Cainozoic Research, 6(1-2), pp. 25-35, March 2009

A new genus of paroxyclaenid (Mammalia: Condylarthra: Paroxyclaenidae: *Paravulpavoides*) from the Upper Middle Eocene of Creechbarrow, Dorset, S. England

David L. Harrison[1]

[1]*Harrison Institute, Bowerwood House, St. Botolph's Road, Sevenoaks, Kent TN13 3AQ, Great Britain; e-mail: hzm@btinternet.com*

Received 22 January 2007; revised version accepted 24 September 2007

Recovery of eight further teeth of a rare and little known paroxyclaenid from the Creechbarrow Limestone Formation has enabled a more detailed comparison with related taxa and the definition of a new genus, *Paravulpavoides*, with a distinctive dental profile.

KEY WORDS: Paroxyclaenid, Middle Eocene, Creechbarrow, England.

Introduction

The taxon *Vulpavoides cooperi* Hooker, 1986, was originally based on one right M1 (the holotype BM M37570) and a doubtfully referred left DP4 fragment (M35646). Hooker (1986: 340). During an ongoing research programme devoted to the Robiacian mammal fauna of Creechbarrow at the Harrison Institute, eight further teeth of this taxon have been recovered, including a new specimen of M1, an M3 and specimens of each of the previously unknown mandibular elements p1 or 2, p3, p4, m1 and m2. This material reveals distinctive differences from previously described paroxyclaenid taxa and necessitates the description of a new genus. The methods employed in this study have been described by Harrison (2002).

Systematic palaeontology

Order Condylarthra Cope, 1881
Family Paroxyclaenidae Weitzel, 1933
Subfamily Paroxyclaeninae Weitzel, 1933
(*sensu* Russell & Godinot, 1988)

Type genus – *Paroxyclaenus* Teilhard de Chardin, 1922.

Included genera – *Kopidodon* Weitzel, 1933; *Vulpavoides* Matthes, 1952, (including *Russellites* Van Valen, 1965); *Pugiodens* Matthes, 1952 (possibly synonymous with *Vulpavoides*) and *Paravulpavoides* gen. nov.

Genus *Paravulpavoides gen. nov.*

Type species – *Vulpavoides cooperi* Hooker, 1986

Paravulpavoides cooperi (Hooker, 1986)
Figures 1-5, 8, 9

1977 *Russellites* sp. Hooker: p. 141.
1980 *Pugiodens* sp. Hooker & Insole: p. 42
1986 *Vulpavoides cooperi* Hooker: p. 340; text-fig. 42 A-D, I-K.

Holotype – Right M1, BM M37570 (Hooker, 1986: text-fig. 42 A-D).

Horizon and locality – Creechbarrow Limestone Formation, Creechbarrow, Dorset. SY 8240 9215. Robiacian (ELMA MP 16).

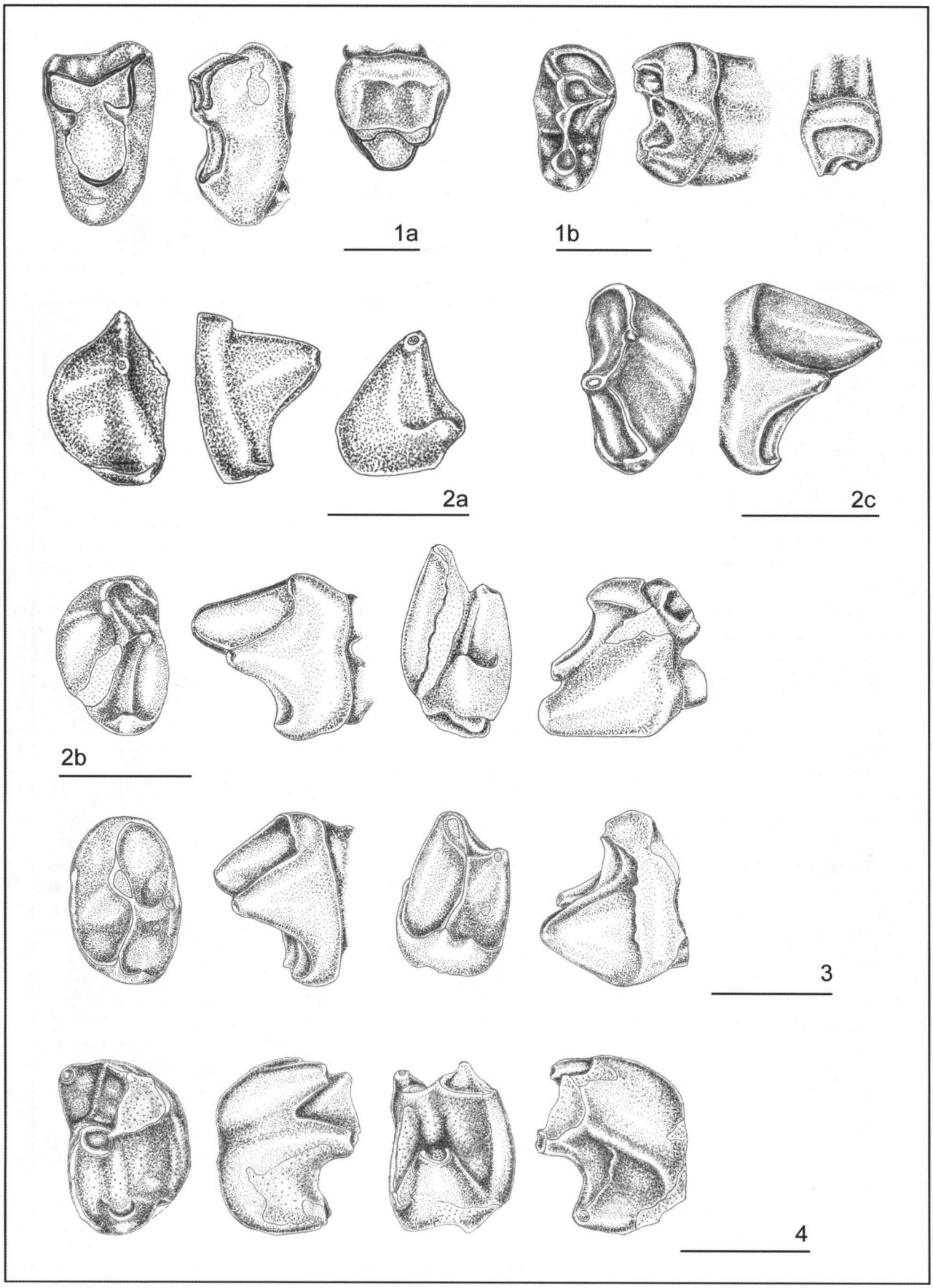
Generic and specific diagnosis – M1 small (CL 3.0 – 3.1 CW 5.1 – 5.2 mm). *Vulpavoides germanica* Matthes, 1952, *V. vanvaleni* Russell & Godinot, 1988, and *V. simplicidens* Van Valen, 1988, larger. M1 relatively short and broad with no paraconule, metaconule weak to absent, paracone and metacone close together, ectoflexus weak. M3 is not greatly reduced with prominent protocone and paracone. The combined crown lengths of p3 and p4 are close to those of m1 and m2 combined. The p3 and p4 are semimolariform, both teeth with discrete cuspate metaconids and absent paraconids. m1 with prominent lingual paraconid, close to the metaconid. m2 smaller, with distinct lingual paraconid, lower and less lingually prominent than m1, and incipient protoconulid, both with reduced talonids.

Differential diagnosis – *Paravulpavoides cooperi* is readily

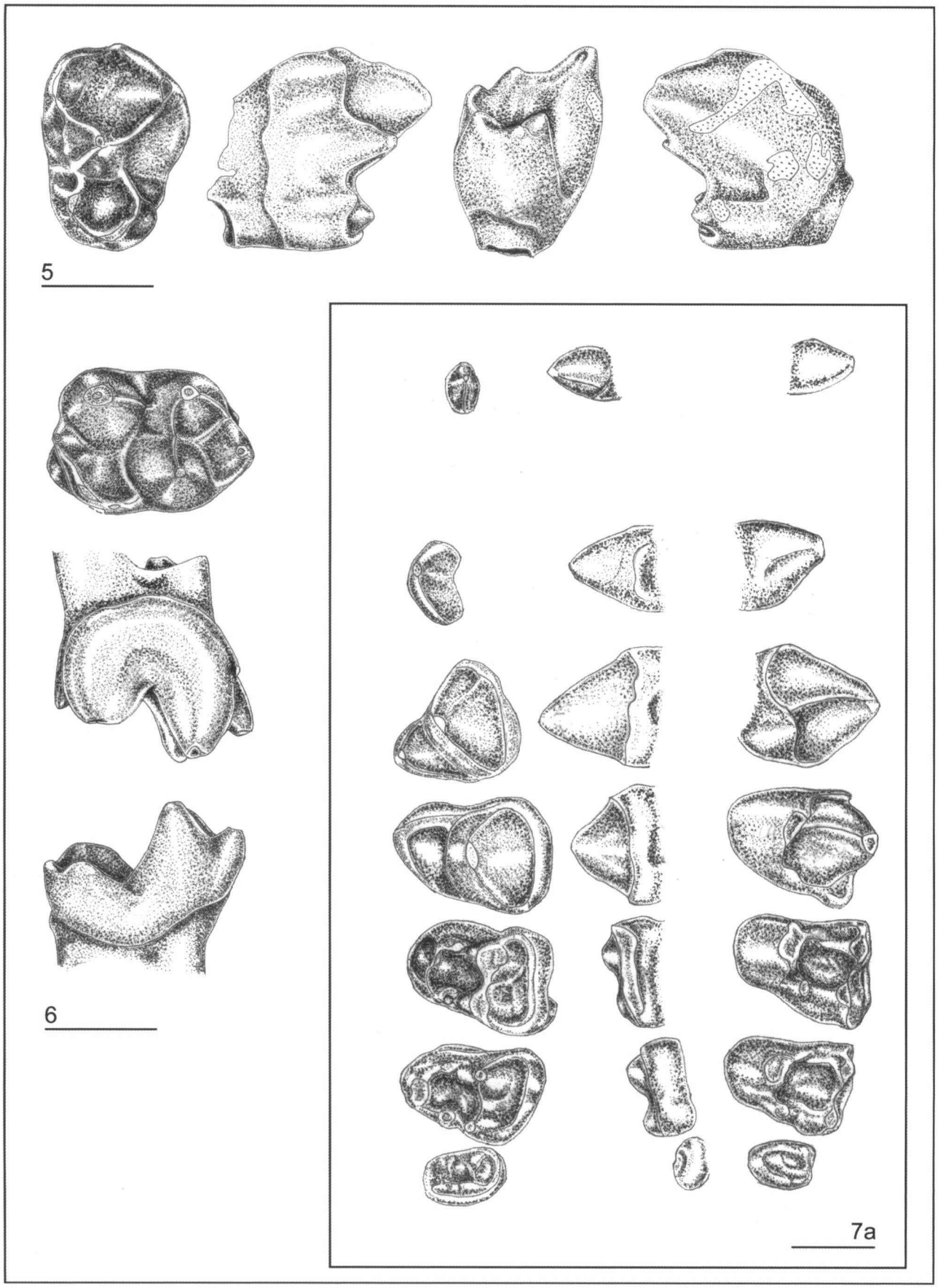
distinguished from the Merialinae by their possession of a premolariform p4. *Vulpavoides germanica* Matthes, 1952, *V. vanvaleni* Russell & Godinot, 1988 and *V. simplicidens* Van Valen, 1988, are all larger and have the M1 longer in relation to its width. The M3 of *P. cooperi* is less reduced than that of *Paroxyclaenus lemuroides* Teilhard de Chardin, 1922, with distinct protocone and paracone. *Paroxyclaenus* additionally has the p3 not molarised, lacking any metaconid. The paraconid of m1 is prominent and hooked in *Paravulpavoides cooperi*, scarcely evident in *Paroxyclaenus*. *Kopidodon macrognathus* has an unmolarised p3, lacking any metaconid. *Pugiodens mirus* has the p3 without paraconid and p4 fully molarised, m1 with protoconulid. *Kinkerishella zaizanica* is a little known taxon, but the talonid of m1 has a high tubular hypoconid, distinct entoconid and hypoconulid (Russell & Godinot, 1988), which distinguish it from *Paravulpavoides*. For more detailed comparisons see Discussion below.

Referred material – (CL = Crown length, CW = Crown width, sin. = sinistral, dex. = dextral) HZM 3.32598 M1 sin. CL 3.10 CW 5.12 mm (Figure 1a). HZM 6.34903 M3 sin. CL 1.76 CW 3.01 mm (Figure 1b). HZM 7.35425 p 1 or 2 sin. CL 2.56 CW 1.92 mm (Figure 2a). HZM 1.32172 p3 sin. CL 3.71 CW 2.50 mm (Figure 2b; 8a–c). HZM 8.37498 p3 dex. CL 4.22 CW 2.46 mm (Figure 2c). HZM 2.32259 p4 sin. CL 4.16 CW 2.88 mm (Figure 3; 8d-f). HZM 4.34112 m1 dex. CL 4.16 CW 2.94 TRI L 2.56 TAL L 1.60 mm (Figure 4). HZM 5.34877 m2 dex. CL 3.71 CW 2.69 TRI L 2.37 TAL L 1.28 mm (Figure 5).

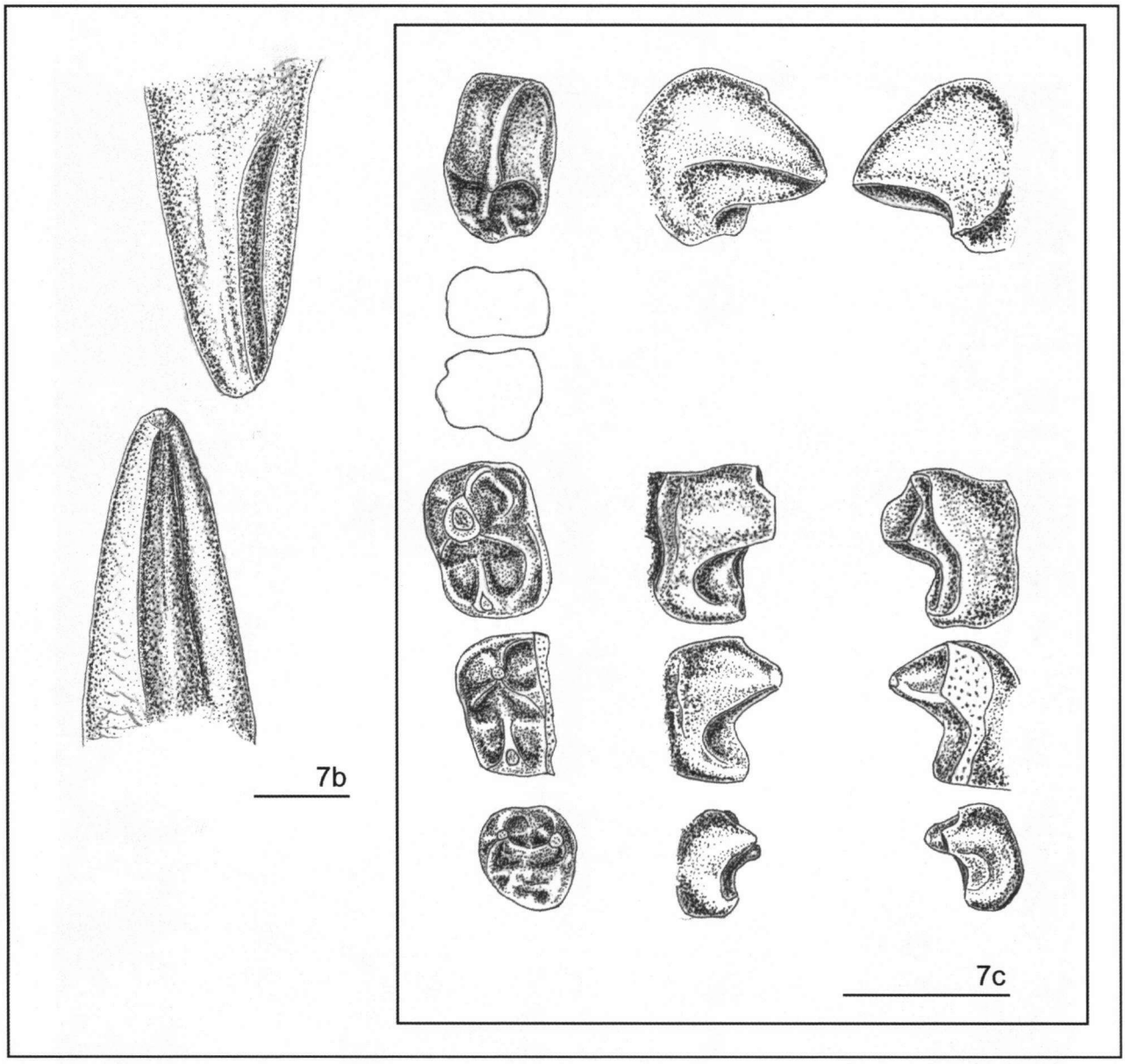
Description – **M1**: HZM 3.32598 M1 sin. is the second known specimen of this element (Figure 1a). The morphology agrees well with that of the holotype (BM M37570), but this specimen exhibits more advanced wear, with dentine exposure throughout the whole protofossa and stylar shelf, only the lingual slopes of the paracone and metacone retaining enamel on the occlusal surface. The latter cusps are close together and the tooth is elongated transversely and shortened mesio-distally, as in the holotype. The metastylar region is similarly rounded and more prominent, indicating that this is a left M1, but the styles are rather more angular and pointed than in the holotype, probably due to individual variation. There is no trace of any hypocone or mesostyle; the ectoflexus is somewhat more evident in this specimen. No paraconule or metaconule is visible, although the adjacent exposure of dentine may possibly have obscured this feature. The ectocingulum is weak as in the holotype and there is no lingual, mesial or distal cingulum. Enamel bordering the protofossa and stylar shelf is thin. Three roots were present, the strongest below the protocone. The slight differences from the holotype seem well within the limits of variation for a single species, especially having regard to the more advanced wear in this specimen.
M3: HZM 6.34903 (Figure 1b) is an intact M3 sin. less worn than the M1. Principal features denoting this specimen as paroxyclaenid are the complete absence of any hypocone or mesial and distal cingula. The transversely elongated form of the M1 is also reflected in this tooth, which has a length/width ratio of 1.71. The paracone is the dominant cusp, the metacone so weak as to be scarcely evident. The protocone is notably robust, its cusp already well worn, but probably not as high as the paracone originally. The distal part of the paracone is worn away. A distinct preprotocrista connects the protocone to the paracone and an ovoid swelling close to the paracone, although worn down, marks the original presence of a paraconule. There is no postprotocrista or metaconule. A buccal cingulum extends from the base of the sharp parastylar crest to the less prominent, more distally situated metastyle. The tooth is slightly 'waisted' between the protocone and the buccal cusp. The buccal margin is oblique and unlike the M1 it is slightly convex. The heavy wear seen in the M1's has similarly produced exposure of dentine distal to the paracone of the M3, extending lingually behind the preprotocrista. A single robust transverse root is present.
p1-2: HZM 7.35425 (Figure 2a) is a p1 or 2 sin. crown of this taxon. It is well preserved apart from marginal enamel erosion mesiolingually. It is strongly bulbous buccally, with the single cusp curved lingually, the lingual surface of the crown gently concave. A distinct distal heel is reminiscent of the p3 and the pointed mesial projection of the crown forms a small ledge. Like the p3 there is no buccal or lingual cingulum. Its paroxyclaenid affinities seem reasonably certain.
p3: HZM 1.32172 is a p3 sin. (Figures 2b, 8a–c). The crown contour is broadly ovoid, more rounded on the buccal aspect and rather flattened lingually. The tooth is blunt and rounded mesially, the heel ovoid and narrower than the trigonid. The protoconid is high and dominant, its buccal surface rounded, the lingual surface remarkably flat. A strong paracristid curves lingually along the crown margin. A slight expansion at its distal end is the only minute trace of a paraconid. The trigonid basin behind the paracristid is open in front of the distinct metaconid, which is situated behind the protoconid with which it forms a marked notch. The heel of the tooth forms a prominent cusp, from which a cristid passes up the posterior aspect of the metaconid almost to its apex. A gutter extends down the disto-buccal side of the metaconid, parallel to an area of enamel loss on the posterior aspect of the protoconid. There is no cingulum on the buccal or lingual aspects of the crown, which are smoothly rounded. The tooth is two-rooted, the posterior root stronger and posteriorly angled.
HZM 8.37498 (Figure 2c) is a p3 dex. It is better preserved than the previous specimen and slightly larger. It is morphologically almost identical, differing only in the more complete absence of any paraconid. In this specimen the paracristid forms a slight angularity in the mesial crown margin. The dominant protoconid is bulbous buccally, without cingulum. The single cusp of the talonid forms a slightly more crestiform heel than in HZM 1.32172 and the posterior cristid ascends to the slightly worn tip of the metaconid.
p4: HZM 2.32259 represents the p4 sin. (Figures 3, 8d-f). It is possibly from the same jaw as HZM 1.32172, since it was excavated from the same hole. No interstitial facets are, however, visible.



Figures 1-4.



Figures 5-7a.



Figures 7b-7c.

Figure 1. *Paravulpavoides cooperi* (Hooker, 1986). (a) HZM 3.32598 M1 sin. (b). HZM 6.34903 M3 sin. Scale = 2 mm. All specimens orientated occlusal (left); oblique distal (centre) and buccal (right).

Figure 2. *Paravulpavoides cooperi* (Hooker, 1986). (a) HZM 7.35425 p1 or 2 sin., occlusal, (left), buccal (centre) and distal (right) views. Scale = 2 mm (b) HZM 1.32172 p3 sin., from left to right occlusal, lingual, distal and buccal views. Scale = 3 mm (c) HZM 8.37498 p3 dex. Occlusal (left) and lingual (right) views. Scale = 3 mm.

Figure 3. *Paravulpavoides cooperi* (Hooker, 1986). HZM 2.32259 p4 sin., from left to right occlusal, lingual, distal and buccal views. Scale = 3 mm.

Figure 4. *Paravulpavoides cooperi* (Hooker, 1986). HZM 4.34112 m1 dex., from left to right occlusal, lingual, distal and buccal views. Scale = 3 mm.

Figure 5. *Paravulpavoides cooperi* (Hooker, 1986). HZM 5.34877 m2 dex, from left to right occlusal, lingual, distal and buccal views. Scale = 3 mm.

Figure 6. *Euhookeria hopwoodi* (Cray, 1973). HZM 1.19050 m1-2 sin. Occlusal (above), lingual (centre) and buccal (below) views. Scale = 3 mm.

Figure 7. *Paroxyclaenus lemuroides* Teilhard de Chardin, 1922. Dentition (drawn from casts of the holotype, Memerlein, Lot, France BM M 42146. (a) Maxillary cheek teeth in occlusal (left row) buccal (centre row) and lingual (right row) views. (b) Left upper canine in lingual (upper) and buccal (lower) views. Scale = 5 mm (c) Mandibular cheek teeth, from left to right occlusal, lingual, and buccal views. Scale = 3 mm.

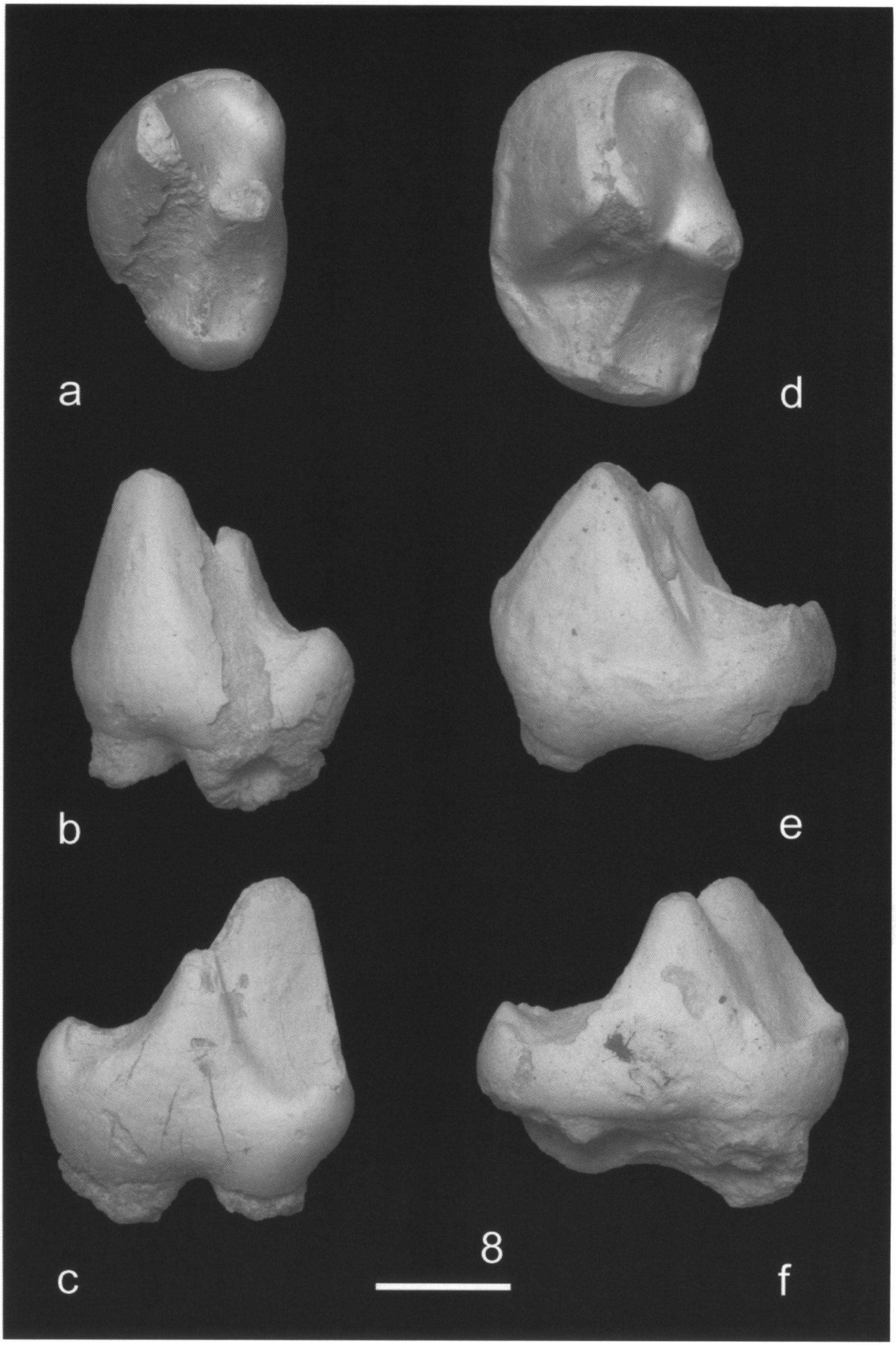


Figure 8. *Paravulpavoides cooperi* (Hooker, 1986). (a-c) HZM 1.32172 p3 sin. (d-f) HZM 2.32259 p4 sin. Occlusal, buccal and lingual views of each. SEM photographs. Scale = 2 mm.

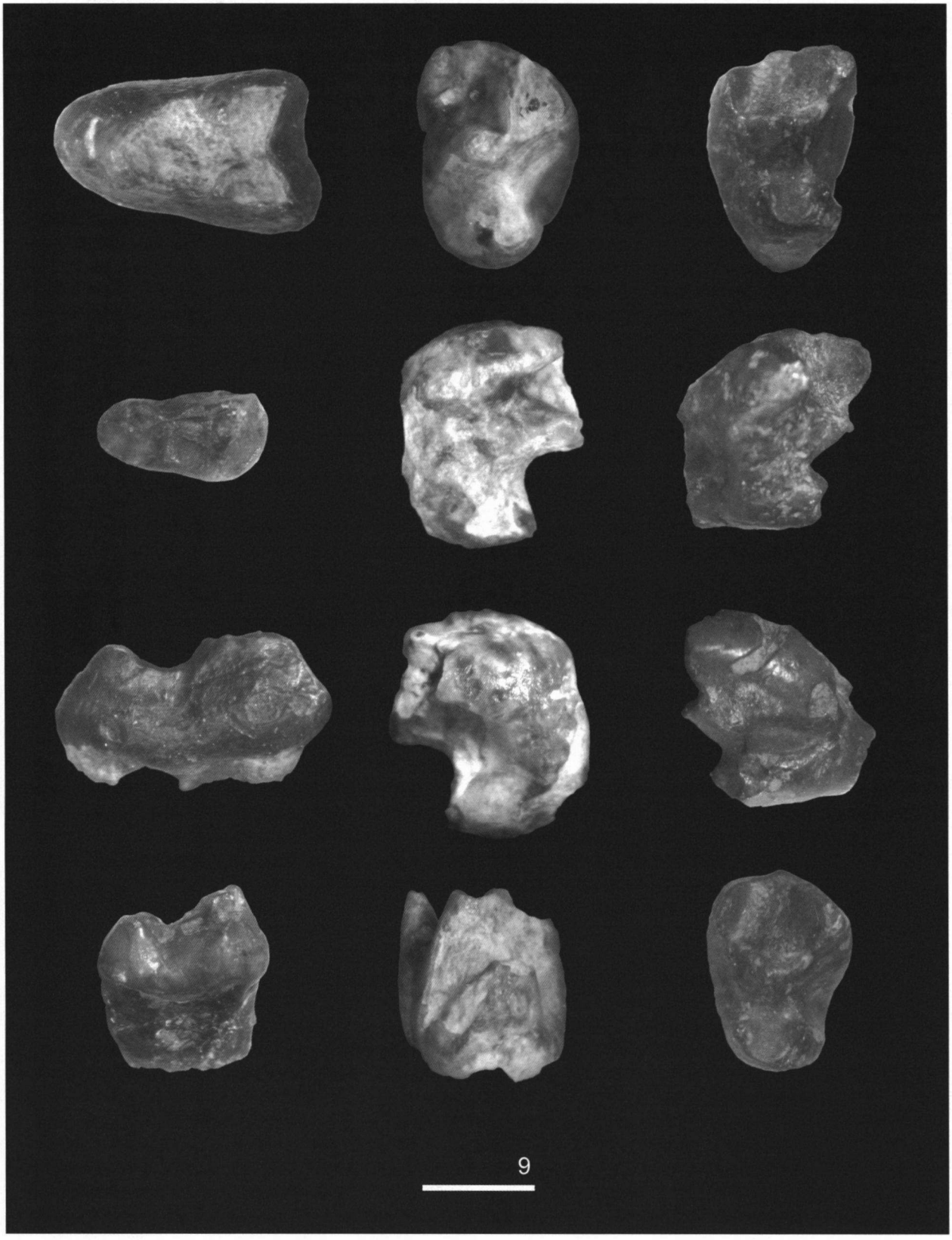


Figure 9. *Paravulpavoides cooperi* (Hooker, 1986). On left row (top-down): HZM 3.32598 M1 sin occlusal view, HZM 6.34903 M3 sin. occlusal view, HZM 3.32598 M1 sin. distal view and HZM 6.34903 M3 sin. distal view. Centre row (top down): HZM 4.34112 m1 dex., occlusal, lingual, buccal and distal views respectively. Right row (top down): HZM 5.34877 m2 dex., occlusal, lingual, buccal and oblique distal views respectively. Scale = 2 mm.

It is more robust and with a generally similar morphology, but with some distinctive differences indicating its more posterior position in the toothrow. It is semimolarised, with the talonid broader than that of the p3; a posterior cristid passes forwards in a slightly sinuous curve more buccally, terminating on the back of the protoconid cusp. The excavated heel of the talonid has an additional small incipient entoconid lingually. The talonid is distinctly shorter than the trigonid, but subequal with it in width. There is a partial, slightly nodular cingulum disto-buccally terminating level with the front of the protoconid cusp. As in the p3 there is no paraconid, but a strongly curving paracristid extends round the front of the trigonid as far as the base of the metaconid. The protoconid is similarly dominant, but lower, the distinct metaconid situated only slightly posterior to it and more widely separated from it. Two roots were present.

m1: HZM 4.34112 is an m1 dex. (Figure 4). The enamel is extensively eroded on the posterior trigonid wall and the lingual aspect of the talonid. The cusp tips of the protoconid and metaconid are also eroded. In spite of this damage the principal morphological features are clear. The tooth is bulbous mesio-buccally, with a subpyriform outline and a slight concavity lingually between the paraconid and metaconid. The protoconid is dominant, with the smaller metaconid fused with its disto-lingual aspect at least as high as the cusps are preserved. The metaconid was originally cuspidate, its tip separate from the protoconid. Although denuded of enamel, it is clear that the posterior trigonid wall is obliquely slanted distally behind the protoconid as far as the junction with the cristid obliqua, then becoming convex behind the metaconid. The paraconid is prominent, lingually situated and lower than the metaconid. The trigonid basin is deep and arcuate, narrowly open between the paraconid and metaconid. Mesially it is closed by the junction of a low preparacristid and preprotocristid. The talonid is reduced, clearly shorter than the trigonid and with a well developed hypoconid. Because of the enamel erosion present on the lingual side of the talonid of this specimen, however, the former presence of a small entoconid and hypoconulid cannot be excluded. The cristid obliqua is broad and straight, attached mesially between the metaconid and protoconid. No cingulum is developed.

m2: HZM 5.34877 (Figure 5) is an intact m2 dex., reasonably well preserved, apart from extensive shallow areas of enamel erosion buccally, two roots originally present. It differs from the m1 described above in its overall smaller size and its more reduced talonid. The cusps of the trigonid are intact; the protoconid is dominant, its cusp situated in a strongly buccal position. A sharp preprotocristid curves lingually to join the preparacristid at a distinct mesial projection (less evident in the m1), forming an incipient protoconulid. The paraconid is elongated, situated lingually, but much lower and less lingually projecting than in the m1. The metaconid is also less robust than in the m1 and the trigonid basin is wider and shallower mesially. The outer wall of the trigonid is very bulbous and globose, like the m1. The talonid is distinctly smaller than that of the m1; the hypoconid is very much smaller, the entoconid higher than the hypoconid; a minute hypoconulid is present, situated closer to the hypoconid than to the entoconid; the talonid basin is shallow and small. Detailed comparison with the talonid of m1 is precluded by the erosion of the distolingual part of the talonid in the m1, with the loss of any entoconid and hypoconulid formerly present. It is however, clear that the m2 talonid is more reduced and its hypoconid much smaller.

Discussion – The Paroxyclaenidae are an enigmatic group of archaic placentals, which have been variously placed by different authors in the Carnivora and Creodonta, 'Condylarthra' and Insectivora. They were also recently considered to be members of the Cimolesta (Russell & Godinot, 1988; McKenna & Bell, 1997), together with other extinct groups such as the Pantolestidae and Apatemyidae, which also occur at Creechbarrow. Following the opinion of Russell & McKenna (1962: 279) based on cranial anatomy and Hooker (1986: 338) the paroxyclaenids are here referred to the 'Condylarthra'. The dentition of paroxyclaenids is complete, resembling in other respects also that of primitive condylarths such as *Phenacodus* and *Hyopsodus*, including enlarged canines and bunodont molars (Lavocat, 1958: figs 20, 26). In other ways, however, it is highly specialised, with relatively enlarged posterior premolars, spaced out cheek teeth and absence of upper molar hypocones, as well as reduction of M3 and m3. A peculiarity of the dentition of paroxyclaenines is the tendency to enlargement and molarisation of the third and fourth posterior upper and lower premolars, generally exceeding the succeeding molars in size. There is significant variation between the various genera in this dental feature as discussed below.

The rather unusual pattern of dental wear occurring in paroxyclaenines suggests a hard diet. Von Koenigswald (1983) describes the distinctive abrasive wear developing on the lingual aspects of the lower molars in *Kopidodon* and *Paroxyclaenus*. This affects particularly the paraconid, metaconid and entoconid, suggesting heavy wear against the cusps and protofossae of the upper molar trigons. *Kopidodon* is known from its skeleton to have been arboreal and may have subsisted on hard fruits, although unfortunately no stomach contents have been found in the well preserved specimens from Messel in Germany (Von Koenigswald *et al.*, 1992). The enlarged and variably molarised posterior premolars suggest a transfer of maximal crushing power forwards in the tooth row, which appears to support such a dietary regime. Enlarged canines were present and in *Paroxyclaenus* the upper canines are particularly massive and straight (Teilhard de Chardin, 1922). These may well have been used to pluck fruit from branches. The latter genus is also known to have a shortened rostral region of the skull and enlarged infraorbital foramina, as well as the most extreme molarisation of p4, all possibly indicative of the modification of the masticatory apparatus in the paroxyclaenines. Some parallels are apparent with the dentition of the fruit bats (Megachiroptera), for example *Pteropus*, in which the canines are large, but the cheek teeth relatively weak and flattened and spaced apart in a similar manner to

Paroxyclaenus. The enlarged posterior premolars of the paroxyclaenines seem well adapted to produce a 'nut-cracker' effect for a relatively hard dietary regime. The approximately equal combined crown lengths of p3 and p4 and m1 and m2 in *Paravulpavoides cooperi* suggests that this genus is somewhat less advanced than *Paroxyclaenus* in the development of this specialised frugivorous dentition. The p3 is however, more molarised in *Paravulpavoides*, supporting its referral to a separate lineage. The length of the diastemata in *Paravulpavoides* is quite unknown at present, although the absence of any interstitial facets between the lower cheek teeth suggest that the teeth were similarly set apart.

Russell & Godinot (1988) have made an extensive revision of the Paroxyclaenidae, recognising two subfamilies. The Merialinae, described as new, comprising *Merialus martinae* Russell & Godinot, 1988, *Euhookeria hopwoodi* (Cray, 1973: fig. 6, formerly *Dyspterna hopwoodi*) and *Spaniella carezi* Crusafont-Pairo & Russell, 1967. These forms are readily distinguished from the nominate Paroxyclaeninae by their possession of a premolariform p4, without a metaconid and lower molars with a lingual paraconid close to the metaconid. It is the members of the nominate subfamily Paroxyclaeninae, comprising the genera *Paroxyclaenus, Kopidodon, Pugiodens* and *Vulpavoides*, which need to be considered in detail below in comparison with the Creechbarrow paroxyclaenid.

Vulpavoides cooperi was described by Hooker (1986) with a single intact M1 as holotype and a possible fragmentary DP4. The mandibular dentition of this rare paroxyclaenid has been unknown hitherto. Comparison with other described genera and species is hampered by the paucity of material and gaps in knowledge of the dentitions and their individual variation. The length/width ratio of the new specimen of M1 (HZM 3.32598) is 1.65, of the holotype 1.73; Russell & Godinot (1988: 326) gave a revised length/width ratio for *V. germanica* of 1.48 and for *V. simplicidens* of 1.38. This ratio in *V. vanvaleni* is 1.58 (or 1.60 as estimated by Russell & Godinot 1988: 326). Comparisons are summarised below. Van Valen (1965: 392) synonymised *Vulpavoides germanica* Matthes, 1952, based on a crushed skull, with *Pugiodens mirus* Matthes, 1952, which was described based on a mandibular ramus. He considered the two specimens occlusally compatible. *Pugiodens mirus* was selected as the senior synonym. Subsequently, Hooker (1986: 339) preferred the use of *Vulpavoides* since the holotype ramus of *Pugiodens* was lost and in any case Tobien (1969: 28, 35) regarded the synonymy of the two genera as somewhat doubtful. Russell & Godinot (1988: 324) have, however, given compelling reasons why *Pugiodens mirus* should be retained as a distinct taxon and this view is followed here. Hooker (1986: 340) has outlined differences between the M1 of *cooperi* and *V. germanica*. (See Diagnosis, above). The M3 of *V. germanica* is only known from its alveolus, which indicates a narrower and longer crown than *Paravulpavoides cooperi* (Van Valen, 1965: Figure 1).

Matthes (1952: 232) gave detailed descriptions and measurements of the mandibular dentition of *Pugiodens mirus*. The p3 is molariform to the extent of having a distinct metaconid, connected to the protoconid by a small crest, but no paraconid is present. It measured CL of 5 mm and CW of 3 mm. The p4 is fully molarised, with a moderately large lingual paraconid (Van Valen, 1965: 391). The talonid is relatively deep and bowl-shaped, the hypoconid larger than the hypoconulid. The p4 is the same length as p3, but broader (CL 5 mm, CW 4 mm) The talonid is shorter than the trigonid (TRI L 3 mm, TAL L 2 mm.). The lower molars are progressively smaller than the p4, with a protoconulid developed in m1 and m2 (m3 is missing, its size only determinable from the alveolus). Matthes (1952) description of the m1 and m2 states that in each the talonid is longer than the trigonid and each possesses a protoconulid situated between the protoconid and paraconid, near to the paraconid. The talonid has a hypoconid, hypoconulid and entoconid. Whichever of the two conflicting views of the taxonomic status of *Pugiodens* is followed, its mandibular dentition clearly differs in important details from the mandibular elements of *Paravulpavoides cooperi* described here. The m1 of *P. cooperi* has no protoconulid, m2 has an incipient one, while the reduced talonid is shorter than the trigonid.

Russellites simplicidens Van Valen 1965 has been transferred by Van Valen (1967: 259) to *Vulpavoides*. Hooker (1986: text-fig. 42: E-H) has shown that M1 in *V. simplicidens* is larger, with more widely spaced paracone and metacone and cuspate paraconule. Its mandibular dentition is unknown.

Vulpavoides vanvaleni described by Russell & Godinot (1988: 326) from the late Lutetian of Bouxwiller Quarry, Alsace, France is known from an M1 and m3. The M1 of this species is slightly larger than *P. cooperi* and has noticeably less transverse proportions and the paracone higher than the metacone (the opposite pertains in *P. cooperi)*; it is also lower crowned and has a larger paraconule. The m3 has the trigonid basin widely open and there is no paraconid. The talonid is short and much narrower than the bulbous, low trigonid. No protostylid is present. The talonid bears a small entoconid and the hypoconid is large. This tooth therefore differs distinctively from the only known lower molars of *P. cooperi* of which the m3 is, however, as yet unknown.

The dentition of *Paroxyclaenus lemuroides* Teilhard de Chardin, 1922, is relatively well known and the known elements of *Paravulpavoides cooperi* are compared here in detail with casts of the holotype of *Paroxyclaenus* in the Natural History Museum (BM M42146 a and b, Phosphorites du Quercy, Memerlein, Lot, France (Figures 7 a, b)). The M1 of *Paroxyclaenus* is more robust. Measurements given by Russell & Mckenna (1962: 275) are CL 4.10 mm, CW 6.0 mm, giving a length/width ratio of 1.40 (1.65 – 1.73 in the two known M1's of *P. cooperi)*. The stylar projections are similarly rounded, but the metastyle of *P. cooperi* is more prominent and the parastyle narrower. The buccal cingulum is scarcely developed and the mesial crown outline is essentially straight, but distinctly concave in *Paroxyclaenus*. The conules are prominent in the genotype, the paraconule fused with the mesio-buccal

aspect of the protocone, the metaconule separated from it by a distinct notch. Both conules are virtually absent in *P. cooperi* although possibly affected by wear in HZM 3.32598. The paracone is slightly higher than the metacone in *Paroxyclaenus*, the reverse is the case in *Paravulpavoides*. The M3 is more robust and structured in *Paravulpavoides*, with distinct protocone and paracone. The p3 is smaller than the relatively massive tooth of *Paroxyclaenus*, which measured CL 5.0 and CW 3.10 mm in the holotype (Russell & McKenna, 1962). This tooth is not molarised, lacking any trace of metaconid, prominent in *P. cooperi*. The talonid is short and slightly rugose, but lacks any defined cusp, in *P. cooperi* a single central talonid cusp is present. The p4 is now lacking in the holotype of *Paroxyclaenus* and measurements are not available. It was originally a massive tooth, exceeding the m1 in size and fully molarised (Teilhard de Chardin, 1922: figs 38, 86). The talonid was only slightly shorter than the trigonid and the entoconid was scarcely developed. The paraconid was low and described by Van Valen (1965: 389) as moderately large and lingually situated. The p4 of *Paravulpavoides* lacks any paraconid, the talonid is distinctly shorter than the trigonid and bears three incipient cusps. The metaconid is distinct, however, but p4 is clearly less completely molarised than *Paroxyclaenus*. It is noteworthy that the m1 of *P. cooperi* is the same length as p4, although with isolated teeth individual variation could affect relative size. The m1 of *Paroxyclaenus* measured CL 4.7 mm and CW 3.4 mm (Russell & Mckenna, 1962: 275). The paraconid of the holotype m1 is low and scarcely evident in marked contrast to the prominent, hooked paraconid of *P. cooperi*, forming a distinct bulge on the mesio-lingual crown margin. The talonid is broader and unreduced in *Paroxyclaenus*, unlike *Paravulpavoides cooperi* and has a single, central hypoconid, which is, however, less prominent.

Kopidodon macrognathus (Wittich, 1902; Tobien, 1969) also has a semimolarised p4, the talonid as long and as wide as the trigonid, the metaconid strong, but the paraconid vestigial. The p3 in this genus is disproportionately large, with a single cusp and not molarised, lacking any metaconid, differing strikingly from *Paravulpavoides* in this respect. The m1-2 of this genus also possess normal trigonids, with the small paraconids situated lingually and the talonids subequal in length with the trigonids (Von Koenigswald, 1983: fig. 4), with variably developed talonid cusps.

Kinkerishella zaisanica Gabunia & Biryukov (1978) from the late Eocene Aksyir beds, Zaisan depression, Kazakhstan, is of obscure affinity, but may be referable to the paroxyclaenines, with only the talonid of m1 and an intact m3 known. The talonid of m1 has a high tubular hypoconid, with distinct entoconid and hypoconulid (Russell & Godinot 1988: 328, holotype m3, fig. 1, C and D). The m3 completely lacks a paraconid.

The subfamilial status of *Paravulpavoides cooperi*.

Comparison with an m1-2 (HZM 1.19050; Figure 6) of *Euhookeria hopwoodi* (Cray, 1973), a member of the subfamily Merialinae, from the Lignite Bed of Headon Hill, shows a striking similarity in the prominent cuspate paraconid, which is, however, even more strongly lingual in *Paravulpavoides cooperi*, forming a projecting bulge on the lingual crown, in front of the metaconid. In *E. hopwoodi* the paraconid is distinctly buccal to the metaconid. In other respects, however, the lower molar of *E. hopwoodi* differs greatly. It possesses a small projecting anterior cingulum, absent in *Paravulpavoides cooperi*. The talonid of *E. hopwoodi* is not reduced. It is as broad and subequal in length with the trigonid and is furnished with three distinct cusps. A large hypoconid is attached to the base of the trigonid much more lingually and the cristid obliqua is very short. A small, but distinct hypoconulid is present as well as a low crestiform entoconid. Allowing for the eroded cusp tips of its protoconid and metaconid, the trigonid of *P. cooperi* was at least as high crowned as this specimen of *E. hopwoodi*.

Cray (1973: 69, fig. 21) figured and described an isolated lower molar of *'Dyspterna' hopwoodi* considered by him to be an m1. It differs from HZM 1.19050 in having a more centrally placed paraconid, the talonid slightly narrower and the anterior cingulum better developed. Russell & Godinot (1988: 322) however, doubt whether this specimen is referable to *E. hopwoodi*, considering its median paraconid anomalous and the tooth most probably an unidentified dyspternine taxon. Since the m1 and m2 of the holotype jaw of *E. hopwoodi* were lacking, the isolated lower molar described and figured here (HZM 1.19050) assumes particular importance. The paroxyclaenid affinities of *Euhookeria hopwoodi* appear rather uncertain, but it is clearly not closely related to *Paravulpavoides*.

The new genus *Paravulpavoides* is a very specialised member of the Paroxyclaeninae, primarily distinguished by the semimolarised p3 and p4. The m1 however, with its reduced talonid and prominent very lingual paraconid, appears unique in the known dentitions of Paroxyclaeninae. The m2 is also distinctive, with its well developed lingual paraconid, incipient protoconulid and reduced talonid with three cusps present. The pronounced mesio-distal shortening of the M1 and M3 has to be added to this distinctive dental profile. Hooker (1986: 340), observing the very shallow mesocylix of the holotype M1 of *'V'. cooperi* concluded that it must have occluded with an m1 with a very reduced talonid. This prediction is now fully confirmed and it is predictable that the M2 will have a reduced mesocylix also.

Although the dentition of *Paravulpavoides cooperi* is still imperfectly known, it is clear that it has a very distinctive dental profile amongst the Paroxyclaeninae. There can be no doubt, in view of the new elements described here, that it represents a distinct genus.

Acknowledgements

The author is again much indebted to ECC International and Imerys Minerals Ltd. for permission to continue this

research on their land, especially Q.G. Palmer, senior geologist and M.E. Arthur. The arduous field work was carried out by the staff and helpers of the Harrison Institute, Sevenoaks. Sally Balcon, Patrick White, James Stephen, Paul Bates, Malcolm Pearch, Chris Michaels, Lorna McGregor, June Cree, Pippa Capon, David and Alison Ward have all taken part and special thanks are due to them. The Systematics Association provided a grant for purchase of a Leica stereomicroscope drawing attachment, which has proved invaluable. Dr Ian Slipper of Greenwich University, Malcolm Pearch and David Ward have kindly assisted with S.E.M and light macrophotography. The author is most indebted to J. J. Hooker for his invaluable help with identification of the material and with discussion of this paper, as well as providing access to specimens in his care. Lars van den Hoek Ostende has made most helpful comments on review, which are gratefully acknowledged.

References

Cope, E.D. 1881. A new type of Perissodactyla. *American Naturalist* 15, 1017-1018.

Cray, P.E. 1973. Marsupialia, Insectivora, Primates, Creodonta and Carnivora from the Headon Beds (Upper Eocene) of Southern England. *Bulletin of the British Museum (Natural History) Geology* 23, 1-102.

Crusafont-Pairo, M. & Russell, D.E. 1967. Un nouveau Paroxyclaenidé de l'Eocène d'Espagne. Bulletin du Muséum national d'Histoire Naturelle Paris 38, 757-773.

Gabunia, L.K. & Biryukov, N.D. 1978. On the presence of a peculiar representative of Arctcyonoids in the Paleogene of Asia. *Bulletin of the Academy of Science of the Georgian S.S.R.* 92, 489-492.

Harrison, D.L. 2002. A new species of Dormouse (Rodentia: Gliridae) from the Creechbarrow Limestone Formation (late Middle Eocene) of Dorset, England. *Tertiary Research* 21, 11-18.

Hooker, J.J. 1986. Mammals from the Bartonian (middle/ late Eocene) of the Hampshire Basin southern England. *Bulletin of the British Museum (Natural History) London (Geology)* 39, 1-478.

Hooker, J.J. 1977. The Creechbarrow limestone – its biota and correlation. *Tertiary Research* London 1, 139-145.

Hooker, J.J. & Insole, A.N. 1980. The distribution of mammals in the English Palaeogene. In Hooker *et al.* The distribution of cartilaginous fish, turtles, birds and mammals in the British Palaeogene. *Tertiary Research* 3, 31-45.

Koenigswald, W. von 1983. Skelettfunde von *Kopidodon* (Condylarthra, Mammalia) aus den mitteleozanen Olschiefer von Messel bei Darmstadt. *Neues Jahrbuch für Geologie und Paläontologie*, Abhandlungen 167, 1-39.

Koenigswald, W. von 1992. The Arboreal *Kopidodon*, a relative of primitive hoofed animals. *In*: Schaal, S. & Ziegler, W. (Eds.). Messel, an insight into the history of life and of the Earth. *Clarendon Press,* Oxford. 322 pp.

Lavocat, R. 1958. Condylarthra. *In*: J.Piveteau. Traité de Paléontologie Tome V1-2, 1-27.

Matthes, H.W. 1952. Die Creodontier aus der Mitteleozänen Braunkohle des Geiseltales. *Hallesches Jahrbuch für Mitteldeutsche Erdgeschichte* 1, 201-240.

McKenna, M.C. & Bell, S.K. 1997. Classification of Mammals Above the Species Level. *Colombia University Press*, New York. 631 pp.

Russell, D.E. & Godinot, M. 1988. The Paroxyclaenidae (Mammalia) and a new form from the Early Eocene of Palette, France. *Paläeontologische Zeitschrift* 62, 319 - 331.

Russell, D.E & McKenna, M.C. 1962. Etude de *Paroxyclaenus*, mammifère des phosphorites du Quercy. *Bulletin de la Société Géologique de France* 3, 274 - 282.

Teilhard de Chardin, P. 1922. Les mammifères de l'Eocène inférieur français et leurs gisements. *Annales de Paléontologie*, 11, 1-116.

Tobien, H. 1969. *Kopidodon* (Condylarthra, Mammalia) aus dem Mitteleozan (Lutetium) von Messel bei Darmstadt (Hessen). *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden* 97, 7-37.

Van Valen, L. 1965. Paroxyclaenidae, an extinct family of Eurasian mammals. *Journal of Mammalogy* 46, 388 - 397.

Van Valen, L. 1967. New Paleocene insectivores and insectivore classification. *Bulletin of the American Museum of Natural History* 135, 217-284.

Weitzel, K. 1933. *Kopidodon macrognathus* Wittich, ein Raubtier aus dem Mitteleozan von Messel. *Notizblatt des Vereins für Erdkunde zu Darmstadt* 14, 81-88.

Wittich, E. 1902. *Cryptopithecus macrognathus* n. spec., ein neue Primate aus dem Braunkohlen von Messel. *Centralblatt für Mineralogie, Geologie und Paläeontologie* 1902, 289-294.