Jones Hopkins University Press).

Plate 1

***Orygotherium tagaiensis* sp. nov.**

Fig. 1: P a r a t y p e: Right M3, a, occlusal, b, buccal, c, lingual, d, anterior; Tagai; Coll. PIN 4338/57

Fig. 2: P a r a t y p e: Right mandible with m1-m3, a, occlusal, b, buccal, c, lingual; Tagai; Coll. PIN 4338/59

Fig. 3: H o l o t y p e: Right mandible with p2-m1, a, occlusal, b, buccal; Tagai; Coll. PIN 4338/61

All figs. x 2.3.

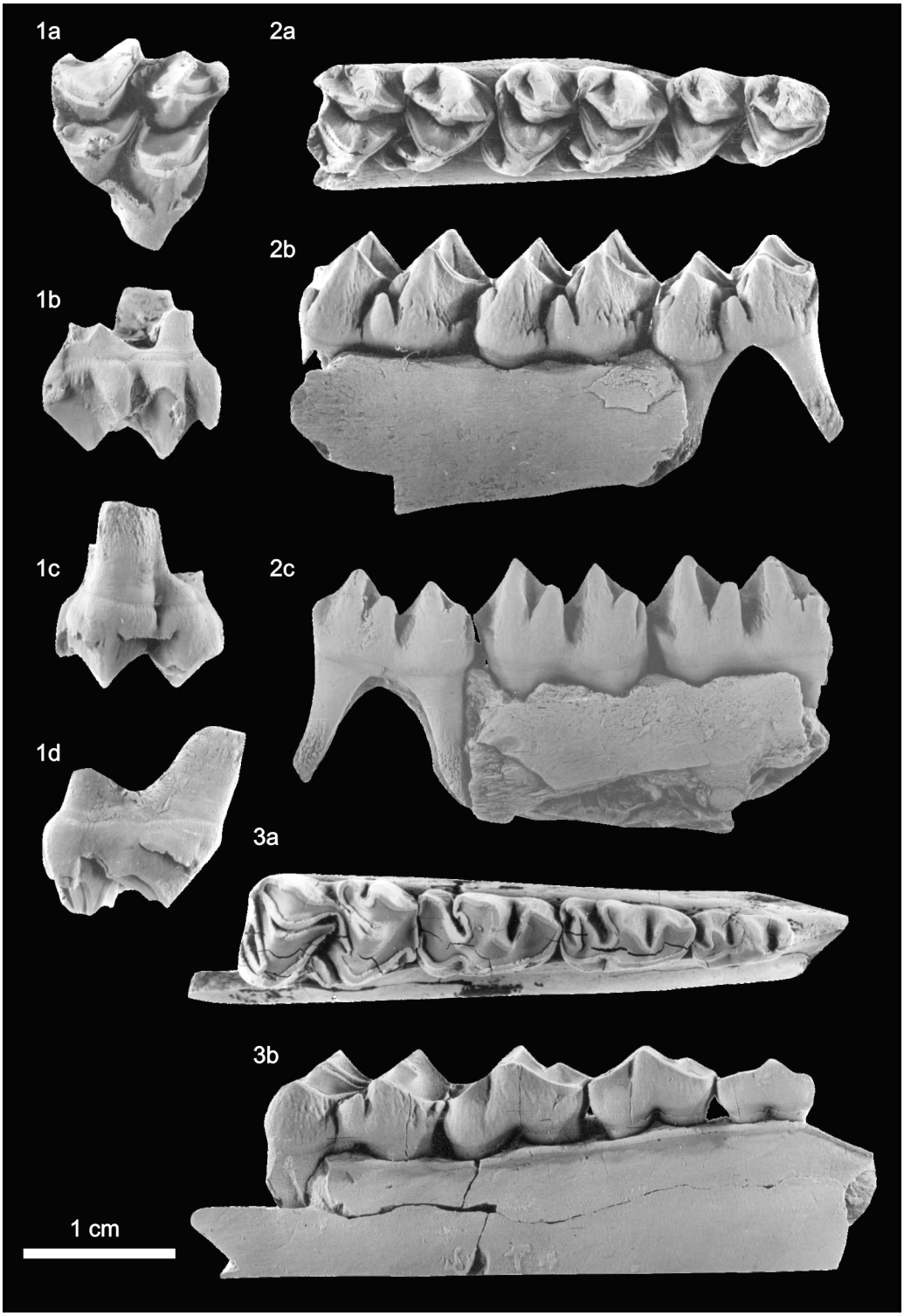

1a
2a
2b
1b
1c
2c
1d
3a
3b
1 cm

Plate 2

***Orygotherium tagaiensis* sp. nov.**

Fig. 1: H o l o t y p e: Right mandible with p2-m1, lingual; Tagai; Coll. PIN 4338/61

***Orygotherium heinzi* sp. nov.**

Fig. 2: P a r a t y p e: Right M1, a, occlusal, b, anterior, c, posterior; Kohfidisch (Ko-III); Coll. NHMW2004z 0051/0002

Fig. 3: Left M3, occlusal; Kohfidisch (Ko-I); Coll. NHMW2004z0051/0003

Fig. 4: Left M1, occlusal; Kohfidisch (Ko-III); Coll. NHMW2004z0051/0004

Fig. 5: Partial left M1, occlusal; Kohfidisch (Ko-III); Coll. NHMW2004z0051/0005

Fig. 6: P a r a t y p e: Right m2, a, occlusal, b, buccal, c, lingual; Kohfidisch (Ko-III); Coll. NHMW2004z0051/0006

Fig. 7: Left m2, occlusal; Kohfidisch (Ko-III); Coll. NHMW2004z0051/0007

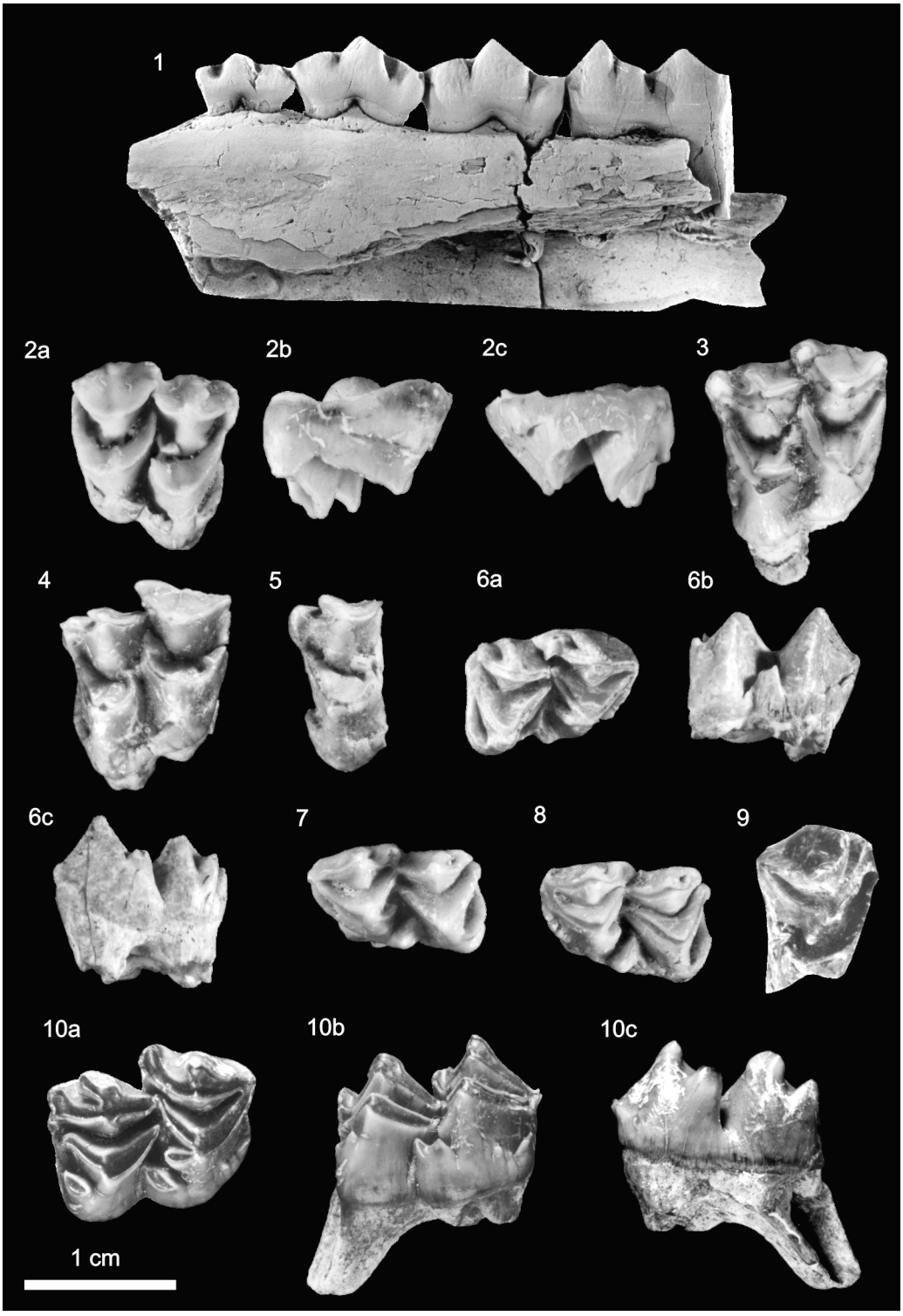
Fig. 8: Left m1, occlusal; Kohfidisch (Ko-III); Coll. NHMW2004z0051/0008

***Orygotherium* sp.**

Fig. 9: Partial left M3, occlusal; Götzendorf; Coll. NHMW2004z0052/0001.

Fig. 10: Right m2, a, occlusal, b, buccal, c, lingual

All figs. x 2.3.


1
2a
2b
2c
3
4
5
6a
6b
6c
7
8
9
10a
10b
10c
1 cm