

## The Paroxyclaenidae (Mammalia) and a new form from the early Eocene of Palette, France

DONALD E. RUSSELL and MARC GODINOT\*

With 2 figures and 2 tables

**Kurzfassung:** Eine neue Gattung und Art der Paroxyclaenidae, *Merialus martinae*, wird beschrieben; dabei wird die Familie revidiert und in zwei Subfamilien, die Paroxyclaeninae und die Merialinae, nov., aufgeteilt. Die zwei Arten von *Dyspterna* werden zwei Gattungen zugewiesen, von denen *Eubookeria* neu ist. Die Subfamilie Dyspterninae KRETZOI, 1943, wird wieder aufgestellt, um *Dyspterna woodi*, *Cryptopithecus* und *Kochictis* zusammenzufassen; die Subfamilie wird zu den Pantolestidae gestellt. *Vulpavoides* wird als valide Gattung angesehen; sie enthält »*Russellites*« *simplicidens*. *V. vanvaleni* n. sp. wird von Bouxwiller beschrieben. Die Gattungen *Künkerishella* und *Dulcidon* und mögliche Beziehungen zwischen den Ptolemaidae und den merialinen Paroxyclaeniden werden diskutiert.

**Abstract:** A new genus and species of the Paroxyclaenidae is described, *Merialus martinae*, and the family is reviewed and divided into two subfamilies, the Paroxyclaeninae and the Merialinae, new. The two species of *Dyspterna* are attributed to two genera, of which *Eubookeria* is new; Dyspterninae KRETZOI, 1943, is resurrected to include *Dyspterna woodi*, *Cryptopithecus* and *Kochictis*; the subfamily is referred to the Pantolestidae. *Vulpavoides* is considered valid and includes "*Russellites*" *simplicidens*; *V. vanvaleni* n. sp. is described from Bouxwiller. *Künkerishella* and *Dulcidon* are discussed, as are possible relationships between the Ptolemaidae and the Merialine paroxyclaenids.

### Introduction

The Palette fossil locality was discovered at the beginning of this century. It is situated near the city of Aix-en-Provence in southern France. For many years its principal claim to fame was that of the type-locality of *Lophiaspis maurettei* (DÉPÉRET, 1910), a taxon based on a well preserved specimen that was transferred from the lophiodontids to the Chalicotheriidae by RADINSKY (1964). The second mammal that has long been known from this locality is a small equid that was tentatively referred to *Hyracotherium* by SAVAGE et al. (1965), and which is now considered a species of the primitive perissodactyl genus *Cymbalophus* HOOKER, 1984 (GODINOT et al., 1987).

New excavations in the fossiliferous sediments of Palette were undertaken by GODINOT in 1979. Careful quarrying has led to the recovery of a small number of exceptionally preserved fossil mammals; one of these is the paromomyid primate *Arcius rougieri* GODINOT, 1984. Alpine tectonism has disturbed the beds in the area and is probably responsible for the microfis-

\*Addresses of the authors: Dr. DONALD E. RUSSELL, Institut de Paléontologie (UA 12, CNRS) 8 rue Buffon, 75005 Paris; Dr. MARC GODINOT, Institut des Sciences de l'Évolution (UA 327 du C.N.R.S., Paléontologie) U.S.T.L., Place Eugène Bataillon, 34060 Montpellier Cedex, France.

uration of the fossil remains; this factor necessitates sometimes difficult preparation in the laboratory, a long process that is still continuing.

Within the new material is the paroxyclaenid mandible described here; the new genus and species is the oldest known member of the family. As other recently discovered fossil material becomes available, including micromammals obtained through matrix processing, a better chronologic assessment of the fauna will be possible. Already, it appears to fit in or near the reference-level of Dormaal, in the earliest part of the Eocene (GODINOT et al., 1987).

### Systematic paleontology

The point of departure for this article was the project to describe new material from Pallette. As has been usual when workers have touched the subject of paroxyclaenids, a general review of the group has resulted (TEILHARD DE CHARDIN 1922, KRETZOI 1943, VAN VALEN 1965, CRUSAFONT & RUSSELL 1967, TOBIEN 1969, VON KOENIGSWALD 1983). This paper is no exception.

While previous authors have considered the group as insectivores, carnivores or condylarths, we adhere to the opinion of MCKENNA (1975 and in manuscript) who uses the Suborder Pantolesta (Order Cimolesta) in which they are included.

The Paroxyclaenidae are moderately small mammals with relatively transverse low-crowned upper molars and low to moderately high-crowned lower molars. A labial shelf is variably developed in the upper molars, which lack lingual cingula and a hypocone. P3/3 and P4/4 are large, with the former subequal in size to the latter; the molars decrease in size from M1/1 to M3/3. Lower molars are typified by a lingually placed paraconid and by the reduction or loss of the entoconid. Canines are large and tend to be grooved.

The nominate subfamily, the Paroxyclaeninae, is here proposed to accommodate the genera *Paroxyclaenus*, *Kopidodon*, *Pugiodens* and *Vulpavoides*. These genera constitute a closely knit group, characterized by molariform tendencies in the lower P/4, which has a well developed metaconid, and by a relatively wide separation between the paraconid and metaconid on the molar trigonids.

The counterpart of this group is the Merialinae, a new subfamily including *Merialus* n. gen., *Spaniella* and *Eubookeria* n. gen. The salient features of these taxa are the presence of a premolariform P/4, without a metaconid, and, on the lower molars, a lingual paraconid closely appressed to the metaconid.

Since its description by KRETZOI (1943), *Kochictis* has been considered related to the Paroxyclaenidae. The specimen is now lost and the published text and figures are inadequate for precise appreciation of its characters. The upper premolars appear to be large, with the P3/ almost as big as the P4/; of the upper molars, only the lingual part of M1/ is preserved. From the drawing of it there seems to have been a short post-cingulum and even a small hypocone (also cited in the text). In the lower teeth, the P/3 is remarkably short for a paroxyclaenid. The P/4 is said to possess a small metaconid. If the lower jaw is from the left side, which appears probable, then the paraconid of the molars is situated not only centrally, but apparently even labial of the midline, a condition that is not at all typical of paroxyclaenids. The trigonid is also unusually high. It follows that *Kochictis* is not easily referable to the Paroxyclaenidae, as described above.

An interesting similarity, however, to *Cryptopithecus* can be observed. This genus was reviewed by HEISSIG (1977) and includes the early Oligocene species *C. sideroolithicus* (from Möhren 13) and the late Eocene *C. ("Opsiclaenodon") major* from the Lower Headon Beds. As in *Kochictis*, the upper P3/ is large and possesses a protoconal lobe; a slight hypocone exists on M1/ (M1/ in *Kochictis* probably also lacked a labial shelf); the paraconid in the lower molars is

median. The presence of a small metaconid on P/4 of *Kochictis* has been noted, a character that is also sometimes indicated in specimens of *C. sideroolithicus*. M/3 is not preserved in *Kochictis* for length relationships.

Another taxon that has been cited in discussions concerning paroxyclaenids is *Dyspterna*. *D. woodi* HOPWOOD, 1927, was described from the early Oligocene Lower Hamstead Beds and is contemporary with *Cryptopithecus sideroolithicus*. Some of the features shared by the two forms are: M/3 smaller than M/2 and similar in morphology to M/2, the talonid not being elongated as in pantolestine pantolestids; the paraconid is median and the hypoconid dominates the talonid. Other resemblances are those that constitute uniting characters within the Pantolestinae, but generic distinction remains unquestionable. As in *Kochictis*, it is probable that the trigonid cusps were higher than those of *Cryptopithecus*.

In view of the basic tendencies that appear to indicate a particular affinity between *Kochictis*, *Cryptopithecus* and *Dyspterna woodi*, we propose that they be set apart in a separate subfamily within the Pantolestidae. For this, the nominate taxa of Kochictinae and Dyspterninae KRETZOI (1943) are available. Because of the disappearance of the type material of *Kochictis* we prefer to use Dyspterninae. The latter can be distinguished from pantolestines by the large size and lingual development of the P3/, the lack of M/3 elongation, and the decrease in molar size from M1 to M3, and from paroxyclaenids by the presence of an upper molar hypocone and little or no labial shelf, and by the medianly placed paraconid of the lower molars.

A second species of *Dyspterna*, *D. hopwoodi*, was proposed by CRAY (1973). This form displays, in the available teeth (C, P/2-P/4, M/3), the characteristics seen in *Merialus* and in *Spaniella*. With its M/3 paraconid situated far lingually and the talonid limited postero-lingually by a crest (thus lacking a differentiated entoconid), *D. hopwoodi* is much better placed among the merialine paroxyclaenids than in the pantolestids.

"*D. hopwoodi*" is from the Upper Headon Beds and is thus late Eocene in age. In labial view especially, the M/3 (the only comparable tooth) is very different in "*D. hopwoodi*" from that of *D. woodi*: instead of a sloping posterior trigonid wall as in the latter, in "*D. hopwoodi*" it is nearly vertical. Another important difference is the height with which the hypoconid contacts the wall of the trigonid in *D. woodi*; in "*D. hopwoodi*" a deep, V-shaped notch separates the hypoconid and protoconid. In occlusal view in *D. woodi*, the hypoconulid is labial and the talonid basin is broad; the hypoconulid is, on the contrary, almost median and the talonid basin narrower and more elongate in "*D. hopwoodi*". While the crown is considerably higher in *D. woodi* than in "*D. hopwoodi*" and the talonid notably shorter, it could be argued that these traits indicate evolutionary divergence within the genus. It is our contention, however, that a basic difference exists between these two taxa and that they cannot be congeneric.

The consequence of our conclusion concerning "*D. hopwoodi*" is the need to propose a new generic name for the species.

### Paroxyclaenidae WEITZEL, 1933

#### Merialinae new

#### *Euhookeria* n. gen.

Type-species: *Euhookeria hopwoodi* (CRAY, 1973).

Distribution: Upper Headon Beds (Lignite Bed), England; late Eocene.

Diagnosis: Differs from the pantolestine Pantolestidae (*Palaeosinopa*, *Bessoecetor*, *Propalaeosinopa*, *Pagonomus*, *Buxolestes*, *Pantolestes*, *Chadronia*) by the paraconid of the lower M/3 situated far lingually and closely appressed to the metaconid; by the absence of a distinct, cusped entoconid and the absence of a cusped, posteriorly projecting hypoconulid in M/3. Differs from the Paroxyclaeninae (*Paroxyclaenus*, *Kopidodon*, *Pugiodens* and *Vulpavoides*) by the

lingual situation of the paraconid, close to the metaconid, and by a simple, premolariform P/4. Differs from *Dyspterna* by the lesser height of the crown of M/3, by the deep, wide notch separating the hypoconid and protoconid, by the steepness of the posterior trigonid wall, and by the more crestiform and more labially placed hypoconid. Differs from *Spaniella* by a larger and more strongly grooved lower canine; by a more blade-like P/2 and P/3; by a longer M/3 and a stronger, more lingually situated paraconid, and by a larger and higher M/3 hypoconid.

Etymology: Named in honor of Dr. J. J. HOOKER for his fundamental studies on the mammals of the European Paleogene.

Discussion: Other distinctions of *E. hopwoodi* from *D. woodi* can be seen in the lack of a cristid obliqua in the former; if one were projected along the axis of the anterior hypoconid crest it would contact the posterior side of the protoconid. In the M/3 of *D. woodi* the cristid obliqua attains the trigonid wall below the protoconid-metaconid notch and continues obliquely upward toward the summit of the metaconid. Comparison is difficult because of the damaged trigonid cusps, but it is possible that the trigonid in *E. hopwoodi* is narrower antero-posteriorly and the paraconid slightly more lingually placed. Development of the antero-labial cingulum is exaggerated in *D. woodi*.

CRAY (1973) referred an isolated lower molar (probably M/1; B. M. M 26053) from the Upper Headon Beds to the species *hopwoodi*, but in our opinion this attribution should be questioned. Although the morphology of the talonid is admittedly similar, the size and situation on the trigonid of the paraconid is rather anomalous for conspecificity. It is quite small, placed medianly, and very far below the level of the protoconid and metaconid. As a general rule in mammals, one can expect the paraconid to be farther lingual in a first molar than in a third; the opposite is surprising. The talonid construction of this specimen eliminates it from the Pantolestinae and indicates affinity to the Dyspterninae. Its trigonid also finds reflection, among the Dyspterninae, in *Cryptopithecus*, *Kochictis* and, to a certain degree, in *Dyspterna woodi*. Talonid morphology is particularly similar to that of the latter species, but M 26053 is not referable to any known taxon. We would place it, pending supplementary material, in the Dyspterninae as an indeterminate species.

The new form from Palette, like *Euhookeria*, can also be placed in the Merialinae.

### *Merialus* n. gen.

Type-species: *Merialus martinae* n. sp.

Distribution: Early Eocene of France.

Etymology: Named after Meyreuil, the Commune on which is situated the Palette locality; its name is of probable Gallic origin (mero, bramble, and ialo, field).

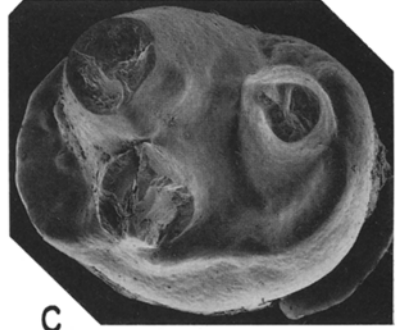
Diagnosis: Differs from the Paroxyclaeninae (*Paroxyclaenus*, *Kopidodon*, *Pugiodens* and *Vulpavoides*) by the molar paraconids being situated close to the metaconids and by the absence of a strong metaconid on P/4. Differs from *Spaniella* by the less inflated P/2–P/3; by the more sharply V-shaped (in occlusal view) trigonids of M/2 and M/3; by the shorter M/2 talonid; and by the stronger, more lingually placed paraconid of M/3. Differs from *Euhookeria* in its less blade-like P/2–P/3; by its shorter and lower crowned M/3, and by its (probably) lower hypoconid.

---

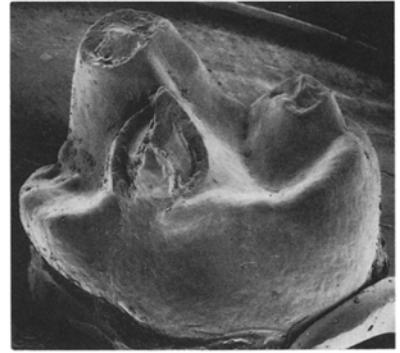
Fig. 1. A and B: *Merialus martinae* n. gen., n. sp., PAT 11, right mandible, Holotype. A: Stereophoto,  $\times 4$ ; B: Lingual view,  $\times 2$ . Collections of the University of Montpellier. – C and D: *Kiinkerishella zaisanica* GABUNIA & BIRYUKOV, 1978, 3K7, 289/1406, right M/3 of the Holotype. C: Occlusal view, D: Lingual view,  $\times 10$ . Collections of the Laboratory of Paleobiology, Institute of Zoology, Academy of Sciences of the Kazakh S.S.R.



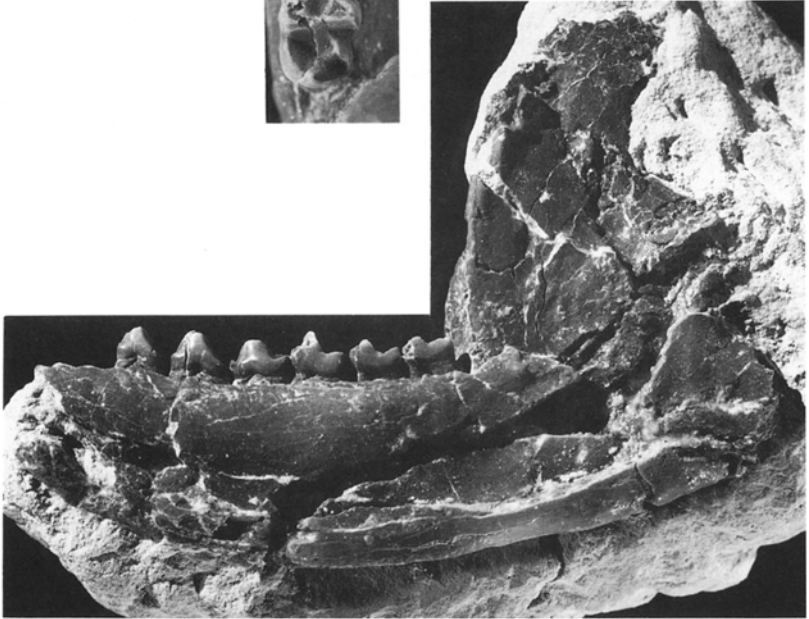
A



C



D



B

*Merialus martinae* n. sp.

Fig. 1A and B

Holotype: Right mandible with P/2-M/3, PAT 11; collections of the University of Montpellier. Horizon and age: Earliest Eocene; Dormaal reference-level.

Diagnosis: As for genus.

Etymology: Dedicated to Madame MARTINE MONS-GILLET, for her untiring devotion to the excavations made at Palette.

Description: From the empty alveolus, P/1 was a single-rooted tooth, with a crown that probably sloped forward. P/2 is supported by two, widely separated roots; the crown is simple, with anterior and posterior crests, each possessing a small tubercle lingually at its base. A short, weak postcingulum exists lingual to the posterior tubercle. P/3 is similar, except bigger; it is subequal in length to the P/4. The latter is wider, however, and possesses a more distinct antero-basal paraconid and a hypoconid; the talonid is basined and limited posteriorly by a small hypoconulid. The top of the tooth is worn, but no trace of a metaconid is perceptible. M/1 is the largest of the molar series, which decreases in size to M/3. In all three teeth the metaconid is subequal in height to the protoconid (despite wear or breakage), and the paraconid is situated antero-lingually on the trigonid. Although well distinct from each other, the paraconid and metaconid are in contact at their bases. A trigonid basin is formed between the protoconid and the two lingual cusps. Trigonid height decreases from M/1 to M/3. The talonid is well basined, between a curving, lingually closing crest (that includes the position of the absent entoconid) and the hypoconid, which is also somewhat crestiform. A minute hypoconulid is situated medianly at the base of the hypoconid. The only cingulum is that present anterolabially.

	L	W		L	W
P/2	3.2	1.8	M/1	4.9	3.0
P/3	4.1	2.3	M/2	3.6	2.9
P/4	4.0	2.5	M/3	3.2	2.7

The height of the mandible is moderate, neither low nor high, and its proportions are masked by crushing. The remaining part of the posterior rim of the canine alveolus indicates a tooth of rather modest size, which is substantiated by the antero-vertical tapering of the front of the mandible. The coronoid process was twisted during fossilization and was, in its natural state, much more procumbent postero-ventrally. As such, the articular condyle would have been nearly in the plane of the occlusal surface of the teeth. This is a condition that appears to typify paroxyclaenids.

*Vulpavoides* and *Pugiodens* were described by MATTHES (1952) from the Geiseltal "obere Mittelkohle". Although *Vulpavoides* has page priority, VAN VALEN (1965) synonymized it with *Pugiodens*. CRUSAFONT & RUSSELL (1967) noted several characters in the lower jaw (which constitutes all that is known of *Pugiodens*) that shed doubt on this synonymy. The M/3, although missing, was apparently subequal in length to the M/2; in the crushed skull that is the type specimen of *Vulpavoides*, the M3/ is by far the smallest in the molar series. The molars of *Pugiodens* are peculiar in that the entoconid appears to be more distinct than is usual, the cristid obliqua appears to contact the posterior trigonid wall more lingually than is usual, and a particularly distinct hypoconulid seems to exist, which is unusual in paroxyclaenids. As the upper teeth (of *Vulpavoides*) do not show any such deviations from the norm, it is permitted to wonder if we are not confronted with two different taxa. Admittedly, the teeth of the single specimen of *Vulpavoides germanica* are rather heavily worn; this fact excludes, in any case, their being associated with the lesser worn teeth of *Pugiodens mirus*.

Table 1. A comparison of significant traits within the groups discussed. It can be seen that the Dyspterninae are in some ways intermediate between the Paroxyclaeninae and Merialinae on the one hand, and the Pantolestinae on the other; the closest affinity is shown to the latter.

	Paroxyclaeninae <sup>1</sup>	Merialinae <sup>2</sup>	Dyspterninae <sup>3</sup>	Pantolestinae <sup>4</sup>
up. mol.	labial shelf present ( <i>Pa.</i> , <i>K.</i> , <i>V.</i> )	yes ( <i>Span.</i> )	no ( <i>Cryp.</i> )	no
	lingual cingula absent ( <i>Pa.</i> , <i>K.</i> , <i>V.</i> )	yes ( <i>Span.</i> )	no ( <i>Cr.</i> , <i>Ko.</i> )	no
	hypocone absent ( <i>Pa.</i> , <i>K.</i> , <i>V.</i> )	yes ( <i>Span.</i> )	no ( <i>Cr.</i> , <i>Ko.</i> )	no
	P3 subequal to P4 ( <i>Pa.</i> , <i>K.</i> , <i>Pu.</i> , <i>V.</i> )	yes ( <i>M.</i> )	yes (uppers) ( <i>Cr.</i> , <i>Ko.</i> )	no
	molars decrease from M1 to M3 ( <i>Pa.</i> , <i>K.</i> , <i>Pu.</i> , <i>V.</i> )	yes ( <i>M.</i> )	yes ( <i>Cr.</i> )	no
low. mol.	P/4 molariform ( <i>Pa.</i> , <i>K.</i> , <i>Pu.</i> )	no ( <i>M.</i> , <i>E.</i> )	no, or slightly ( <i>Cr.</i> , <i>Ko.</i> )	no
	Paraconid lingual, well separated from metaconid ( <i>Pa.</i> , <i>K.</i> , <i>Pu.</i> )	yes closely appressed ( <i>M.</i> , <i>Span.</i> , <i>E.</i> )	no, median ( <i>Cr.</i> , <i>Ko.</i> , <i>Dy.</i> )	no, median
	Entoconid reduced or absent ( <i>Pa.</i> , <i>K.</i> , <i>Pu.</i> )	yes ( <i>M.</i> , <i>Span.</i> , <i>E.</i> )	yes, ( <i>Cr.</i> , <i>Dy.</i> , <i>Ko.</i> ?)	no

<sup>1</sup> including *Paroxyclaenus*, *Kopidodon*, *Pugiodens*, *Vulpavoides*.

<sup>2</sup> *Merialus*, *Spaniella*, *Euhookeria*.

<sup>3</sup> *Dyspterna*, *Cryptopithecus*, *Kochictis*.

<sup>4</sup> *Palaeosinopa*, *Bessoecetor*, *Propalaeosinopa*, *Pagonomus*, *Buxolestes*, *Pantolestes*, *Chadronia*.

TOBIEN (1969) also doubted this synonymy and resuscitated *Vulpavoides*. HOOKER (1986) agreed and pursued this concept, but left a doubt as to whether or not *Pugiodens* should be referred to *Vulpavoides*. This reversal of the synonymized taxon resulted from the doubt that persists concerning the synonymy, the fact that the type mandible of *Pugiodens* has been lost since at least 1963, and from personal choice. In our opinion, it is doubtful that the synonymy can ever be firmly established, especially with the loss of one of the contestants. We propose to retain the name *Pugiodens* for the lower jaw that has been figured; we also retain it as a somewhat aberrant paroxyclaenine. We concur that *Vulpavoides* should be used as a valid taxon.

The fate of the Egerkingen specimen named *Russellites simplicidens* by VAN VALEN (1965) is intimately linked to that of *Vulpavoides*. While TOBIEN (1969) and VON KOENIGSWALD (1983) regarded *Russellites* as valid, VAN VALEN later (in 1967) synonymized his genus with *Pugiodens*, which he considered to include *Vulpavoides*. HOOKER (1986), regarding *Vulpavoides* valid, synonymized *Russellites* with it. As noted at the moment of its creation, the two upper molars of the holotype of "*Russellites*" are indeed quite similar to those of *Vulpavoides*. We follow HOOKER in calling the specimen *Vulpavoides simplicidens*; it could be noted that the exact provenance of this specimen from the Egerkingen fissures is not known.

On the basis of a single upper molar from the Bartonian Creechbarrow Limestone in England, HOOKER (1986) proposed the new species *Vulpavoides cooperi*; in his discussion he described an upper molar from Bouxwiller (France) and referred it to *V. simplicidens*. We contend that the latter is specifically distinct. This confronts us with the conflict posed by the maxim that intones "species should not be multiplied beyond necessity" (VAN VALEN 1967), and the reasoning put forth by HOOKER (referring to his new species) which states that the distinctness of the new form and the rarity of all members of the Paroxyclaenidae justify sufficiently its creation. Our decision is that we believe in the specificity of the Bouxwiller form; to

refer to it by name is both a convenience and an aid to comprehension. It should be added that the specimens have been cited since JAEGER (1966).

In comparing the upper M1/ (Bchs 656) we discovered discrepancies in the dimensions of the M1/ of *V. germanica* given by MATTHES (1952: 230) and repeated by TOBIEN (1969: 31). Measurement of the figures made by VAN VALEN (1965: 390) give 4.5 mm for the length (vs. 5 in MATTHES) and 6.68 mm for the width (8, in MATTHES). We accept VAN VALEN's drawings as accurate. For *V. simplicidens*, however, we prefer a maximum measurement of the width, while he measured from the middle of the labial border. This results in the width of M1/ equaling 5.68 mm, rather than the 5.5 cited by VAN VALEN. These differences of proportion alter the width/length relationships. For example, the M1/ width/length ratio of *V. germanica* now becomes 1.48; that of *V. simplicidens*, 1.38. In Bchs 656 the M1/ ratio varies between 1.58 and 1.60, depending on the estimation of its total width. This indicates a tooth that is broader antero-posteriorly and not so extended transversely. The extreme in transverseness is found in *V. cooperi*, with a ratio of 1.73. These relationships are a reflection especially of the antero-posterior diameter of the labial part of the teeth; when this diameter is measured at the level of the protocone *V. germanica* is shown to be lingually the broadest, *V. cooperi* the narrowest, and *V. simplicidens*, with Bchs 656, are intermediate.

But proportions are not all. Despite undeniable points of similarity, Bchs 656 differs from *V. simplicidens* by a number of morphologic traits. HOOKER (1986: 340) noted that Bchs 656 differs from the M1/ in the type of *V. simplicidens* by the obtuseness of the postero-labial angle and the more sharply pointed character of the antero-labial angle; the nature of these angles is reversed in *V. simplicidens*. We would add that the labial shelf in Bchs 656 is regularly concave, while in *V. simplicidens* the paracone produces a notable bulge that extends as far as the ectoconulum; in consequence, the labial shelf is essentially reduced to a concavity labial only to the metacone. The crest between the metacone and the metastylar region (the postmetacrista) is rectilinear in Bchs 656 and is notched, or concave, in *V. simplicidens*. There is furthermore, in occlusal view, a difference in profile between the lobes of the labial shelf in Bchs 656 and in *V. simplicidens*; in the former the ectoflexus occurs about midway between them, producing subequal lobes; in *V. simplicidens* the ectoflexus is displaced anteriorly, separating a short, rounded parastylar area and a longer metastylar lobe. The conules are considerably more developed in Bchs 656, and the metaconule, which is situated closer to the protocone, is connected to the latter by a strong postprotocrista; this crest is absent in *V. simplicidens*. Particularly noteworthy is the placement of the protocone in Bchs 656, relatively far from the lingual border of the tooth; in *V. simplicidens* the protocone is significantly closer to this border. In lingual view it is possible to observe an obliquity of the protocone in *V. simplicidens*; it appears to slope anteriorly towards the summit of the cusp. In Bchs 656 the protocone is more equilibrated and hence more simply vertical.

Lacking a reasonable sample of teeth from Bouxwiller and from Egerkingen that would permit a solid appreciation of the variability that surely exists within these taxa, it is not possible to distinguish which of the above characters are only manifestations of this variability. Taken as a whole, however, it seems likely that the differences that typify the Bouxwiller specimen translate specific individuality.

*Vulpavoides vanvaleni* n. sp.

Fig. 2E-H

Holotype: Bchs 656, left M1/.

Referred specimen: Bchs 351, left M/3; both are from the collections of the Naturhistorisches Museum Basel, Bâle, Switzerland.

Provenance and age: Bouxwiller (Buchweiler) Quarry (from the upper levels of the brown-beige marl), Alsace, France; late Lutetian (sensu FRANZEN & HAUBOLD 1986).



Diagnosis: Bchs 656 differs from the M1/ of *Vulpavoides germanica* MATTHES (1952) by its smaller size, by its less transverse proportions, and by a more moderate, centrally placed ectoflexus. It differs from the M1/ of *V. simplicidens* (VAN VALEN, 1965) also by its less transverse proportions, by a greater concavity of the labial shelf, by the rectilinearity of the postmetacrista, by the situation of the metaconule, closer to the protocone, by the presence of a post-protocrista, and by the non-obliquity, in lingual view, of the protocone. It differs from *V. cooperi* HOOKER (1986) by its slightly larger size, by its notably less transverse proportions, by its paracone being higher than the metacone (the opposite is true in *V. cooperi*), and by a larger paraconule; it is also lower crowned.

Etymology: Dedicated to LEIGH VAN VALEN, in recognition of his numerous contributions to paleontology, including those on paroxyclaenids.

	L	W
M1/ Bchs 656	3.4	5.4 (or 5.5 estimated)
M/3 Bchs 351	3.6	2.8

Discussion: By the morphology of its trigonid Bchs 351 can be referred to the Paroxyclaeninae. The trigonid basin is widely open antero-lingually and there is no paraconid appressed to the metaconid. In fact, the paraconid is lacking. The talonid is short and much narrower than the rather bulbous, low trigonid. While there is no trace of a hypoconulid, a small entoconid is present, closely behind the metaconid, attesting to a certain peculiarity of this species.

Although similar in proportions to the M/3 of *Paroxyclaenus*, Bchs 351 is larger and endowed with a much larger hypoconid. A faint paraconid is still present in *Paroxyclaenus*, and the entoconid, if truly present (wear obscures the region), was situated farther posteriorly.

Compared to the M/3 in *Kopidodon*, Bchs 351 is similar in lacking a paraconid, but differs in that its hypoconid is larger and not situated so posteriorly. The entoconid in *Kopidodon* is much larger, less crestiform and is also placed closer to the posterior border of the tooth.

M/3 is not preserved in the type specimen of *Pugiodens mirus*, but the length of the alveolus is 4 mm. MATTHES (1952), on the basis measurements obtained by X-rays of the mandible, calculated that the trigonid of M/3 would have been 1.5 mm long and the trigonid, 2.5 mm. These proportions are nearly reversed in Bchs 351, but the measurements were taken at the occlusal surface. In view of the important development of the paraconid in the other molars of *P. mirus* (as well as on P/4 and even P/3), and its total absence on the M/3 of *V. vanvaleni*, it is probable that the latter differs from *P. mirus* in this respect. From Egerkingen a P/4 referable perhaps to *V. vanvaleni* is known to exist (pers. comm., VAN VALEN 1966). No lower teeth are known of *V. simplicidens* nor of *V. cooperi*.

The locality of Bouxwiller is equivalent to the "obere Mittelkohle" of Geiseltal in age (FRANZEN & HAUBOLD 1986), that is, contemporary with the top third of the Lutetian middle Eocene. Since the Bartonian is now also considered as part of the middle Eocene (CAVELIER & POMEROL 1986), the stratigraphic situation of Bouxwiller and the "obere Mittelkohle" would be approximately in the middle of the middle Eocene.

The genus *Dulcidon* was created by VAN VALEN (1965) for a single upper molar from the middle Eocene of Pakistan, and regarded as the first Asian representative of the Paroxyclaenidae. TOBIEN (1969) removed it from the family and GINGERICH & RUSSELL (1981: 237) placed it in the Artiodactyla, close to their recently described *Chorlakkia*. Additional teeth are now known of *Dulcidon*.

Despite the retreat of *Dulcidon* from the ranks of the Paroxyclaenidae, the family is probably still represented in Asia. *Kiinkerishella zaisanica*, described by GABUNIA & BIRYUKOV (1978), from the late Eocene lower part of the Aksyir beds in the Zaisan Depression, Kazakhstan, appears to be referable to the group. Only the talonid of M/1 and the M/3 are known.

The M/1 talonid (in place in a fragmentary mandible) suggests a rather high crowned tooth. The talonid itself is short, with a high somewhat tubular hypoconid. The presence of a distinct entoconid and hypoconulid is in contrast to the usual condition in paroxyclaenids. The M/3 is considerably smaller than the M/1 and completely lacks a paraconid; the open trigonid basin is continued antero-labially around the base of the protoconid by a cingulum. On the talonid, the hypoconid is short and high; there is no entoconid or hypoconulid.

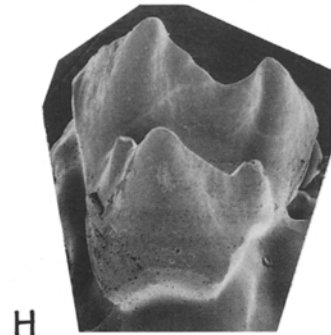
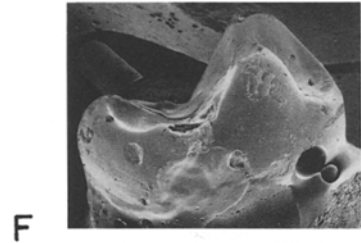
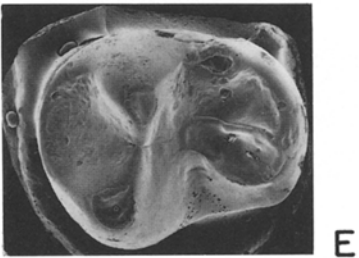
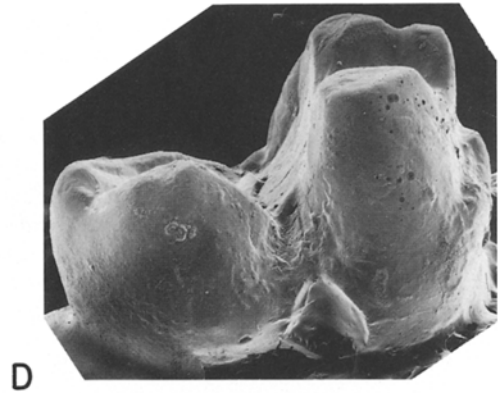
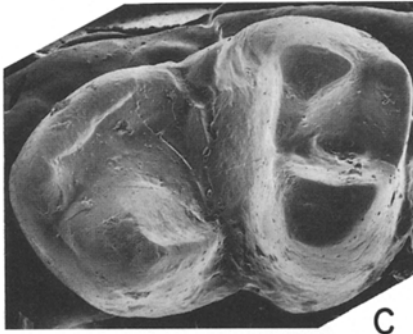
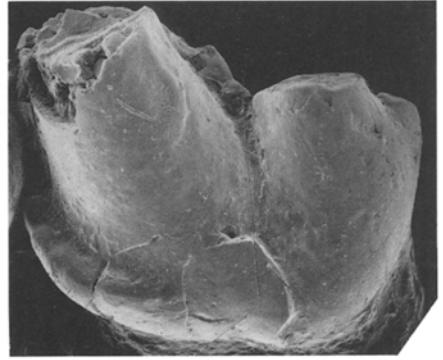
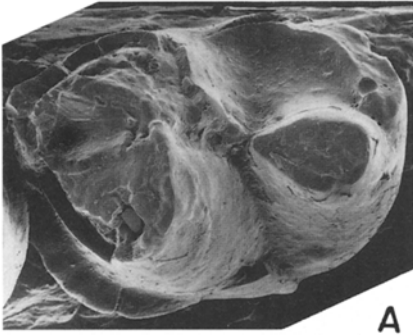
*Kiinkerishella* is unique in several respects, but seems to be related to the paroxyclaenines. Given the relative inaccessibility of the specimen, we figure here the type M/3 (Fig. 1C, D).

*Ptolemaia lyonsi* and the family Ptolemaidae were proposed by OSBORN in 1908; further material from the Fayum was described by SIMONS & GINGERICH (1974). VAN VALEN (1966) suggested pantolestid affinity for the genus, an opinion shared by MCKENNA (pers. comm., 1986). We would add that perhaps a particular relationship to the merialine paroxyclaenids is discernable. P/3 and P/4 are large, and it has been suggested that P/4 was a premolariform tooth, lacking a metaconid. The lower molars decrease in size from M/1 to M/3; the paraconid is close to the metaconid and situated far lingually. Comparison of the occlusal views of the M/3's in *Ptolemaia* and in *Euhookeria* reveals considerable similarity, especially in the morphology and orientation of the trigonid; the posterior surface of the protoconid is also similar in its steepness. The teeth of *Ptolemaia* are much higher crowned and it would be precipitous to propose the derivation of the African Oligocene form from *Euhookeria*; the resemblance between them, however, merits reflection.

Table 2. Temporal distribution of the Paroxyclaenidae and the dyspternine Pantolestidae. All species are in stratigraphical sequence, except *Paroxyclaenus* and *Kiinkerishella*.

	Paroxyclaeninae	Merialinae	Dyspterninae	
late Oligo.			<i>Kochictis centennii</i>	
mid. Oligo.				
early Oligo.			<i>Dyspterna woodi</i>	<i>Cryptopithecus sideroolithicus</i>
late Eocene	<i>Paroxyclaenus lemuroides</i> <i>Kiinkerishella zaisanica</i>	<i>Euhookeria hopwoodi</i>	Dyspterninae indet. <i>Cryptopithecus major</i>	
mid. Eocene	<i>Vulpavoides cooperi</i> <i>Vulpavoides simplicidens</i> <i>Vulpavoides vanvaleni</i> <i>Vulpavoides germanica</i> <i>Pugiodens mirus</i> <i>Kopidodon macrognathus</i>			
early Eocene		<i>Spaniella carezi</i> <i>Merialus martinae</i>		

Fig. 2. A and B: *Dyspterna woodi* HOPWOOD, 1927, M13125, left M/3 of the Holotype. A: Occlusal view, B: Labial view;  $\times 10$ . Collections of the British Museum (N.H.). - C and D: *Euhookeria hopwoodi* (CRAY, 1973), n. gen., M26052, right M/3 of the Holotype. C: Occlusal view, D: Labial view;  $\times 10$ . Collections of the British Museum (N.H.). - E to H: *Vulpavoides vanvaleni* n. sp. - E and F: Bchs 351, left M/3. E: Occlusal view; F: Lingual view,  $\times 10$ . G and H: Bchs 656, left M/1, Holotype. G: Occlusal view, H: Lingual view;  $\times 10$ . Collections of the Naturhistorisches Museum Basel.



The enigmatic *Simidectes* from the late Eocene of California bears some resemblance in its M/2–M/3 in labial view to those teeth in *Dyspterna woodi*, but in occlusal view they are quite different. With a broad trigonid basin, the lower molars of *Simidectes* are also reminiscent of those in the Paroxyclaeninae, although the paraconid is situated much more labially. The genus seems well placed in the Pantolestia, as incertae sedis.

RICH (1971) attributed to the Paroxyclaenidae a surprisingly large number of isolated teeth from the early Eocene of the Paris Basin. Paroxyclaenids are usually rare elements in any fauna. Apart from this objection, it is sometimes difficult to distinguish isolated paroxyclaenid teeth from those of miacids. Much more material is now available (although still in the form of isolated teeth) and a revision is scheduled for the near future; both paroxyclaenid subfamilies appear to be present, however.

### Conclusion

Prompted by the discovery of a new paroxyclaenid in the locality of Palette, we have been led to review the group as a whole. Following this, the division of the family into two subfamilies has been deemed necessary. The two species of *Dyspterna* have been recognized as attributable to two distinct genera, *Dyspterna* and *Euhookeria* n. gen.; the type species of the former, *Dyspterna woodi*, and *Kochictis centennii* have been included in KRETZOI's subfamily, the Dyspterninae, along with the species of *Cryptopithecus*. The group is referred to the Pantolestidae. The problem of the *Vulpavoides*–*Pugiodens* synonymy has been examined and both genera retained as valid. "*Russellites*" *simplicidens* is considered a species of *Vulpavoides* and a new species of the genus, *V. vanvaleni*, is created for material from Bouxwiller.

It has been judged useful to figure *Kiinkerishella*, a paroxyclaenid from Kazakhstan and the only member of the family in Asia. *Dulcidon*, formerly attributed to the group, is now recognized as an artiodactyl.

A relationship is suggested between the African *Ptolemaia* and the merialine *Euhookeria*.

## Literature

- CAVELIER, C. & POMEROL, C. (1986): Stratigraphy of the Paleogene. – Bull. Soc. géol. France, (8), II (2): 255–265; Paris.
- CRAY, P. (1973): Marsupialia, Insectivora, Primates, Creodonta and Carnivora from the Headon Beds (Upper Eocene) of Southern England. – Bull. Brit. Mus. (N.H.) Geology, 23 (1): 1–102; London.
- CRUSAFONT-PAIRO, M. & RUSSELL, D.É. (1967): Un nouveau Paroxyclaenidé de l'Eocène d'Espagne. – Bull. Mus. nat. Hist. Nat., 2 sér., 38 (5): 757–773; Paris.
- DEPERET, C. (1910): Etudes sur la famille des lophodontidés. – Bull. Soc. géol. France, 4 (10): 558–577; Paris.
- FRANZEN, J. L. & HAUBOLD, H. (1986): The Middle Eocene of European Mammalian Stratigraphy. Definition of the Geiseltalian. – Modern Geology, 10: 159–170; U.K.
- GABUNIA, L. K. & BIRYUKOV, N. D. (1978): On the presence of a peculiar representative of Arctocyonoids in the Paleogene of Asia. – Bull. Acad. Sci. Georgian S.S.R., 92 (2): 489–492; Tbilisi. [in Russian]
- GINGERICH, P. D. & RUSSELL, D. E. (1981): *Pakicetus inachus*, a new archaeocete (Mammalia, Cetacea) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). – Contrib. Mus. Paleont. Univ. Michigan, 25 (11): 235–246; Ann Arbor.
- GODINOT, M. (1984): Un nouveau genre de Paromomyidae (Primates) de l'Eocène inférieur d'Europe. – Folia primat., 43: 84–96; Basel.
- GODINOT, M.; CROCHET J.-Y.; HARTENBERGER, J.-L.; LANGE-BADRE, B.; RUSSELL, D. E. & SIGE, B. (1987): Nouvelles données sur les mammifères de Palette (Eocène inférieur, Provence). – Münch. Geowiss. Abh. (A) 10: 273–288; München.
- HEISSIG, K. (1977): Neues Material von *Cryptopithecus* (Mammalia, Pantolestidae) aus dem Mitteloligozän von "Möhren 13" in Mittelfranken. – Mitt. Bayer. Staatslg. Paläont. hist. Geol., 17: 213–225; München.
- HOOKE, J. J. (1984): A primitive ceratomorph (Perissodactyla, Mammalia) from the early Tertiary of Europe. – Zool. J. Linnean Soc., 82: 229–244; London.
- 1986: Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. – Bull. Brit. Mus. (N.H.), Geology, 39 (4): 191–478; London.
- JAEGER, J. J. (1966): Révision de la faune de Mammifères du Lutétien de Bouxwiller (Bas-Rhin). – Unpubl. Thesis, Fac. Sci. Univ. Strasbourg, Inst. Géol.
- KOENIGSWALD, W. v. (1983): Skelettfunde von *Kopidodon* (Condylarthra, Mammalia) aus dem mittel-eozänen Ölschiefer von Messel bei Darmstadt. – N. Jb. Geol. Paläont. Abh., 167 (1): 1–39; Stuttgart.
- KRETZOI, M. (1943): *Kochictis centemii* n. g. n. sp., ein altertümlicher Creodonte aus dem Oberoligozän Siebenbürgens. – Föld. Közl., 73 (1–3): 190–195; Budapest.
- MCKENNA, M. C. (1975): Toward a Phylogenetic Classification of the Mammalia. – [In:] LUCKETT, W. P. & SZALAY, F. S. (eds.): Phylogeny of the Primates: 21–46; Plenum Press, New York.
- MATTHES, H. W. (1952): Die Creodontier aus der mitteleozänen Braunkohle des Geiseltales. – Hallesches Jb. Mitt. Erdgesch., 1: 201–240; Halle.
- OSBORN, H. F. (1908): New fossil mammals from the Fayûm Oligocene, Egypt. – Bull. Amer. Mus. Nat. Hist., 24 (16): 265–272; New York.
- RADINSKY, L. B. (1964): *Paleomoropus*, a new Early Eocene Chalicotheres (Mammalia, Perissodactyla), and a Revision of Eocene chalicotheres. – Amer. Mus. Novitates, 2179: 1–28; New York.
- RICH, T. H. (1971): Deltatheridia, Carnivora, and Condylarthra (Mammalia) of the early Eocene, Paris Basin, France. – Univ. Calif. Publ. Geol. Sci., 88: 1–72; Berkeley.
- SAVAGE, D. E.; RUSSELL, D. E. & LOUIS, P. (1965): European Eocene Equidae (Perissodactyla). – Univ. Calif. Publ. Geol. Sci., 56: 1–94; Berkeley.
- TEILHARD DE CHARDIN, P. (1922): Mammifères de l'Eocène inférieur français. – Ann. Paléont., 11: 9–116; Paris.
- TOBIEN, H. (1969): *Kopidodon* (Condylarthra, Mammalia) aus dem Mitteleozän (Lutetium) von Messel bei Darmstadt (Hessen). – Notizbl. hess. L. – Amt Bodenforsch., 97: 7–37; Wiesbaden.
- SIMONS, E. L. & GINGERICH, P. D. (1974): New carnivorous mammals from the Oligocene of Egypt. – Ann. Geol. Surv. Egypt, 4: 157–166; Cairo.
- VAN VALEN, L. (1965): Paroxyclaenidae, an extinct family of Eurasian Mammals. – J. Mammal., 46 (3): 388–397; Lawrence.
- (1966): Deltatheridia, a New Order of Mammals. – Bull. Amer. Mus. Nat. Hist., 132 (1): 1–126; New York.
- (1967): New Paleocene insectivores and insectivore classification. – Bull. Amer. Mus. Nat. Hist., 135 (5): 217–284; New York.