

ADDITIONS TO THE GEISELTAL MAMMALIAN FAUNAS, MIDDLE EOCENE: DIDELPHIDAE, NYCTITHERIIDAE, MYRMECOPHAGIDAE

by

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CONTENT

	Page
Abstract, Kurzfassung	96
Introduction	96
Systematic paleontology	96
Marsupialia, Didelphidae	96
<i>Amphiperatherium giselense</i> (HELLER 1936)	97
<i>Amphiperatherium</i> aff. <i>maximum</i> CROCHET 1979	97
<i>Amphiperatherium goethei</i> CROCHET 1979	100
<i>Peratherium</i> aff. <i>monspeliense</i> CROCHET 1979	101
<i>Microtarsioides voigti</i> WEIGELT 1933	105
Lipotyphla, Nyctitheriidae	106
<i>Saturninia ceciliensis</i> n. sp.	106
Edentata, Myrmecophagidae	109
<i>Eurotamandua joresi</i> STORCH 1981	109
Comparison Messel — Geiseltal	112
References	112
Legend of plate	114

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Key-words: Marsupialia, Didelphidae, Lipotyphla, Nyctitheriidae, Edentata, Myrmecophagidae, Geiseltalian, Middle Eocene, MP 11-13, Geiseltal, German Democratic Republic.

Schlüssel-Worte: Marsupialia, Didelphidae, Lipotyphla, Nyctitheriidae, Edentata, Myrmecophagidae, Geiseltalium, Mittel-Eozän, MP 11-13, Geiseltal, Deutsche Demokratische Republik.

Mots-clés: Marsupialia, Didelphidae, Lipotyphla, Nyctitheriidae, Edentata, Myrmecophagidae, Geiseltalien, Eocène moyen, MP 11-13, Geiseltal, République Démocratique Allemande.

ABSTRACT

New and hitherto unpublished mammals from the stratigraphical levels Unterkohle, Untere Mittelkohle and Obere Mittelkohle of the Geiseltal near Halle, GDR, are described (= biochronological levels MP 11-13, Geiseltalian *sensu* Franzen & Haubold 1986a, b). The marsupial taxa *Amphiperatherium* aff. *maximum* (MP 12), *A. goethei* (MP 12), and *Peratherium* aff. *monspeliense* (MP 12 and 13) are recorded for the first time. A lectotype for *Amphiperatherium giselense* is designated, and the alleged primate *Microtarsioides voigti* is assigned to Marsupialia, incertae sedis. A new insectivore species, *Saturninia ceciliensis* n. sp., is described (MP 13). The anteater *Eurotamandua joresi* is recorded for the first time outside its type locality, Grube Messel, FRG (MP 11). The present humerus and ulna display the autapomorphic features of the myrmecophagids.

KURZFASSUNG

Beschrieben werden bislang unveröffentlichte Säugerfunde aus den Formationsgliedern Unterkohle, Untere Mittelkohle und Obere Mittelkohle des Geiseltals bei Halle, DDR (= Biochronologische Einheiten MP 11-13, Geiseltalium *sensu* Franzen & Haubold 1986a, b). Erstmals nachgewiesen werden die Beuteltiere *Amphiperatherium* aff. *maximum* (MP 12), *A. goethei* (MP 12), und *Peratherium* aff. *monspeliense* (MP 12 und 13). Ein Lectotypus für *Amphiperatherium giselense* wird designiert, und der vermeintliche Primate *Microtarsioides voigti* den Marsupialia, incertae sedis, zugeordnet. Eine neue Insektivoren-Art, *Saturninia ceciliensis* n. sp., wird aufgestellt (MP 13). Der Ameisenbär *Eurotamandua joresi* wird erstmals außerhalb der Typus-Lokalität Grube Messel, BRD, nachgewiesen (MP 11). Die vorliegenden Humerus und Ulna besitzen die autapomorphen Merkmale der Myrmecophagiden.

INTRODUCTION

The present paper is a further contribution to the revision and completion of the Geiseltal mammalian faunas. We report on marsupial, lipotyphlan and myrmecophagidan remains which have not been published previously, and we review some relevant type specimens. All specimens are housed in the Geiseltalmuseum collections of the Martin-Luther-University Halle-Wittenberg (GMH).

The European continental Middle Eocene has been recently subdivided into three Paleogene mammal units, MP 11-13 (see Schmidt-Kittler 1987). This subdivision is mainly based on the faunal sequence represented by the Geiseltal Unterkohle (MP 11), the Geiseltal Untere Mittelkohle (MP 12), and the Geiseltal Obere Mittelkohle (MP 13), which consequently were selected for reference localities (Franzen & Haubold 1986a, b, 1987, Schmidt-Kittler 1987). Franzen & Haubold (*l.c.*) proposed the new term Geiseltalian as an European land-mammal age to replace the marine Lutetian. Since biochronology is essentially based on a detailed knowledge of the animals involved, we feel that our additions to the Geiseltal Middle Eocene reference localities might be of some common interest. Further, our joint studies aim at an evaluation of dissimilarities and similarities between the lower Middle Eocene Geiseltal and Messel mammalian faunas.

SYSTEMATIC PALEONTOLOGY

Infraclass METATHERIA HUXLEY 1880

Order MARSUPIALIA ILLIGER 1811

Family DIDELPHIDAE GRAY 1827

Genus *AMPHIPERATHERIUM* FILHOL 1879

Type species: Amphiperatherium frequens (MEYER 1846).

Diagnosis: see Crochet (1980: 59).

Amphiperatherium giselense (HELLER 1936)

(Pl. 1, fig. 1)

Designation of a lectotype

Heller (1936) in his description of *Peratherium giselense* did not specifically designate a holotype. His type material was composed of specimen GMH CeIV-7285, a crushed skull with associated right mandible (Heller 1936, pl. 1, figs. 1-2), and specimen GMH CeIV-7286, a right maxillary fragment with C1/ and P2/-M4/ (Heller 1936, pl. 1, figs. 3-4). Locality and horizon for both syntypes are Grube Cecilie, site IV (Trichter NO), Geiseltal near Halle, GDR; Obere Mittelkohle (MP 13), Upper Geiseltalian. Referred specimens (Heller 1936: 316) were GMH CeI-7287, a badly corroded mandibular fragment with P2/-M3/ (figured by Heller 1930, pl. 1, fig. 2a-b), and GMH CeI-7288, a badly corroded maxillary fragment with C1/-M4/ (figured by Heller 1930, pl. 1, fig. 1a-b), both from Grube Cecilie, site I, Oberes Hauptmittel (MP 13-14).

We select and designate as lectotype for *Amphiperatherium giselense* (HELLER 1936): Geiseltalmuseum, Martin-Luther-University Halle, GMH CeIV-7285, crushed skull with associated incomplete right mandible, with right C1/, P1/-P3/, M1/-M4/, C1/, P1/-P3/, M1/-trigonid, alveoli for M1/-talonid and M2/-M4/, and with partly fragmentary or wanting upper and lower right incisors (pl. 1, fig. 1; Heller 1936, pl. 1, figs. 1-2).

We made no attempt to clarify the specific status of the poorly preserved referred material.

The original diagnosis of *giselense* was essentially based on small size. Only few and approximate data for the lectotype dentition were given by Heller. Therefore, we here present our measurements taken from the actual specimen and X-ray pictures. *A. giselense* is the smallest of the known Geiseltal marsupials (e.g., alveoli lengths for M2/-M4/: 4.6 mm in *giselense*, 5.35 mm in *A. goethei*, and 5.8 mm in *P. aff. monspeliense*).

Measurements

Tooth length:	Length of tooth-row:	Length of alveoli:
M2/ 1,60	C1/-M4/ 12,2	C1/-M4/ 12,5
M3/ 1,56	P1/-P3/ 4,4	M1/-M4/ 5,8
M4/ 1,12	M1/-M4/ 5,7	M1/ 1,44
	P1/-P3/ 4,8	M2/ 1,60
		M3/ 1,60
		M4/ 1,44
		M1/ 1,44
		M2/ 1,60
		M3/ 1,60
		M4/ 1,2

Amphiperatherium aff. maximum CROCHET 1979

Material: Crushed skull fragment, lacking braincase, with partly fragmentary incisors, canines, left M1/ and right M3/, and with left P3/, M2/ and right P1/ extracted; other

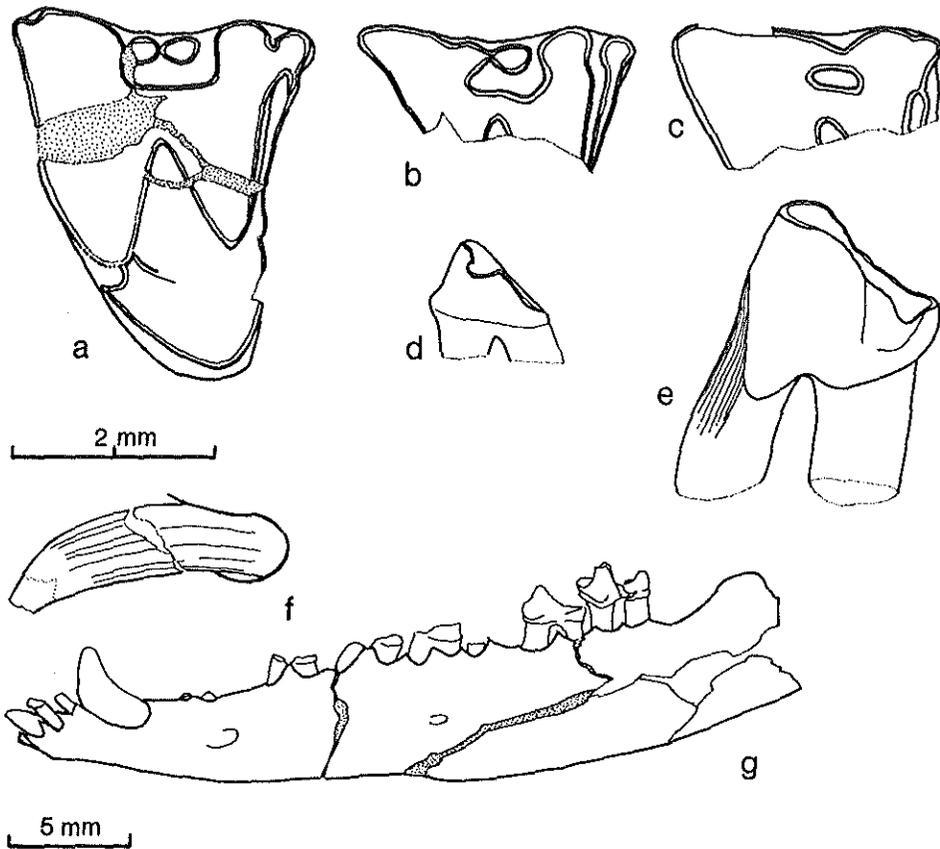


Figure 1. – *Amphiperatherium* aff. *maximum* CROCHET 1979, specimen GMH XXII-604. Geiseltal near Halle, GDR; Untere Mittelkohle, MP 12. a: r. M3/, occlusal view; b: l. M2/ (inverse), occlusal view; c: l. M1/ (inverse), occlusal view; d: r. P1/, labial view; e: l. P3/, lingual view; f: r. C1/, lingual view; g: lower jaw fragment, labial view. 2 mm scale refers to a-e, 5 mm scale refers to f-g.

cheek teeth badly damaged. Right edentulous jaw fragment; left jaw fragment, lacking ascending ramus, with partly fragmentary incisors, canine and M/3-4, and with roots of P/1-M/2. GMH XXII-604.

Horizon: Untere Mittelkohle; MP 12, Middle Geiseltalian.

Measurements

Tooth length x width:		Length of alveoli:	Length of diastema:	
P1/	1,20 x 0,52	I/1-M/4	26,0	
P3/	2,28 x 1,16	C/1-M/4	23,4	
M1/	2,64 x –	M/1-M/4	9,7	
M2/	2,72 x –	M/1	2,28	
M3/	2,84 x 3,40	M/2	2,44	
M4/	(2,96) x 1,56	M/3	2,52	
		M/4	2,48	
			C/1-P/1	1,20
			P/1-P/2	1,88

Most teeth of the Geiseltal specimen are fragmentary and its molars are heavily

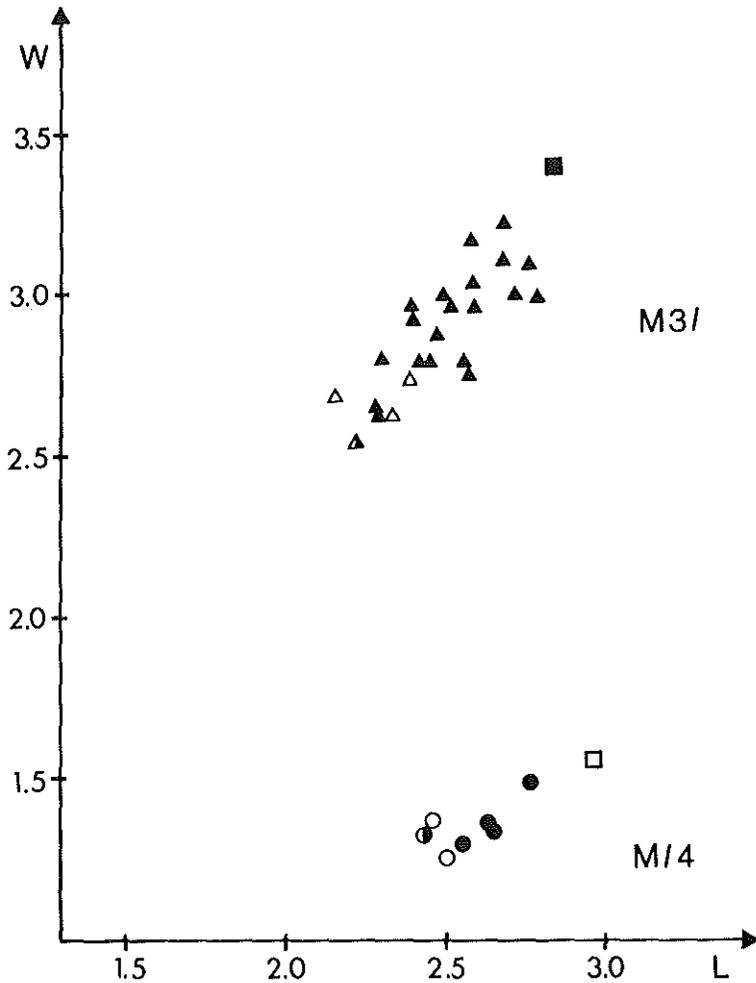


Figure 2. – Length (L) / Width (W) scatter diagram of M3/ and M/4 of *Amphiperatherium* aff. *maximum*, Geiselt specimen GMH XXII-604 (□■), and of *A. maximum* (▲●), *A. bastbergense* (△○), and *A. fontense* (▲●). Measurements of *A. m.*, *A. b.*, and *A. f.* from Crochet (1980).

worn. Yet various preserved features clearly demonstrate affinities with the *Amphiperatherium* lineage no. 5 of Crochet (1980), comprising the species *maximum*, *bastbergense*, *fontense*, and *ambiguum*. Correspondence includes:

- Large size. Tooth size of the Geiselt specimen is within the size range of the largest species, *maximum* or even beyond it (M3/ and M/4, see fig. 2). Actually, it represents the largest *Amphiperatherium* specimen known so far.
- Marked longirostry. The horizontal branch of the lower jaw is relatively high below the molars and evenly tapering from the level of P/3 anteriorly. The mandible is elongated anteriorly, with C/1-P/1-P/2-P/3 being separated by diastemata (fig. 1g). Thus, it compares well with preserved mandibles of *fontense* and *ambiguum* (Crochet 1980, figs. 123, 130). There is also agreement in the size and position of the two mental foramina (fig. 1g).
- Long protocone lobe (protofossa of Crochet 1980). On the ± completely preserved

M3/ (fig. 1a) the length of the protocone lobe is about 60% of the tooth length, what is in agreement with *maximum* and *bastbergense* according to Crochet's (1980) figures 108 and 114b.

- Marked dilambdodonty. The styler shelf adjacent to styler cusp C on M1-3/ is narrow despite the fact that the teeth are extensively worn out. Reduction of the styler shelf at cusp C seems to agree fairly well with that of the *bastbergense* holotype (cf. fig. 1a-c, Crochet's fig. 114b).
- Strong styler cusp C. The rather massive cusp C is doubled on M3/ and probably on M2/ (fig. 1a-b). The mesial cusp C is separated from B while the distal one is connected with D, supposedly even in slightly worn teeth.
- Shallow ectoflexus. It is weakly indicated on M1-2/ and slightly deeper and symmetrical on M3/ (fig. 1a-c).

A. maximum (Lower Eocene, MP 8-10, of the Paris basin) is somewhat larger than *bastbergense* (Upper Middle Eocene, MP 13-14, of France and Switzerland). The Geiseltal specimen falls within and beyond the size category of *maximum* and we therefore link it nomenclaturally with this species.

There are only slight morphological differences among the species of lineage no.

5. Evolutionary trends between *maximum* and its probable descendant *bastbergense* on M1-3/ are towards:

- 1) crestlike connexion and closer position of styler cusps A and B,
- 2) slightly narrower paracingulum,
- 3) slightly shallower ectoflexus,
- 4) slightly weaker conuli, and
- 5) reduction of styler cusp A.

The Geiseltal specimen seems to be closer to *maximum* in characters 1), 2) and 5), and closer to *bastbergense* in character 3). Nothing can be said about 4) except that there was a metaconule on M3/.

For the morphology of the preserved Geiseltal P1/ and P3/ see fig. 1d-e. C1/ is hypertrophied, laterally compressed, and it is equipped with weak ridges longitudinally (fig. 1f). There are 5 upper and 4 lower incisors. I/2 is enlarged compared with I/1 and I/3-4, which are subequal (fig. 1g). The posterior edge of the infraorbital foramen is above P3/.

Amphiperatherium goethei CROCHET 1979
(Text-fig. 6a-c)

Material: Right mandibular fragment with M/2-M/4, M/2 being extensively worn; anterior edge of coronoid process and masseteric fossa partially preserved. GMH XVIII-223.

Horizon: Lowermost Untere Mittelkohle; MP 12, Middle Geiseltalian.

Measurements

Tooth length	x width:	Length of alveoli:
M/3 1,88	x 1,10	M/2-M/4 5,35
M/4 1,84	x 1,00	

The specific assignment of the Geiseltal specimen is based on size and morphology. Molar size compares well with *goethei* (cf. Crochet 1980, fig. 104) and it falls slightly beyond the size range of *bourdellense* (cf. Crochet 1980, fig. 53). *A. giselense* and its supposed ancestral form, *A. sp. 1* of Crochet (1980), also would fit stratigraphically and they are similar morphologically, but both are distinctly smaller than the Geiseltal specimen.

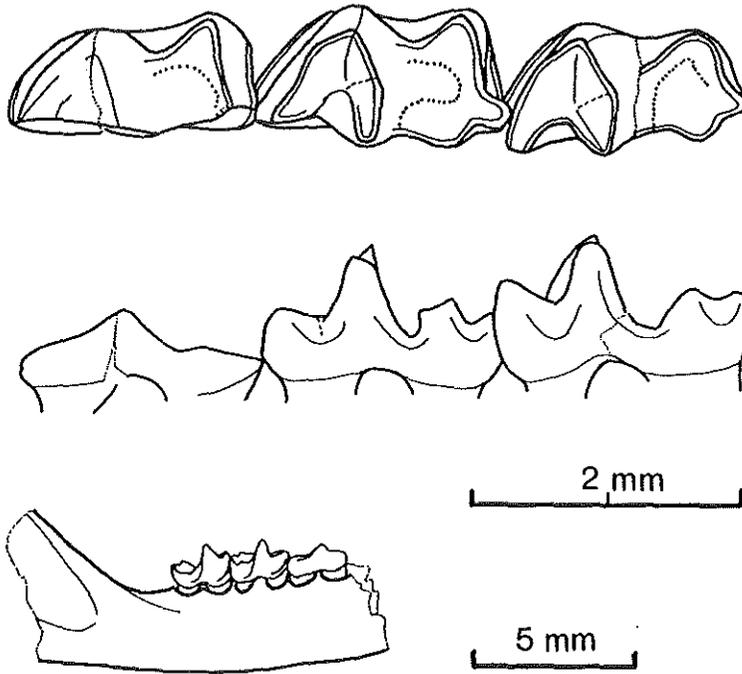


Figure 3. – *Amphiperatherium goethei* CROCHET 1979, specimen GMH XVIII-223, Geiseltal near Halle, GDR; lowermost Untere Mittelkohle, MP 12. M/2-M/4 in occlusal and lingual view (above), and lower jaw fragment in labial view (below).

Morphologically, the fairly high and elongate entoconid of the Geiseltal specimen (fig. 3) is characteristic of *goethei* rather than *bourdellense*. Compared to *bourdellense*, the postcristid of M/2-3 is less obliquely set and the hypoconulid of M/3-4 is less protruding distally; in these characters again there is better agreement of the Geiseltal specimen with *goethei*.

Additional features of the Geiseltal lower molars are (fig. 3): paraconid rather prominent; protoconid only slightly mesial to metaconid; talonid distinctly shorter and slightly wider than trigonid on M/3, and reduced in width on M/4 (around 80% of trigonid width); crista obliqua joins protoconid midway between trigonid notch and labial edge on M/3 and somewhat more lingually on M/4; precingulid terminates at protoconid; trigonid basin is open lingually; entoconid higher than hypoconulid on M/3, and both are subequal on M/4.

Genus *PERATHERIUM* AYMARD 1850

Type species: *Peratherium elegans* (AYMARD 1846).

Diagnosis: See Crochet (1980: 143).

Peratherium aff. *monspeliense* CROCHET 1979

(Text-fig. 4a-c, 5a-d)

Material: Left mandibular fragment with P/2 and M/4, and with alveoli for P/1, P/3,

and M/1-3; anterior edge of ascending ramus and of masseteric fossa partly preserved. GMH LII-46.

Horizon: Untere Mittelkohle; MP 12, Middle Geiseltalian.

Material: Left corpus mandibulae with I/1-C/1 and P/2-M/4; molars lingually in part fragmentary. GMH XLI-5.

Horizon: Obere Mittelkohle; MP 13, Upper Geiseltalian.

Measurements

	GMH LII-46	GMH XLI-5
Tooth length x width:		
P/2	1,60 x 0,68	1,64 x 0,72
P/3	—	1,68 x 0,76
M/1	—	1,96 x 1,12
M/3	—	2,12 x 1,28
M/4	2,08 x 1,16	—
Length of tooth-row:		
I/1-M/4	—	17,5
C/1-M/4	—	15,2
P/2-M/4	11,2	11,0
M/1-M/4	—	7,8
Length of alveoli:		
M/1	1,80	1,88
M/2	2,00	1,96
M/3	2,12	2,04
M/4	1,84	—
M/1-M/4	7,60	(7,50)
Length of diastema:		
P/1-P/2	1,00	0,52

Specimen GMH LII-46, MP 12, differs from GMH XLI-5, MP 13, by its deeper and more robust horizontal ramus and by its longer P/1-P/2 diastema (figs. 4c, 5d); both differences may be due to different individual age of the animals (cf. Crochet 1980, fig. 5). Otherwise, both specimens agree in size and morphology and they are referred to one taxon.

Specimen GMH LII-46: A single M/4 of *P. monspeliense* which has been figured (Crochet 1980, fig. 227) is rather distinctive specifically. GMH LII-46 (fig. 4b) morphologically almost duplicates this specimen from Mas de Gimel, MP 10. Common distinctive characters are:

- the metaconid is only very slightly distal to the protoconid,
- the hypoconulid is rather prominent and strictly lingual in position,
- trigonid and talonid are of equal length,
- the trigonid basin is deep, and
- the entoconid is relatively high.

Additional features which are less distinctive specifically are: relatively high and pointed main cuspids; a rather strong precingulid which terminates at the protoconid; talonid width clearly less than trigonid width; termination of the crista obliqua relatively high up against the posterior trigonid wall.

P/2 of specimen GMH LII-46 (fig. 4a) morphologically agrees fairly well with

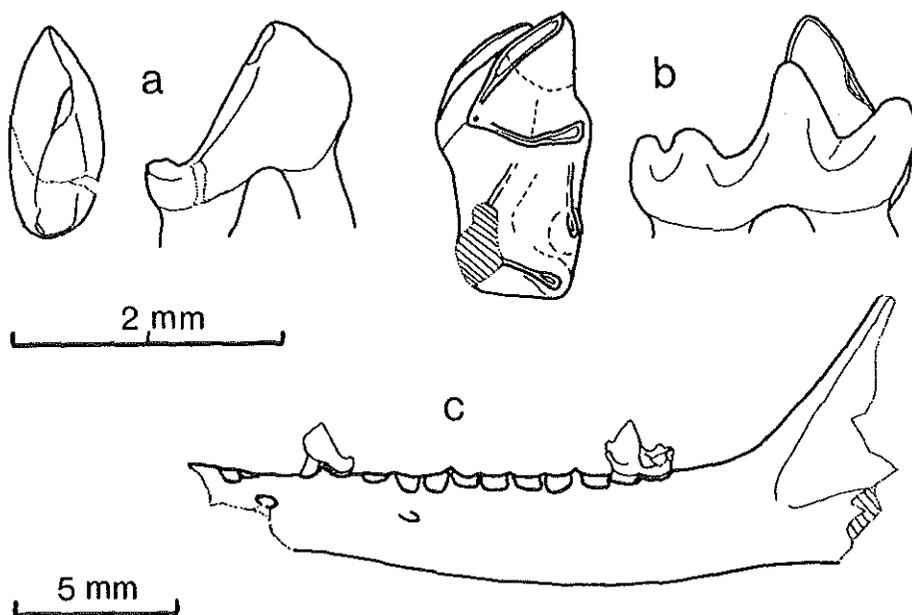


Figure 4. – *Peratherium* aff. *monspeliense* CROCHET 1979, specimen GMH LII-46. Geiseltal near Halle, GDR; Untere Mittelkohle, MP 12. a: l. P/2 in occlusal (left) and lingual (right) view; b: l. M/4 in occlusal (left) and lingual (right) view; c: l. lower jaw fragment in labial view.

that of the holotype of *P. perrierense* which is a supposed member of the *monspeliense* lineage (Crochet 1980, fig. 232; no *monspeliense* P/2 is known). The single cusp is centred over the anterior root, there is a sharp anterior crest, and two sloping posterior ridges delimit a distinct posterior heel.

Specimen GMH XLI-5: M/4 (fig. 5a-b) is badly damaged, and its paraconid and talonid are somewhat displaced. Nevertheless, distinctive features like the strictly lingual hypoconulid, the high entoconid, and corresponding trigonid and talonid lengths can be substantiated. P/2, too, compares well with GMH LII-46.

M/2-3 (fig. 5a-b) of GMH XLI-5 likewise fit the descriptions for the type material of *P. monspeliense* (no M/1 is included in the type series). The protoconid is only slightly mesial to the metaconid; trigonid and talonid are of subequal length and width; the conical entoconid is strong and high (on M/3, in which the talonid is completely preserved, the entoconid clearly surpasses the hypoconid); the strong hypoconulid reaches to the lingual crown margin; pre- and postcingulid are well developed; the crista obliqua terminates slightly labially of the trigonid notch and it is ascending the posterior trigonid wall for some distance. The height of the protoconid is constantly increasing from M/1 to M/4 (fig. 5).

No lower antemolar dentition of *P. monspeliense* has been described so far. P/2 and P/3 (fig. 5a-b) of specimen GMH XLI-5 are subequal in size (P/3 slightly larger than P/2). P/3 differs from P/2 in possessing a weak precingulid and in having a more expanded and more deeply basined posterior heel. The alveoli of P/1 are separated by short diastemata from P/2 and C/1, respectively. C/1 (fig. 5c) is moderately strong; in labial view its posterior outline is almost straight and its anterior edge is becoming

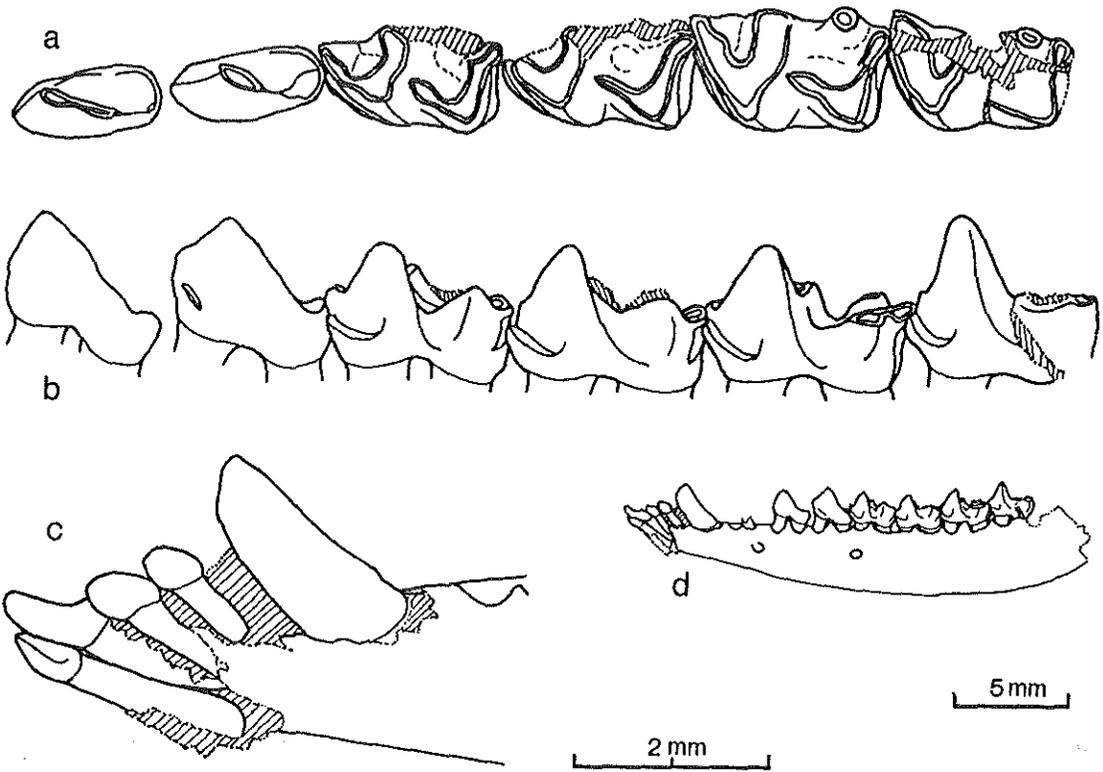


Figure 5. – *Peratherium* aff. *monspeliense* CROCHET 1979, specimen GMH XLI-5. Geiseltal near Halle, GDR; Obere Mittelkohle, MP 13. a: l. P/2-M/4 in occlusal view; b: l. P/2-M/4 in labial view; c: l. I/1-C/1 in labial view; d: l. lower jaw fragment in labial view. 2 mm scale refers to a-c, 5 mm scale refers to d.

strongly convex apically. The incisors (fig. 5c) are crowded, procumbent, and spatulate. I/2 is enlarged in comparison with I/1, I/3 and I/4, which are subequal in size (I/4 is slightly smaller than I/1 and I/3).

P. monspeliense (MP 10) and *perrierense* (MP 16-17) are supposed to represent a lineage. Evolutionary trends seen within this lineage include an increase of tooth size and an increasing length of the lower molars from M/1 through M/2 to M/3. In *monspeliense*, M/2 and M/3 are of similar length (no M/1 is known), whereas the molars of *perrierense* become longer from M/1 to M/3.

In both criteria of absolute and relative molar size, the Geiseltal specimens look a little more advanced than *monspeliense*: the Geiseltal M/3-4 are slightly larger than the specimens from the type locality of *monspeliense*, Mas de Gimel. *P. perrierense*, on the other hand, is still decidedly larger. The alveoli lengths of both Geiseltal specimens increase from M/1 to M/3 (in GMH LII-46, alveoli lengths decrease from M/3 to M/4; in *perrierense*, M/4 may be either longer or shorter than M/3). The Geiseltal lower jaws may represent a new species. For the moment we link these specimens nomenclaturally with the morphologically closest taxon, *P. monspeliense*.

MARSUPIALIA, incertae sedis

Microtarsioides voighti WEIGELT 1933

(Pl. 1, fig. 2)

Material: Holotype, poorly preserved and delicate skeleton of a very young individual. GMH CeIII-4235.

Type locality and horizon: Grube Cecilie, site III (Leichenfeld 2), Geiseltal near Halle, GDR; Oberes Hauptmittel-lowermost Oberkohle, MP 13/14, Uppermost Geiseltalian/? Lowermost Robiacian.

The mammalian fauna of the Geiseltal Oberes Hauptmittel-lowermost Oberkohle comprises two enigmatic taxa, *Microtarsioides voighti* WEIGELT 1933 and *Ceciliolemur delasaucei* WEIGELT 1933. Both have been originally assigned to primates: *Microtarsioides* has been referred to superfamily Tarsiioidea, family incertae sedis, and to house *Ceciliolemur*, the superfamily Ceciliolemuroidea consisting of a single family Ceciliolemuridae has been established (Weigelt 1933). Both of these taxa are based on a poorly preserved skeleton of a very young individual (pl. 1, fig. 2).

Accordingly, the taxonomic position has been judged controversially. Simpson (1945: 64) questionably assigned both to Prosimii of uncertain infraorder or family. Matthes (1958: 49 and 58) considered *Ceciliolemur* to be an insectivore and he grouped *Microtarsioides* among Tarsiioidea, incertae sedis. Simons (1962: 30) examined the two type specimens and he found no basis for referring either of these specimens to the primates; he presumed that they belong to the same species (of uncertain affinities) and that they are even from the same "litter". Van Valen (1967: 266) provisionally included *Ceciliolemur* (synonym = *Microtarsioides*) in the Insectivora, incertae sedis. Szalay (1976: 366) closely compared the type specimens and concluded that both of these taxa have been based on very young individuals of marsupials, both probably of the same species of *Peratherium*. Haubold (1983: 160) on the other hand presented evidence against close relationships of *Ceciliolemur* and *Microtarsioides*; he left the taxonomic status of the two undecided.

On the basis of our current understanding of the actual type specimens we refer *Ceciliolemur* to the order Primates, incertae sedis, and *Microtarsioides* to the order Marsupialia, incertae sedis. The juvenile age and the poor preservation make any more precise assignment hazardous.

Primate-like features of *Ceciliolemur* are the following:

- On the right lower jaw only two deciduous incisors can be substantiated, one of which is being replaced by a permanent tooth (nothing can be said about the left front dentition).
- The terminal phalanges of the hands and feet broaden; they evidently have been equipped with nails.
- Supposedly there was a complete postorbital bar (there is no much doubt about its dorsal portion).

On the other hand, the structure of the lower jaw of *Microtarsioides* provides a character diagnostic of marsupials: the angular process is typically inflected medially. Besides, the leading edge of the coronoid process is strongly inclined posteriorly as can be seen likewise in the Geiseltal *Amphiperatherium* and *Peratherium* specimens. Finally, two bony chips which extend from the crushed pubic bones cranially probably represent epipubic bones.

Infraclass EUTHERIA GILL 1872
 Order LIPOTYPHILA HAECKEL 1866
 Family NYCTITHERIIDAE SIMPSON 1928

Genus *SATURNINIA* STEHLIN 1940

Type species: Saturninia gracilis STEHLIN 1940.

Diagnosis: See Sigé (1976: 11).

Saturninia ceciliensis n. sp.

(Text-fig. 6a-c)

Etymology: From its type locality, "Grube Cecilie".

Holotype: GMH CeIV-2882, right lower jaw fragment with M/1-3 (fig. 6a-c). The metaconids are more or less broken, M/1 is corroded to some extent, and the thin enamel cover is partly lacking.

Type locality: Grube Cecilie, site IV (Trichter NO), Geiseltal near Halle, GDR.

Stratum typicum: Obere Mittelkohle (MP 13), Upper Geiseltalian (= Upper Lutetian), Middle Eocene.

Diagnosis: Middle-sized species of *Saturninia*. On M/1-3, the crista obliqua terminates at posterior wall of protoconid, not ascending trigonid wall; hypoflexids shallow; talonids long; hypoconulids somewhat lingual of midline; entoconids crest-like; post-cingulids lacking.

Measurements

	Tooth length	x	width:
M/1	1,56	x	(1,12)
M/2	1,60	x	1,12
M/3	1,52	x	1,04
M/1-M/3	4,52		

Description and comparison

The Geiseltal lower molars show a suite of characters which is highly diagnostic of nyctitheriids and within this family, of the genus *Saturninia* (cf. Sigé 1976, Krishtalka 1976):

- the trigonid is elevated and open lingually, the paraconid is low;
- the talonid is deeply basined and about as wide as the trigonid on M/1-2, narrower on M/3;
- the hypoconulid is submedial in position and projecting distally;
- the hypoconid is higher than the entoconid and it does not become flat with wear;
- there is no mesoconid on the crista obliqua;
- M/3 is not reduced, its talonid is long;
- talonids and trigonids have angular occlusal outlines; and
- the cusps are sharp, subconical to subcrescentic.

Named *Saturninia* species are known from the Bartonian (MP 15) to late Ludian (MP 20) of western and central Europe (Sigé 1976). They all differ morphologically from the Geiseltal specimen.

The crista obliqua of the Geiseltal molars meets the posterior wall of the protoconid labially of the trigonid notch. As a result, the hypoflexid is rather shallow. In all previously described species the crista obliqua terminates on the metaconid and consequently, the hypoflexid is markedly deeper. The crista obliqua of the Geiseltal M/1-2 continues on the flat trigonid wall for a very short distance only, while in known

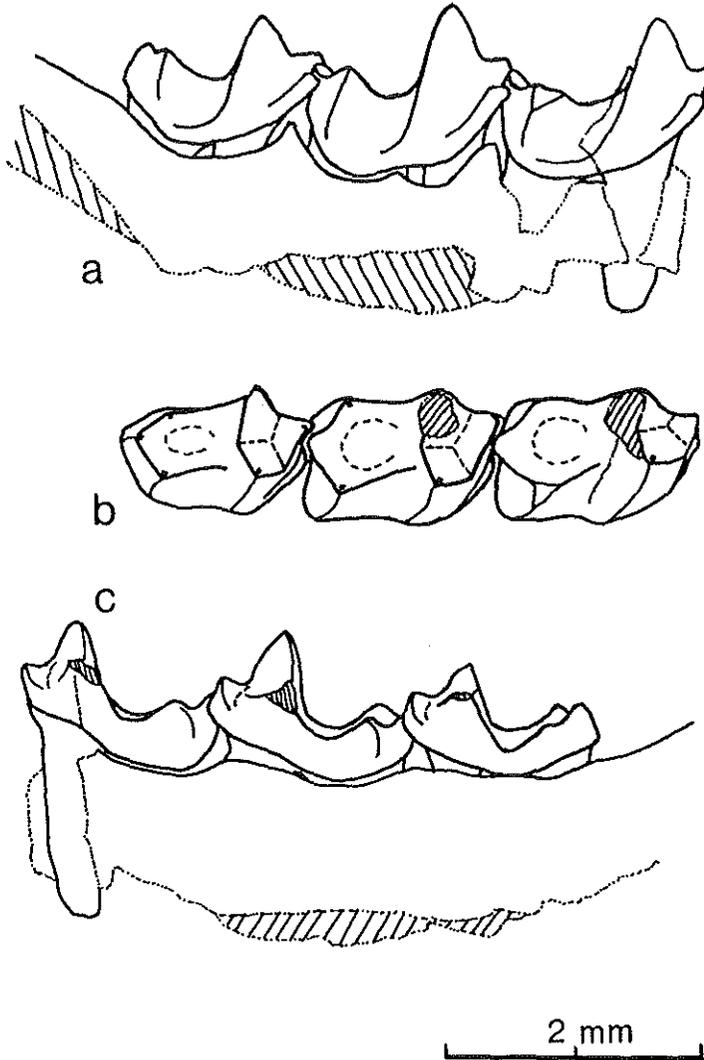


Figure 6. — *Saturninia ceciliensis* n. sp., holotype GMH CeIV-2882. Grube Cecilie, Geiseltal near Halle, GDR; Obere Mittelkohle, MP 13. R. M/1-M/3 in labial (a), occlusal (b) and lingual (c) view.

species it is ascending the metaconid, occasionally running up to its apex. As an exception, the crista obliqua of *S. grandis* is not ascending; yet unlike the Geiseltal specimen (and *Saturninia* species in general) the crista obliqua seems to bear a small mesoconid (Sigé 1976, fig. 73; cf. Hooker 1986).

The Geiseltal molars lack a postcingulid. Thus, they are distinguished from *S. gracilis*, *intermedia*, and *mamertensis*. A rather distinctive feature of the Geiseltal species are the unreduced long talonids. Trigonid and talonid are of equal length on M/1-2, and the talonid length slightly exceeds the trigonid length on M/3. The talonid is relatively shorter—in some of the species markedly so—in *S. gracilis*, *mamertensis*, *grisollensis*, *tobieni*, *intermedia*, and *hartenbergeri*. The Geiseltal

specimen in this respect compares well, however, with *S. beata* (cf. Sigé 1976, figs. 55, 57) and *grandis* (cf. Sigé 1976, fig. 73). The configuration, including the inclination, of the Geiseltal trigonids agrees with that in known species except for *S. mamertensis*, in which the trigonids are more erect.

The Geiseltal lower molars are of subequal length. Judging from associated M/1-3 of *S. gracilis*, *grisollensis*, *hartenbergeri*, and *beata* (tabs. in Sigé 1976, measurements for other species are not available), there usually is some reduction in size from M/1 distally. Thus, the length of the Geiseltal M/1 is close to the mean for *hartenbergeri*, its M/2 and M/3 length, however, fall beyond the size range for this species. *S. gracilis*, *mamertensis*, *grisollensis*, *tobieni*, and *intermedia* have slightly to distinctly smaller molars than the Geiseltal specimen, while *S. beata* and *grandis* average somewhat more.

It is premature to link the Geiseltal species with one of Sigé's (1976) supposed evolutionary lineages on the basis of a single series of lower molars only. But we feel that it is more closely related to *S. grandis* and *beata* than to any other species. Common features of the three are:

- crista obliqua without an accentuated continuation on the posterior wall of the trigonid,
- hypoconulids strong and projecting,
- postcingulids lacking,
- talonids long, and
- paraconids crest-like.

One character, however, may exclude the Geiseltal species from an ancestor-descendant relationship with *S. grandis* and/or *beata*. Its entoconids are crest-like and relatively low, while they are cusperate and stronger in *grandis* and *beata*. We hesitate to regard a reduced entoconid as the primitive condition in *Saturninia*. Early records of the genus do not contribute to the question of character polarity. The geologically oldest record is from Mas de Gimel, MP-Unit 10 (= cf. *Saturninia* sp.; Cappetta *et al.* 1968) but this assignment seems questionable (Sigé 1976). *Saturninia* is then known from Saint-Martin-de-Londres, MP 12 (= *Saturninia* sp.; Crochet *et al.* 1988), and from Bouxwiller, MP 13 (= *Saturninia* sp.; Sigé 1976), but so far no lower molars have been described.

There is broad consensus that the ancestry of *Saturninia* is to be sought among primitive nyctitheriids of the *Leptacodon* group, typically represented by a species like *L. tener* MATTHEW & GRANGER 1921 from the Tiffanian of North America (Krishtalka 1976, McKenna 1960, Robinson 1968, Sigé 1976). European Paleocene and Early Eocene (MP 1-10) nyctitheriids have been provisionally referred to *Leptacodon* (Godfriaux & Thaler 1972, Godinot 1981, Russell *et al.* 1982, Savage & Russell 1983). This material needs to be reviewed. A M/1 or M/2 of cf. *Leptacodon* sp. from Rians, MP 7 (Godinot 1981, fig. 7c-e) differs morphologically from the Geiseltal M/1-2 in having a more lingual position of both the hypoconulid and the mesial termination of the crista obliqua, and in having a stronger hypoconid. If we accept *L. tener* as a plesiomorphic model, two of the diagnostic characters of the Geiseltal species must be considered primitive for *Saturninia*. These are the labial position of the crista obliqua on M/1-2, and the submedial position of the hypoconulid on M/1-3 (for *L. tener*, see Krishtalka 1976, fig. 1A; McKenna 1968, figs. 3-4; Simpson 1935, fig. 4). *L. tener* differs from the Geiseltal species, however, in having cusperate and stronger paraconids and entoconids.

Other nyctitheriid genera which evolved independently in Europe, North America, and possibly Asia (Russell & Dashzeveg 1986) from a *Leptacodon*-like stock differ morphologically from the Geiseltal species and need not concern us here in detail.

Scraeva CRAY 1973 is distinguished by the presence of a mesoconid. In *Nyctitherium* MARSH 1872, the hypoconulid is twinned with the entoconid. In *Pontifactor* WEST 1974, the trigonid is not open lingually but anteroposteriorly compressed, and a mesoconid occurs on the crista obliqua.

Order EDENTATA CUVIER 1798

Family MYRMECOPHAGIDAE BONAPARTE 1838

Genus *EUROTAMANDUA* STORCH 1981

Type species: *Eurotamandua joresi* STORCH 1981.

Diagnosis: see Storch (1981: 253).

Eurotamandua joresi STORCH 1981

(Pl. 1, fig. 3-4)

Material: Right humerus without proximal epiphysis; entepicondylar and trochlear regions and proximal part of supinator crest are broken. GMH XIV-4318. Right ulna without proximal and distal epiphyses; proximal bit of coronoid process broken. GMH XIV-3912.

Horizon: Unterkohle; MP 11, Lower Geiseltalian.

Measurements

Humerus:	Maximum length	63,2
	Maximum width proximally	20,8
Ulna:	Maximum length	85,0
	Length of olecranon	24,2
	Maximum width distally	12,5

Description

Eurotamandua joresi has been originally described on the basis of a single, virtually complete skeleton from Grube Messel near Darmstadt, FRG. Since then, the Messel oil shale pit has produced no additional specimens, although excavations have intensified rather. In the course of examining a large quantity of isolated postcranial bones at the Geiseltalmuseum in Halle, Jens Franzen (Senckenberg-Museum, Frankfurt am Main) and the present authors discovered one humerus and one ulna, which at once suggested an *Eurotamandua* nature. Close comparisons with the Messel type specimen in Frankfurt confirmed agreement in size and morphology. Both the Geiseltal and Messel specimens are from the same biostratigraphical level, MP 11. The type is represented by an articulated skeleton so that humerus and ulna are partially covered by other forelimb elements and visible in fixed views only (Storch 1981, fig. 9a-b). Thus, the new Geiseltal specimens can add considerably to the knowledge of their morphology.

Humerus

(Pl. 1, fig. 4a, b)

The humerus is robust and it is equipped with strong muscular crests. The pectoral crest is long and prominent distally. It is faintly concave laterally and it is directed toward the capitulum. Its distal end is not developed into an anteromedially directed prominent flange and it is not limited by a definite trough or groove.

The deltoid tubercle is prominent and projects laterally about midway along the

shaft. A well-defined deltoid crest converges from the deltoid tubercle toward the distal end of the pectoral crest. The surface between the pectoral and deltoid crests is not developed into an elevated deltopectoral shelf, but is low and excavated.

The shaft exhibits no evidence of a distinct teres tubercle, yet muscle scars for insertion of the teres major are situated on its medial border, about opposite to the deltoid tubercle.

The supinator crest is extraordinarily pronounced. Its proximal edge winds back to merge with the posterolateral face of the shaft.

The distal end of the humerus is very wide medio-laterally (its entepicondylar part is missing in the Geiseltal specimen but it is well exposed in the type). The capitulum is large and strongly spherical; lateral to the capitulum, an anterior articular groove and narrow flange are developed. The entepicondyle (Storch 1981, fig. 9a-b) is markedly extended medially and it has an angular outline. Its medial margin is long and straight longitudinally. The distal edge of the entepicondyle is also long and nearly straight; it is displaced proximally with respect to the trochlea, thus forming an extended notch for the passage of forearm muscles.

The entepicondylar foramen is preserved by part of its anteroproximal edge. Obviously, the foramen was situated rather proximally and the entepicondylar bridge was very wide transversally.

Posteriorly above the capitulum the humerus has a small circular olecranon fossa.

Ulna

(Pl. 1, fig. 3a-c)

The ulna is robust. Its shaft is straight, and the large and relatively deep olecranon is slightly incurved. The shaft is moderately compressed laterally; in cross-section it is convex medially and gently excavated laterally. The thickness is about the same along the whole length of the shaft.

The anconaeal process of the semilunar notch is elevated only along the lateral face of the ulna; thus it does not produce a bill-shaped outline in lateral view of the bone. The radial facet of the ulna is rugose rather; it is not expanded into a tongueshaped lateral process, i.e. a processus coronoideus lateralis is lacking. The well-developed medial coronoid process projects anteromedially.

Mediodistally to the trochlear facet of the semilunar notch is a definite longitudinal pit. The interosseous crest is not sharp; it is rugose distally.

Comparisons

The recent *Tamandua* is a powerful hook-and-pull digger. Its forelimbs have important capabilities to tear apart hard carton nests of termites and ant-infested wood with the large second and even larger third claws. Beside the obtainment of food, the forelimbs play a major role in defense and arboreal habits. These biological roles are reflected in very distinctive osteological specializations of the forelimb, part of which are autapomorphic of anteaters (Myrmecophagidae) (see Taylor 1978 and 1985, and Hildebrand 1985 for anatomical descriptions and functional implications).

Humerus and ulna of *Eurotamandua* were highly adapted for fossorial habits and they show distinctive myrmecophagid specializations (as does the entire skeleton; Storch 1981). Thus, *Eurotamandua* like its recent relative, evidently was a forceful hook-and-pull digger. The Messel type specimen contributes further evidence: Its gut contents are preserved and they consist of insect cuticulae (presumably of termites), grains of sand, and of numerous particles of cemented wood which compare very well with the wall material of hard carton nests of recent termites (Richter 1987, Storch &

Richter 1988).

The most striking feature of the forelimb of the recent *Tamandua* and *Myrmecophaga* is the modification of the medial head of the triceps muscle. This large portion passes through a distinctive very wide and rather deep notch delimited by the distal border of the large entepicondyle and the medial margin of the trochlea, to become continuous with the tendon of the deep digital flexor. Thus, it becomes an accessory flexor of the distal phalanges, above all of the strong digit III. The entepicondylar distal notch is in line with the axis of rotation of the elbow joint. Thus, contraction of the medial triceps head has scant effects upon movement of the elbow and the claws may be flexed to full effect even when the limb is fully extended. These specializations are unique to *Tamandua* and *Myrmecophaga*. *Eurotamandua* as can be clearly seen on the type specimen, almost duplicates the configuration of the entepicondyle and the entepicondylar notch of *Tamandua*.

Beside capabilities for powerful flexion of the claws, *Tamandua* and *Myrmecophaga* possess enhanced capabilities for strong axial rotation of the humerus. Lateral rotation is increased primarily by lateral expansion of the deltoid tubercle: its effect is to displace the insertion of the spinodeltoid muscle laterally thus increasing its moment arm for rotation. "This feature is characteristic of xenarthrans and reaches its extreme in vermilinguas" (Taylor 1985: 167). *Eurotamandua* displays a widely flaring deltoid tubercle; actually its deltopectoral region is very similar to that of *Myrmecophaga* except for the somewhat more proximal position of the deltoid tubercle.

Pholidotans (Manidae) and the early Tertiary palaeonodons are the closest ecological analogues of myrmecophagids. Manids feed on termites and ants and they are forceful scratch-diggers; palaeonodons supposedly had similar habits (see Emry 1970, Rose 1978 and 1979, and Simpson 1931). Accordingly, the three groups display resemblances in many skeletal features which have been enumerated by several authors. McKenna (1987: 78) assigned *Eurotamandua* to the palaeonodons, and Novacek (1982: 35) saw no definite reason to exclude *Eurotamandua* from the Pholidota; therefore, we include the humeri and ulnae of these mammals in our comparison. (By the way, the xenarthrous condition of *Eurotamandua* is not "reconstructed" as stated by Novacek. It is precisely drawn on the basis of the actual specimen in an oblique dorsal view, the centra of the vertebrae are not visible; cf. Storch 1981, fig. 8a-b. We can see no differences to the "xenarthry characteristic of edentates".)

The humerus and the ulna of *Eurotamandua* are similar to those of palaeonodons and pholidotans in being stout, the humerus in having strong muscular crests and processes. But no features are demonstrably synapomorphic with one or the other of these orders.

The deltopectoral regions of the humeri, and hence the muscular arrangements of the forelimbs, of manids and palaeonodons (excluded from comparisons are the highly subterranean Oligocene *Epoicotherium* and *Xenocranium*; cf. Rose & Emry 1983) are definitely specialized unlike those of *Eurotamandua* and the myrmecophagids on the whole: the pectoral crest in manids and the elevated deltopectoral shelf in palaeonodons, respectively, are elongated distally to the upper end of the entepicondylar bridge; their lower end is prominent and characteristically turned over anterointernally so that it extends beyond the medial outline of the shaft; their distal termination is abruptly limited by a groove or trough for the passage of the biceps tendon; pectoral crest and deltopectoral shelf are directed distally toward the entepicondyle rather than toward the capitulum as in *Eurotamandua* and extant myrmecophagids. The deltoid tubercle is a low process on the proximolateral side of the humerus at best (humeri of various manids and palaeonodons are figured in Emry 1970, Koenigswald 1969, Rose 1979, Simpson 1931).

The specializations of the myrmecophagid entepicondyle are lacking in manids and palaeanodonts. The extant *Manis temminckii* and certain fossil *Necromanis* species have amongst manids a more anteroposteriorly flattened entepicondyle with a proximodistally somewhat more expanded medial end (Emry 1970), but they do not fit the characteristic myrmecophagid condition, particularly of the distal margin (cf. Emry 1970, fig. 3).

The semilunar notch of the ulna of pholidotans and palaeanodontans (see figures in Emry 1970, Koenigswald 1969, Schoch 1984, Simpson 1931) differs from that of *Eurotamandua* and extant myrmecophagids in having an elevated anconaeal process in lateral view and in having a laterally extended radial lip (= proc. coronoideus lateralis) in anterior view. Corresponding to the typically reduced anconaeal process, the olecranon fossa is rather small and circular in *Eurotamandua*, *Tamandua*, and *Myrmecophaga*, as compared to the transversally elongate fossa in the two other groups.

COMPARISON MESSEL — GEISELTAL

Of the taxa presented, only *Eurotamandua joresi* is common to both faunas. It should be noted that both records are from the same biochronological level, the lower Geiseltalian (MP 11).

Several marsupial specimens are known from the Messel pit but determinations and descriptions are not yet completed (W. von Koenigswald & G. Storch, in prep.). It can be stated, however, that the lineage of large-sized *Amphiperatherium* species which is represented by *A. aff. maximum* in the Geiseltal Untere Mittelkohle, is also known from Messel. So far, *Saturninia* (or *Leptacodon*) is unknown from Messel.

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LEGEND OF PLATE

PLATE 1

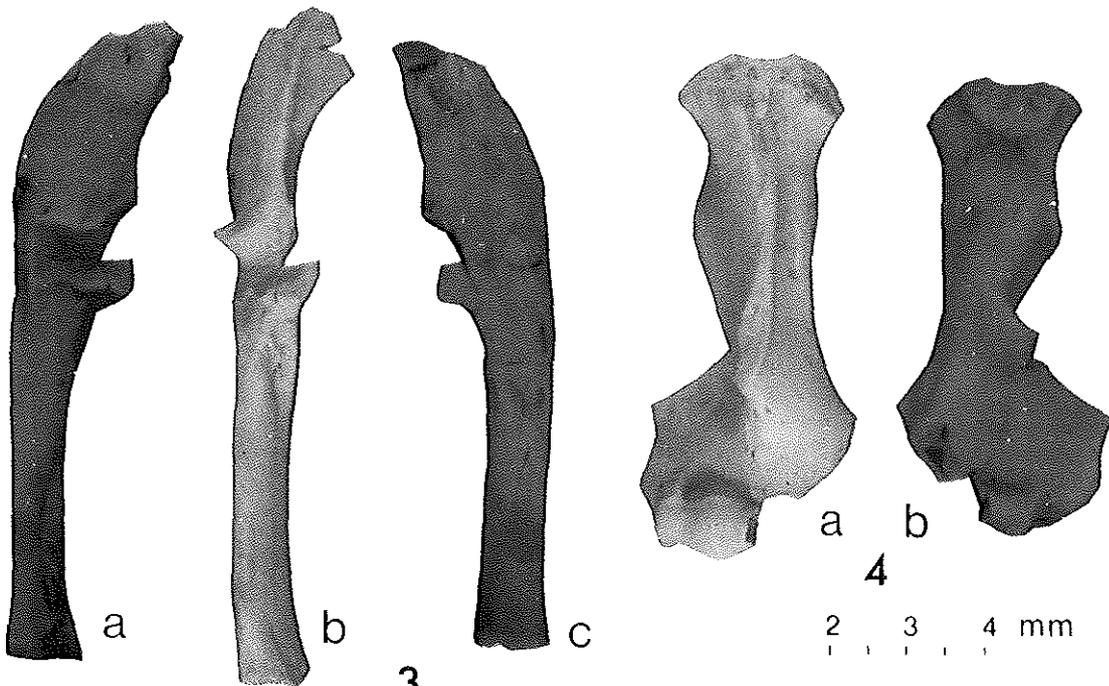
- Fig. 1. – *Amphiperatherium giselense* (HELLER 1936), lectotype GMH CeIV-7285 (X-ray photograph). Grube Cecilie, Geiseltal near Halle, GDR; Obere Mittelkohle, MP 13.
- Fig. 2. – *Microtarsioides voigti* WEIGELT 1933, holotype GMH CeIII-4235. Grube Cecilie, Geiseltal near Halle, GDR; Oberes Hauptmittel-lowermost Oberkohle, MP13/14. Approx. $\times 1,26$.
- Figs. 3-4. – *Eurotamandua joresi* STORCH 1981, specimens GMH XIV-3912 and GMH XIV-4318. Geiseltal near Halle, GDR; Unterkohle, MP 11. 3: r. ulna in lateral (a), anterior (b), and medial (c) view. 4: r. humerus in anterior (a) and posterior (b) view.



1



2



3

4

2 3 4 mm