0012-9402/04/020213-8
DOI 10.1007/s00015-004-1115-8
Birkhäuser Verlag, Basel, 2004

Eclogae geol. Helv. 97 (2004) 213–220

First fossil primates from Eckfeld Maar, Middle Eocene (Eifel, Germany)

JENS LORENZ FRANZEN

Key words: Primates, Europe, Eocene, *Europolemur*, *Periconodon*, taxonomy, biochronology, palaeoecology, palaeobiogeography, taphonomy

ABSTRACT

Two isolated upper molars and a mandible with an almost complete dentition represent the first primates from the Middle Eocene Eckfeld maar (SW Eifel, Germany). They are described and determined as the cercamoniines *Europolemur klatti* and *Periconodon* sp. respectively. The specimens result from excavations undertaken in 1995 by the "Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz". Taxonomy, biochronology, palaeoecology, palaeobiogeography, and the taphonomy of the discoveries are discussed.

ZUSAMMENFASSUNG

Unter den Funden der Grabungskampagne 1995 des Naturhistorischen Museums Mainz/Landessammlung für Naturkunde Rheinland-Pfalz im Mitteleozän des Eckfelder Maares (SW-Eifel) fanden sich in Gestalt zweier Molaren und einer Mandibel mit fast vollständiger Bezahnung die ersten Primaten aus dieser Fossillagerstätte. Sie werden hier beschrieben und bestimmt als die Cercamoniinen *Europolemur klatti* und *Periconodon* sp. Taxonomie, Biochronologie, Paläoökologie, Paläobiogeographie und Taphonomie der Funde werden diskutiert.

Introduction

Known since the 19th century for its well preserved Paleogene leaves (Lutz et al. 2000: 144), the Maar of Eckfeld (SW-Eifel, Germany) became an important site of Middle Eocene vertebrates and mammals since 1987 through the excavations carried out by the "Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz" under the leadership of Franz Otto Neuffer and Herbert Lutz (Lutz 1993a, b). Up to now 16 species of mammals have been discovered indicating a late Geiseltalian (MP 13) age of this locality (Franzen 1993, 1994) which was recently dated at 44.3 ± 0.4 million years BP (Mertz et al. 2000). Biochronologically it is the same level as the "obere Mittelkohle" (upper middle coal seam) of the Geiseltal near Halle (Germany), Bouxwiller, and the upper part of the Paris Limestone ("Calcaire Grossier Supérieur"), as well as Egerkingen γ (Switzerland) (Franzen 1994). Messel and the "untere Unterkohle" (lower part of the lower coal seam) of the Geiseltal are about 3 million years older (Mertz, pers. comm.). Numerous well preserved plants and insects permit a reconstruction of the palaeoecological background (Nickel 1996; Lutz 1997; Wilde 1989, 1995; Wilde & Frankenhäuser 1993). The scenario was obviously a small freshwater lake a few hundred meters in diameter surrounded by a dense paratropical rain forest (Lutz et al. 2000).

It was not until 1995 that the first prosimian primates, typical for such an environment, were found. They are represented by two isolated upper molars, and a fragmentary mandible bearing an almost complete series of cheek-teeth. This material is here described, determined, and discussed for the first time.

Taxonomy

Order Primates

Family Notharctidae TROUESSART 1879
Subfamily Cercamoniinae GINGERICH 1975
Genus *Europolemur* WEIGELT 1933

Diagnosis (emended after Hooker 1986: 267 and Thalmann 1994: 50). – Medium to large sized adapiform primates; dental formula 2•1•3•3/2•1•3•3. Upper canines big and pointed;

Forschungsinstitut Senckenberg Frankfurt am Main, Germany, and Naturhistorisches Museum Basel, Switzerland. Address: Dr. Jens L. Franzen, Jakobistr. 10, D–79822 Titisee-Neustadt, Germany. E-mail: jlfranzen@t-online.de

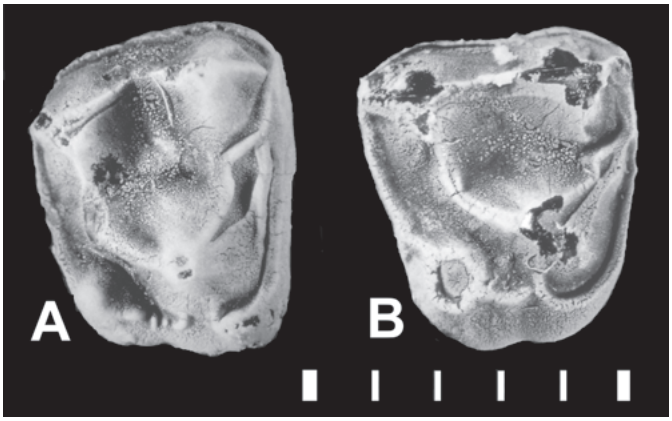

Fig. 1. *Europolemur klatti*, Eckfeld (Eifel), Germany. (Eckfeld collection of the Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz). Right upper molars. Occlusal view. Scale indicated. Scale = 5 mm.- A) M^2 d. (PW1995/70-LS). B) M^1 d. (PW1995/69-LS). – Photos: Naturhistorisches Museum Basel, Severino Dahint.

upper molars without postflexus; postprotocrista (crista obliqua) prominent; no metaconulus; M^3 smaller and shorter than M^2; P^4 much shorter than broad, with a weak parastyle; P_4 with a small and unicuspid talonid and a metaconid present to absent; protocristid of M_{1-2} nearly transversely oriented. Protoconid of P_3 little higher than that of P_4.

Europolemur klatti (WEIGELT 1933)

Fig. 1 A, B

Material. – isolated M^1d (PW1995/69-LS) and M^2d (PW1995/70-LS).

Measurements. – See table 1.
Lmax is the maximum length of the crown. Lbc is the length of the buccal wall of the crown. B is the breadth parallel to the anterior contour of the crown. D1 is the mesiobuccal-distolingual diagonal distance, and D2 is the mesiolingual-distobuccal diagonal of the crown respectively.

Description. – M^1: The colour of the enamel is black to dark brown. The morphology of the tooth corresponds almost perfectly with the left M^1 (BUX 80.82) described and figured by Godinot (1988: 386–387, fig. 3c) from Bouxwiller under the name *Europolemur dunaifi* (TATTERSALL & SCHWARTZ 1983)[2] although the specimen from Eckfeld is somewhat bigger. Its horizontal outline is subquadratic and more or less isometric except for its lingually protruding hypocone. There is a deep notch in the middle of the lingual wall (entoflexus), and a smaller one mesiolingually from the hypocone. Para- and metacone are almost equal in size. The parastyle is very weak, metastyle absent. There is no indication of a mesostyle. A sharp centrocrista runs in a straight line up and down the para- and the metacone. The protocone is situated near the centre of the tooth, just a little bit displaced mesiolingually, although still remote from the lingual cingulum. There is a clear-cut paraconule while a metaconulus is lacking. The ectocingulum is fine, sharp, and continuous except for a short interval distal to the metacone. On the mesial and lingual side a broad bulge-like cingulum extends from the parastyle to the distolingual wall of the protocone where it ends in an apically oriented hook. Another part of the cingulum originates at the notch below the protocone, forms a small hypocone, and fuses into the distal cingulum which extends to the distolingual corner of the tooth. Mesial to the paracone and distal to the metacone ecto- and entocingulum meet the centrocrista in small points. On the lingual side, the cingulum is much higher than buccally. There are three roots, two smaller ones of more or less equal size buccally and one on the lingual side being twice as big.

M^2: The enamel of this tooth is somewhat brighter than that of M^1, particularly at the cones, and on the lingual wall. The tooth displays a more rectangular trapezoidal horizontal outline with the buccal and the lingual wall diverging in a mesial direction. M^2 differs from M^1 in being considerably broader than long. Paracone and metacone are more or less equal in size. The protocone is situated relatively more lingually. The paraconule is well expressed while the metaloph is somewhat damaged at the place where a metaconule should be. The remaining parts, however, suggest that a metaconule was absent. Parastyle and metastyle are lacking. As in M^1 the ectocingulum is fine, sharp and continuous, although it fades away near the distal corner of the tooth. The pre- and entocingulum is bulge-like, and runs from the mesiobuccal corner of the tooth to the mesiolingual flank of the protocone where it forms a small pericone. Behind that it turns in an apical direction and disappears. Above the well expressed lingual notch it is substituted by a few tiny tubercula. Distolingual to the protocone the cingulum gives rise to a rather strong hypocone. On the distal side of the tooth, the cingulum is shelf like, and runs continuously to meet the ectocingulum at a point where the straight centrocrista comes down from the metacone. Summarising, the M^2 from Eckfeld resembles the type of *Europolemur dunaifae* from Bouxwiller figured by Godinot (1988: plate 1, Fig. A – Bchs 648) as an M^1 or M^2. There is, however, no pericone in the specimen from Bouxwiller which is also somewhat smaller and less trapezoidal in horizontal outline. Contrasting with the specimen from Eckfeld its entocingulum is continuous and ends distally at the top of the hypocone. Based on these differences the tooth from Bouxwiller is better considered as an M^1 instead of an M^2.

Tab. 1. Measurements of *Europolemur klatti* (WEIGELT 1933) from Eckfeld.

no.	pos.	Lmax	Lbc	B	D1	D2
PW1995/69-LS	M^1d	4,52	4,39	5,22	5,50	5,35
PW1995/70-LS	M^2d	4,33	4,30	5,50	5,54	5,60

[2] Corresponding with the gender of the patroness of that name, Mrs. Andrea Dunaif, it must be *dunaifae* and not *dunaifi* (article 31.1.2. IRZN).

Tab. 2. Variation of lengths and breadths of the M^{1-2} of *Europolemur*.

	provenance	length of $M^{1,2}$	breadth of $M^{1,2}$	reference
E. koenigswaldi	Messel	4.80 – 4.90	6.00	own measurements
E. kelleri	Messel	5,60 – 5,90	–	own measurements
E. klatti	Geiseltal	3.86 – 4.72	4.66 – 5.92	Thalmann 1994
E. "dunaifae" (= E. klatti)	Bouxwiller	4.07 – 4.87	4.51 – 6.12	Godinot 1988
E. klatti	Eckfeld	4.33 – 4.52	5.22 – 5.50	own measurements
E. collinsonae	Creechbarrow	4,9	6,2	Hooker 1986

Discussion. – Both teeth from Eckfeld belong obviously to the same taxon. The degree of abrasion and the rareness of such discoveries make it highly probable that they derive from the same individual. Size and morphology of the dental pattern point among the Adapiformes to the Cercamoniinae (Franzen 1994; Godinot 1998: 219), particularly to the genus *Europolemur* because of the absent metaconule. *E. koenigswaldi* FRANZEN 1987, and *E. kelleri* FRANZEN 2000, from Messel are larger, especially in the protocone area while the hypocone is smaller. A pericone is evidently variably present, and cannot be considered characteristic for a distinct species *E. dunaifae.*

Since the features presented by Tattersall & Schwartz (1983) as characteristic occur generally in that genus, *E. dunaifae* sinks into the synonymy of *E. klatti* (WEIGELT 1933) which is morphometrically indistinguishable (table 2). *E. koenigswaldi* is clearly more primitive because of its less expressed entocingulum and smaller hypocone which is also situated more lingually (Franzen 1987: 166). *Europolemur collinsonae* HOOKER 1986, from the Robiacian (Bartonian) of Creechbarrow (England), is not only larger, but has a hypocone that is nearly as big as the protocone, a buccally flexed centrocrista, and a distally arched postprotocrista (Hooker 1986: 273).

Up to now, *E. klatti* was only known from the late Geiseltalian (MP 13) of the Geiseltal near Halle. Now, Eckfeld together with Bouxwiller documents the occurrence of that species also west of the Oberrheingraben.

Genus *Periconodon* STEHLIN 1916

Diagnosis (Stehlin 1916: 1429–1430, emended). – Very small cercamoniine primate with P_1 (D_1), and a pericone on the upper molars. Lower cheek-teeth relatively long and slender. Paracristid short, without any trace of a paraconid. Paralophid and premetacristid confluent. Metaconid of molars not bulging, higher than protoconid. Metaconid of P_4 weak, lacking on P_3. Preentocristid and postmetacristid confluent. Entoconid lacking on M_3.

Periconodon sp.

Fig. 2A–C

Material. – Left fragmentary mandible with – P_3-M_3 and a fragmentary P_2 (PW 1995/68-LS). The specimen comes from the "Haupt-Turbidit (HT)" within a series of laminated bituminous freshwater claystone (Lutz 1993a–c).

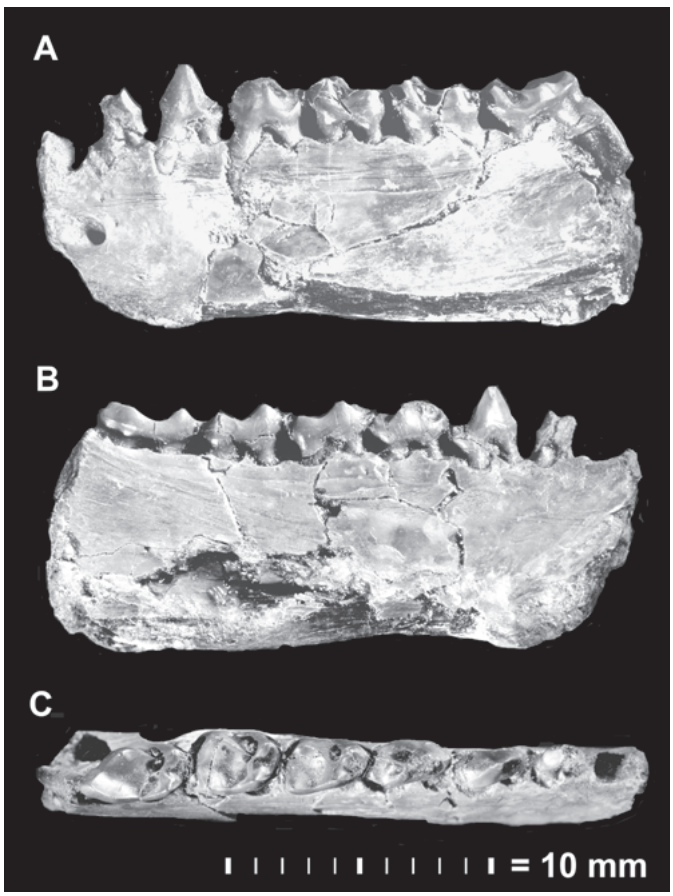

Fig. 2. *Periconodon* sp., ramus mandibulae s. with M_3-P_3, a fragmentary P_2, and the alveolae of P_1 and the canine, Eckfeld (Eifel), Germany (Eckfeld collection of the Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz, no. PW 1995/68-LS). Scale indicated.- A) buccal view, B) lingual view, C) occlusal view.- Photos: Naturhistorisches Museum Basel, Severino Dahint.

Measurements. – See table 3.

Description. – The specimen consists of a fragmentary left mandibular ramus with P_3-M_3, a fragmentary P_2, the alveolus of P_1, and half of the alveolus of the canine. Seen from the lateral and the medial side, the ramus is almost equally high all

Table 3. Measurements of *Periconodon* sp. from Bouxwiller (PW 1995/68-LS) compared with *Periconodon jaegeri* GODINOT 1988 and *P. huerzeleri* GINGERICH 1977 from Bouxwiller, *Microadapis sciureus* (STEHLIN 1916) from Egerkingen γ (holotype, Eh 750) as well as *Buxella magna* Godinot 1988 (type series; after GODINOT 1988: 392), and *Buxella prisca* GODINOT 1988 (type series; after Godinot 1988: 392) from Bouxwiller.

	Periconodon sp.				*P. jaegeri*		*P. huerzeleri*		*Microadapis sciureus*,				*Buxella magna*		*Buxella prisca*	
taxon	Eckfeld own measurements				Bouxwiller (after Godinot 1988)		Bouxwiller (after Godinot 1988)		holotype own measurements (Museum Basel, Eh 750)				type series (after Godinot 1988)		type series (after Godinot 1988)	
measurement	L	B1	B2	B3	L	Bmax	L	Bmax	L	B1	B2	B3	L	Bmax	L	B
M3	4,20	(2,1)	(2,1)	(1,02)	3,70-4,02	2,10-2,41	3,00–3,75	1,78–2,32	3.63	2.00	1.92	1.04	–	–	3.63	2.02
M2	3,69	(1,42)	(2,51)	–	3,24	2,82	2,90–3,13	2,31–2,48	3.58	2.25	2.42	–	3.32	2.55	3.00	2.19
M1	3.50	1.85	2.13	–	3,05	2,71	2,94–3,18	2,13–2,50	3.42	2.08	2.25	–	3.16	2.28	2.54–3.09	1.99–2.20
P4	3,18	(1,53)	(1,72)	–	–	–	2,67	1,54	2.50	1.75	–	–	–	–	–	–
P3	2,74	(1,34)	(1,21)	–	–	–	–	–	2.17	1.42	–	–	–	–	2.62	1.24
P2	(1,85)	–	(0,89)	–	–	–	–	–	1.75	1.29	–	–	–	–	–	–
P1	–	–	–	–	–	–	–	–	1.33	1.0	–	–	–	–	–	–
C	–	–	–	–	–	–	–	–	2,25	1,75	–	–	–	–	–	–

along its length. It is broken off just behind M_3, and at the alveolus of the canine. It is also crushed on the buccal and even more so on the lingual side. In spite of this damage a very large foramen mentale surrounded by three small ones is visible at medium height of the ramus just below the interspace between P_2 and P_1. Interesting are many small dot like impressions all over the buccal side of the ramus below P_2 and P_3, while there are only a few in a corresponding position on the lingual side (see p. 219). Another foramen mentale of medium size is recognised below the interface of P_3 and P_4, just below medium height of the ramus. There is no diastema developed between C and P_1 nor between P_1 and P_2.

The teeth:

The descriptions are based on teeth of which the enamel is almost completely dissolved by chemical erosion from alligator digestive tract except for a few relics in depressions and particularly at the contact between neighbouring teeth. Therefore, characters such as the cingulid are smoother compared with uneroded specimens.

P_1 is only represented by its empty alveolus. It had one root, and it was presumably unicuspid, the only cusp being mesially located and inclined.

P_2 was evidently unicuspid and biradicular. Originally it was about 2/3 of the length of P_3. Ecto- and entocingulid are bulging but weak, and only distally better developed. A smooth centrocristid runs straight from the mesial to the distal end of the crown where it meets the cingulid in tiny peaks.

P_3 is also unicuspid and biradicular being surrounded on the buccal and the distal side by a sharp continuous crest. The cingulid is almost entirely suppressed except mesiobuccally.

P_4 is morphologically a duplicate of P_3 except for its somewhat bigger size, a more elevated distal centrocristid, and a clearly developed metaconid. It displays a rudimentary trigonid. The tip of the protoconid is broken off but glued to the tooth again. Its original height seems to be a little bit less than that of P_3. The ectocingulid is weak and bulging but continuous while the entocingulid is almost completely suppressed, except for a hint mesiolingually.

All molars are characterised by rather low cusps, a deep and wide talonid basin, and a rather small trigonid without any trace of a paraconid. The protocristid connecting the proto- and the metaconid is more transversely oriented in M_3, and becomes more and more oblique in M_2 and M_1. The metaconid is the main cusp in all molars. It is a little bit higher than the protoconid which exceeds the height of the hypoconid. There is no hypoconulid developed in M_2 nor in M_1.

M_1 is about the same length as M_2 but is considerably narrower. The premetacristid is almost sagittally oriented. The trigonid opens more lingually than in M_2. Buccally, a hypoconid and distolingually an entoconid is developed on the crest surrounding the talonid basin. The talonid basin is large although a little bit smaller than in M_2. A bulge like ectocingulid is particularly expressed below and in front of the protoconid while the entocingulid is almost entirely reduced.

M_2 is much broader than M_1. Protoconid and metaconid are less prominent. The premetacristid is more transversely directed than in M_1, so that the trigonid opens more mesially. The premetacristid is confluent with a rather high paracristid, so that the trigonid is entirely surrounded by a flat crest. M_2 displays the largest talonid basin of all molars. The ectocingulid is much weaker than in M_1. It is only slightly expressed distal to the hypoconid, at the medivallum (entoflexid) and particularly mesially. The entocingulid is completely reduced.

M_3 is the longest lower molar but considerably narrower than M_2. It is about as broad as M_1. Its talonid basin is distally extended with a small hypoconulid at its end. There is a hypoconid on its surrounding crest while an entoconid is only slightly indicated by a swelling of the lingual crest surrounding the talonid basin. There is a fissure in that crest separating the hypoconulid from the hypoconid. The bulge-like ectocingulid

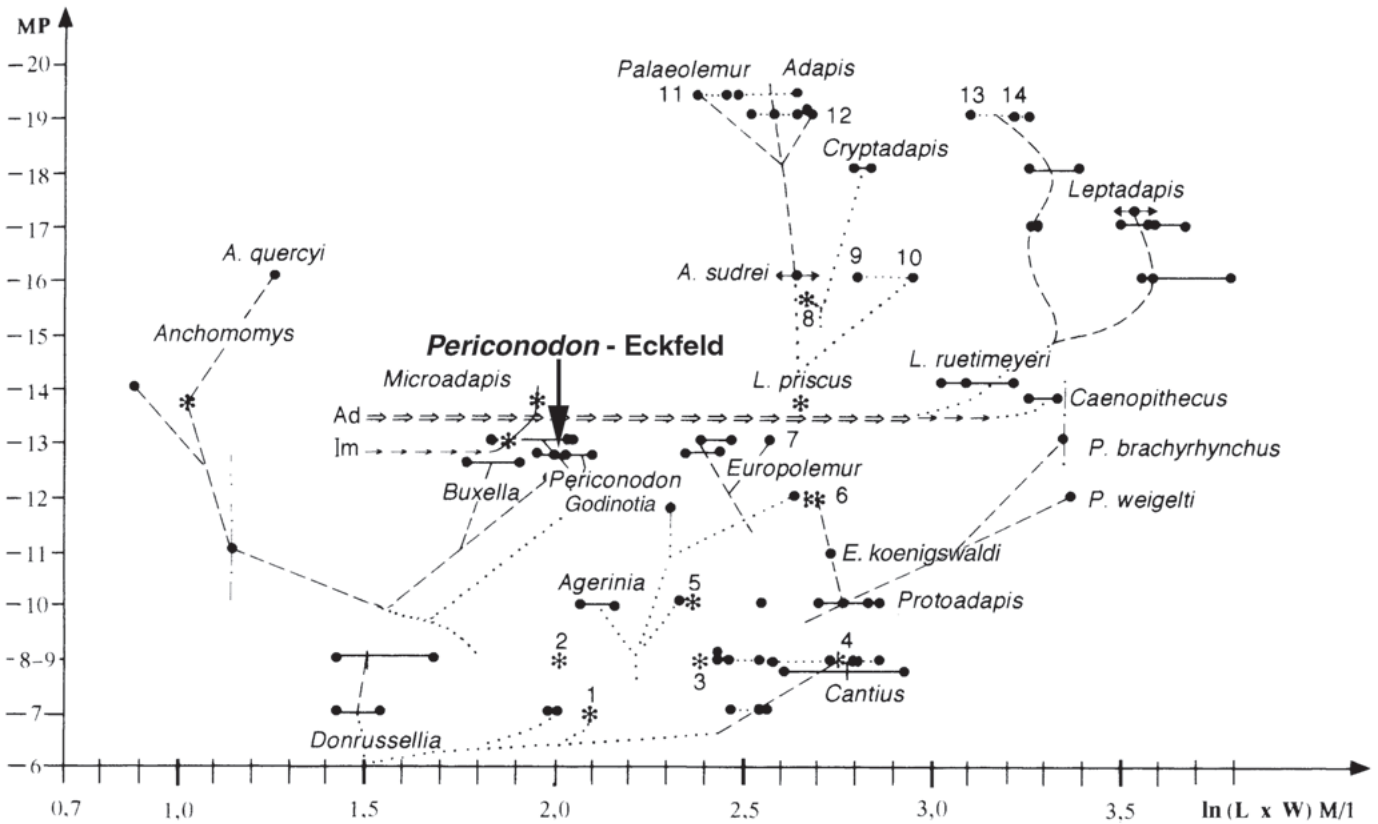

Fig. 3. Stratophenetic diagram of European Eocene adapiform primates based on Godinot (1998: Fig. 5). Abscissa is ln (not log!) of M_1 area (maximum length x maximum width). Ordinate is the sequence of mammalian reference-levels for Europe. *Periconodon* sp. from Eckfeld falls into the *Periconodon* field. Added is *Europolemur koenigswaldi* from Messel (MP 11) which fits with the transition from *Protoadapis* of MP 10 to *Europolemur klatti* of MP 13 (Geiseltal oMK). Corrected is the position and name of "*Pronycticebus*". Following Franzen (2000) this is now *Godinotia.* The measurements, however, do not derive from *Godinotia neglecta* of Messel (MP 11) but from the holotype of this species of Geiseltal uMK (MP 12).

is weaker below the protoconid and behind the hypoconid. An entocingulid is not developed.

Discussion. – The small primate resembles morphometrically *Microadapis sciureus* described by Stehlin (1916) under the name *Adapis sciureus* from Egerkingen γ (Switzerland). A close examination, however, points to a series of differences in detail:

- The premolars are considerably longer and narrower than in *Microadapis sciureus.*
- P_2 shows two roots instead of one in *Microadapis sciureus*.
- Contrasting with *Microadapis sciureus*, the roots are far more divergent.
- The main cuspid of P_3 is absolutely and relatively higher and more pointed than the molars in the species from Eckfeld compared to *Microadapis sciureus*.
- The metaconid is a distinct cusp in *Microadapis sciureus* while there is only a slight swelling of the protocristid in the P_4 from Eckfeld.
- The occlusal relief is much flatter in the taxon from Eckfeld.
- The talonid basin of the molars is considerably larger compared with the trigonid, and
- because of a mesial shift of the metaconid, also longer.
- The angle formed by the postmetacristid- and preentocristid is clearly more than 90° in the species from Eckfeld while it is clearly less than 90° in *Microadapis sciureus.*
- The cingulids, particularly the entocingulid, are sharp in *Microadapis sciureus* while they are bulging in the species from Eckfeld.
- The ramus horizontalis is higher in the species from Eckfeld.
- There are two larger foramina mentalia in the species from Eckfeld while there is only one in *Microadapis sciureus* which is considerably smaller than the anterior one of the Eckfeld specimen.

Summarising, it is clear that the specimen from Eckfeld does not belong to *Microadapis sciureus*, nor to the Adapinae at all. It is the morphology of the premolars, particularly the lack a distinct metaconid on P_4,which is indicative of the Cercamoniinae. In the adapines the P_4 is normally molarised

except in *Microadapis* while the premolars are not as pointed as in the cercamoniines, or in the species from Eckfeld.

Among the Cercamoniinae only the genera *Periconodon*, *Anchomomys*, and *Buxella* are comparable because of their small size. Except for its still smaller size, *Anchomomys* differs from the Eckfeld specimen by the presence of a paraconid and a hypoconulid on M_{1-2}, and the total absence of a metaconid on P_4.

Buxella is about the same size as the specimen from Eckfeld but its cheek-teeth are relatively broader (compare Godinot 1988: 392). While those of *Buxella prisca* GODINOT 1988 are shorter at the same breadths, those of *Buxella magna* GODINOT 1988 are broader at the same lengths. This holds true even when it is considered that the solution of the enamel in the specimen from Eckfeld has a stronger effect on the breadths than on the lengths because relics of enamel are still preserved between the teeth at their contact facies. The cuspids on the lingual side of the lower molars (metaconid and entoconid) are relatively higher and steeper in *Buxella* than in the specimen from Eckfeld. Like *Europolemur* and contrasting with *Buxella* there is no fissure separating a paraconid from the premetacristid in the molars of the species from Eckfeld. The paracristid is more transversally oriented while it runs more distolingually in *Buxella*.

Altogether it is concluded that the specimen from Eckfeld matches perfectly the characters diagnostic for *Periconodon* (see also Fig. 3). The species, however, remains enigmatic because the specimen from Eckfeld is clearly larger than *P. jaegeri*, the larger of the two species known from Bouxwiller, and also the wrinkling of the enamel, typical for that species (Godinot 1988: 389), is lacking. It is questionable, however, if and to what extent the wrinkling may be affected by the solution of the enamel. The breadth of the teeth surely is affected while the length is surely not. Therefore, the specimen from Eckfeld is definitely larger than *P. jaegeri* (see Table 2).

Considering *P. huerzeleri* GINGERICH 1977, the smaller of the two species from Bouxwiller, the holotype of that species (MBA-Bchs. 495) displays a rather small M_3 while a paratype (MBA-Bchs. 494) corresponds in this respect with the specimen from Eckfeld. Altogether, *P. huerzeleri* is considerably smaller than the specimen from Eckfeld.

Periconodon helleri (SCHWARTZ, TATTERSALL & HAUBOLD 1983) from the "oberes Hauptmittel (OHM)" = MP 13/14 of the Geiseltal as well as *P. helveticus* (RÜTIMEYER 1891) from Egerkingen are only known by maxillary teeth. Therefore, they cannot be compared.

Consequently, at the present stage of knowledge and considering possible effects of enamel solution it appears best to leave the species determination of the Eckfeld specimen open.

The Eckfeld mammal fauna

Including the primates there are now 16 mammal species known from the Eckfeld locality.

Chiroptera	indet.
Primates	
Notharctidae:	
Cercamoniinae:	*Europolemur klatti* (WEIGELT 1933)
	Periconodon sp.
Perissodactyla	
Equidae:	*Propalaeotherium parvulum* (LAURILLARD 1849)
	Propalaeotherium voigti (MATTHES 1977)
	Propalaeotherium isselanum (CUVIER 1824)
Palaeotheriidae:	*Paraplagiolophus codiciensis* (GAUDRY 1865)
	Palaeotherium castrense castrense NOULET 1863
Lophiodontidae:	*Lophiodon leptorhynchum* FILHOL 1888
Artiodactyla	
Diacodexeidae:	*Lutzia eckfeldensis* FRANZEN 1994
Dichobunidae:	*Hyperdichobune hammeli* SUDRE 1972
	Neufferia manderscheidi FRANZEN 1994
Cebochoeridae:	*Cebochoerus* cf. *ruetimeyeri* STEHLIN 1908
	Gervachoerus cf. *jaegeri* (SUDRE 1978)
Haplobunodontidae:	*Haplobunodon solodurense* STEHLIN 1908
Rodentia	
Paramyidae:	*Ailuravus picteti* RÜTIMEYER 1891

75% of the species are ungulates (perissodactyls and artiodactyls in equal parts) while 12,5% are primates. Poor in species (only one) but numerous in individuals are the rodents, represented up to now only by *Ailuravus picteti.* Also the isolated astragalus originally regarded as a carnivore (Franzen 1994: 201) belongs to *Ailuravus picteti* as recent comparisons have shown. Bats are restricted to an indeterminable fragment of a wing.

Biochronology

The co-occurrence of *Europolemur klatti* and *Periconodon* is also known from Bouxwiller as well as the "obere Mittelkohle" and the "Oberes Hauptmittel (OHM)" of the Geiseltal. The presence of these taxa therefore confirms the biochronologic correlation of Eckfeld with the upper Geiseltalian = MP 13 – 13/14 (Franzen 1994).

Palaeoecology and palaeobiogeography

Interestingly, the primates of the Eckfeld locality correspond with those from the Geiseltal while there are considerable differences between the ungulate faunas west of the Oberrheingraben and those from the east (Franzen 1994, 1995, 2003).

This may be explained by different biotopes, at Eckfeld a crater lake at an altitude of 460–480 m as a minimum (Pirrung & Büchel 1994: 46), while the Geiseltal was at that time a marshy, at other places also dry environment (Erfurt & Altner 2003) rather close to sea level. So palaeoecologic conditions may have been different for ground-dwelling ungulates while arboreal primates were not so much affected.

In any case, the congruence of the primate fauna of Eckfeld with that of the Geiseltal contradicts the hypothesis that the differing palaeobiogeographic distribution of the ungulates has to do with the Oberrheingraben sinking at this time, because such a scenario should have affected the primates too (Franzen 1994, 1995, 2003). On the other hand, we have to concede that there are only 2 primate taxa with 3 specimens known from Eckfeld while there are 56 specimens representing 13 primate species at the Geiseltal (Thalmann 1994: 68).

Taphonomy

The enamel of the teeth of the *Periconodon* specimen is almost completely dissolved. This is a strong argument that the animal was digested by a crocodile (Fisher 1981). The alternative possibility that the enamel was dissolved as result of acid lake water can be excluded because the contemporary teeth of *Europolemur klatti* do not display any solution grooves. They also show no effect of cracking due to desiccation or to abrasion during transport. They seem to have fallen from a primate carcass decomposing on the lake shore, and were subsequently transported into the lake by debris flows (Lutz 1993c: 106). In the *Periconodon* specimen the removal of the enamel is not restricted to the cusps but occurs also in the depressions (Fisher 1981). The hypothesis of crocodile digestion is strongly corroborated by bite marks occurring on the buccal and the lingual side of the anterior part of the ramus horizontalis (Fig. 2A, B). It is the snout where crocodiles normally attack and grasp their victims.

Conclusions

While two isolated upper molars represent the cercamoniine *Europolemur klatti*, a mandible with an almost complete dentition belongs to an indeterminable species of *Periconodon*. Being otherwise known only from the late Geiseltalian (MP 13) of Bouxwiller (Alsace, eastern France), as well as the "obere Mittelkohle (oMK)" and the "Oberes Hauptmittel (OHM)" of the Geiseltal this primate assemblage confirms the biochronologic correlation of Eckfeld with the time interval MP 13 – MP 13/14. Considerable differences between the ungulate faunas west and east of the Oberrheingraben may be explained by the special swamp-like environment of the Eocene Geiseltal. While bite marks in the front of the mandible and the solution of tooth enamel point in the case of the *Periconodon* specimen to crocodile digestion, the isolated molars of *E. klatti* may have fallen from a carcass decomposing on the lake shore.

Acknowledgements

I am indebted to director Otto Neuffer, Herbert Lutz and Gabriele Gruber, leading the excavations of the "Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz" at the locality of Eckfeld at the time of the discovery of the primates. Thanks go also to the digging team and to Thomas Engel who prepared the specimens as well as to director Christian Meyer and Burkart Engesser of the "Naturhistorisches Museum Basel" for my working place as well as to Severino Dahint of the same institute for the photos. I am also very grateful to Kenneth D. Rose (Johns Hopkins University, Baltimore) who read the manuscript critically and improved its English. Finally, I thank Philip D. Gingerich, an anonymous referee, and Iwan Stössel-Sittig as editor who still improved the article.

This is contribution no. 97 of the series "Fossilfundstätte Eckfelder Maar (Mittel-Eozän)".

REFERENCES

Erfurt, J. & Altner, H. 2003: Habitus-Rekonstruktion von Anthracobunodon weigelti (Artiodactyla, Mammalia) aus dem Eozän des Geiseltales. In: Erkenntnisjäger – Kultur und Umwelt des frühen Menschen (Festschrift für Dietrich Mania) (Ed. by Burdukiewicz, J.M., Fiedler, L., Heinrich, W.-D. & Justus, A.). Veröffentl. Landesamt. Archäol. Sachsen-Anhalt 57, 153–175.

Fisher, D.C. 1981: Crocodilian scatology, microvertebrate concentrations, and enamel-less teeth. Paleobiology 7 (2), 262–275.

Franzen, J.L. 1987: Ein neuer Primate aus dem Mitteleozän der Grube Messel (Deutschland, S-Hessen). Cour. Forsch.-Inst Senckenberg 91, 151–187.

Franzen, J.L. 1993: Das biostratigraphische Alter der Fossillagerstätte Eckfelder Maar bei Manderscheid (Eifel). Mainzer Naturwiss. Arch. 31, 201–214.

Franzen, J.L. 1994: Neue Säugerfunde aus dem Eozän des Eckfelder Maares bei Manderscheid (Eifel). Mainzer Naturwiss. Arch. Bh 16, 189–211.

Franzen, J.L. 1995: Die Equoidea des europäischen Mitteleozäns. Hallesches Jb. Geowiss. B 17, 31–45.

Franzen, J.L. 2000: Der sechste Messel-Primate (Mammalia, Notharctidae, Cercamoniinae). Senckenbergiana lethaea 80 (1), 289–303.

Franzen, J.L. 2003: Mammalian faunal turnover in the Eocene of central Europe. In: Causes and Consequences of Globally Warm Climates in the Early Paleogene (Ed. by Wing, S.L., Gingerich, P.D., Schmitz, B. & Thomas, E.). Geological Society of America Special Papers 369, 455–461; Boulder, Colorado.

Godinot, M. 1988: Les Primates adapidés de Bouxwiller (Eocène Moyen, Alsace) et leur apport à la compréhension de la faune de Messel et à l'évolution des Anchomomyini. In: Der eozäne Messelsee – Eocene Lake Messel (Ed. by Franzen, J.L. & Michaelis, W.). Courier Forsch.-Inst. Senckenberg 107, 383–407.

Godinot, M. 1998: A summary of Adapiform Systematics and Phylogeny.- Folia Primatol. 69 (suppl. 1), 218–249.

Hooker, J.J. 1986: Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. Bull. Brit. Mus. (Natur. Hist.) 39 (4), 191–478.

Lutz, H. 1993a: Grabungskampagne im "Eckfelder Maar": 1992. Mitt. rhein. naturforsch. Ges. 14, 53–59.

Lutz, H. 1993b: Zur Sedimentologie der Leithorizonte des "Eckfelder Maares" bei Manderscheid/Eifel (Mittel-Eozän; Deutschland). Mainzer Naturwiss. Arch. 31, 65–83.

Lutz, H. 1993c: Zur Taphonomie der aquatischen und terrestrischen Fauna des "Eckfelder Maares" (Mittel-Eozän; Deutschland): Ergebnisse aus den Grabungen 1990–1992. Mainzer Naturwiss. Arch. 31, 85–113.

Lutz, H. 1997: Taphocoenosen terrestrischer Insekten in aquatischen Sedimenten – ein Beitrag zur Rekonstruktion des Paläoenvironments. N. Jb. Geol. Paläontol. Abh. 203, 173–210.

LUTZ, H., NEUFFER, F.O., HARMS, F.-J., SCHAAL, S., MICKLICH, N., GRUBER, G., SCHWEIGERT, G. & LORENZ, V. 2000: Tertiäre Maare als Fossillagerstätten: Eckfeld, Messel, Randeck, Höwenegg, Öhningen. Tertiary maars as fossil deposits: Eckfeld, Messel, Randeck, Höwenegg, Öhningen. In: Exkursionsführer. Field Trip Guidebook. Internationale Maar-Tagung. International Maar Conference, Daun/Vulkaneifel, August 17–27, 2000 (Ed. by NEUFFER, F.O. & LUTZ, H.). Mainzer Naturwiss. Archiv, Bh. 24, 125–160.

MERTZ, D., SWISHER, C.C., FRANZEN, J.L., NEUFFER, F.O. & LUTZ, H. 2000: Numerical dating of the Eckfeld Maar Fossil Site (Eifel/Germany): A calibration mark for the Eocene time scale. Naturwissenschaften 87, 270–274.

NICKEL, B. 1996: Die mitteleozäne Mikroflora von Eckfeld bei Manderscheid/Eifel. Mainzer Naturwissenschaftliches Archiv Bh. 18, 1–147.

PIRRUNG, B.M. & BÜCHEL, G. 1994: Das Eckfelder Maar – ein tertiäres Maar der Hocheifel. Mainzer Naturwissenschaftliches Archiv Bh. 16, 39–53.

STEHLIN, H.G. 1916: Die Säugetiere des schweizerischen Eocaens. Critischer Catalog der Materialien. Siebter Teil, 2. Hälfte: *Caenopithecus – Necrolemur – Microchoerus – Nannopithex – Anchomomys – Periconodon – Amphichiromys – Heterochiromys* – Nachträge zu *Adapis* – Schlussbetrachtungen zu den Primaten. Abh. schweiz. paläontol. Ges. 41, 1297–1552.

TATTERSALL, I. & SCHWARTZ, J.H. 1983: A New Genus and Species of Adapid Primate from the Middle Eocene of Alsace, and a New Genus for *'Adapis' ruetimeyeri* Stehlin, 1912. Folia primatol. 41, 231–239.

THALMANN, U. 1994: Die Primaten aus dem eozänen Geiseltal bei Halle/Saale (Deutschland). Cour. Forsch.-Inst. Senckenberg 175, 1–161.

WEIGELT, J. 1933: Neue Primaten aus der mitteleozänen (oberlutetischen) Braunkohle des Geiseltales. Nova Acta Leopoldina (N.F.) 1 (2/3): 97–156.

WILDE, V. 1989: Vorläufige Mitteilungen zur Flora aus dem Alttertiär von Eckfeld – Ergebnisse einer ersten Durchsicht des Fundmateriales aus den Grabungen von 1987 und 1988. Mainzer Naturwiss. Arch. 27, 23–31.

WILDE, V. 1995: Die Makroflora aus dem Mitteleozän des Geiseltalgebietes, kurze Übersicht und Vergleiche. Hallesches Jb. Geowiss B 17, 121–138.

WILDE, V. & FRANKENHÄUSER, H. 1993: Initial Results on the Importance of a Flora from the Middle Eocene of Eckfeld (Eifel, W.-Germany). In: Paleolimnology of European Maar Lakes (Ed. by NEGENDANK, J.F.W. & ZOLITSCHKA, B.). Lecture Notes in Earth Sciences 49, 499–503.

Manuscript received May 24, 2003
Revision accepted March 15, 2004