*Cainozoic Research*, **9**(1), pp. 65-85, June 2012

# New additions to the late middle Eocene mammal fauna of Creechbarrow, Dorset, southern England

**David L. Harrison[1], Paul J.J. Bates[1], Malcolm Pearch[1], Chris Michaels[1, 2] & David J. Ward[3, 4]**

[1]*Harrison Institute, Centre for Systematics and Biodiversity Research, Bowerwood House, 15 St. Botolph's Road, Sevenoaks, Kent, TN13 3AQ, Great Britain*
[2]*Michael Smith Building, Faculty of Life Sciences, University of Manchester, Manchester, M13 9PT, Great Britain*
[3]*Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, Great Britain, and 81 Crofton Lane, Orpington, Kent, BR5, 1HB, Great Britain*
[4]*Corresponding author; e-mail: david@fossil.ws*

Received 24 January 2012; revised version accepted 26 March 2012

Nine little known mammalian taxa are here added to the known late middle Eocene fauna of Creechbarrow, Dorset, UK. They include three lipotyphlan insectivores, *Eotalpa anglica, Saturninia* aff. *mamertensis* and *Cryptotopos hartenbergeri*; a rare adapid primate *Adapis laharpi*; two artiodactyls *Dichobune robertiana* and *Amphirhagatherium louisi*. Two species of miacid carnivore are confirmed as occurring in the fauna, *Paramiacis exilis* and *Paramiacis teilhardi*, and a creodont carnivore *Allopterodon minor* is also included, as well as new specimens of some other little known taxa.

KEY WORDS: Creechbarrow Limestone, late middle Eocene, lipotyphlan insectivore, adapid primate, artiodactyl, miacid carnivore, creodont.

## Introduction

Hooker's (1986) monographic work on the Bartonian mammals of Britain laid the foundation for the study of the unique fauna of Creechbarrow, the only known terrestrial deposit of Bartonian age in Britain, now commonly referred to as Robiacian, because of its strong correlation with the French site of Robiac.

The Harrison Institute initiated an on-going research project at the site in 1997 and this has already resulted in the publication of the first glirid dormouse from the site, *Glamys hookeri* Harrison, 2002, as well as a new genus of paramyid rodent, *Patriarchamys batesi* Harrison, 2006. A new genus of paroxyclaenid condylarth, *Paravulpavoides,* based on Hooker's *Vulpavoides cooperi* has also been described (Harrison, 2009). The rare remains of Microchiroptera and Microchiropteramorpha found at the site have been described (Harrison & Hooker, 2010) including a new species, *Archaeonycteris relicta* Harrison & Hooker, 2010. The present paper places the limited detailed knowledge of the above little known Creechbarrow taxa on record, after which this project will conclude with a review of the glirid rodents of the site. The methods of extraction employed are as described in Harrison (2002) with use of acetic and calcium formate buffered formic acid to reduce limestone clasts.

List of abbreviations

| | |
|---|---|
| c | lower canine |
| CL | crown length |
| CW | crown width |
| HH | Headon Hill, Isle of Wight, UK |
| HZM | Harrison Zoological Museum (now the Harrison Institute), Sevenoaks, Kent, UK |
| LLL | length of the lingual lobe of M1-2 mesio-distally |
| m | mean (of a range of measurements) |
| NHMUK | Natural History Museum, London, UK |
| RBN | Robiac Nord |
| TAL W | talonid width |
| TRI L | trigonid length |
| TRI W | trigonid width |

## Systematic palaeontology

Order Lipotyphla Haeckel, 1866
Family Talpidae Fischer von Waldheim, 1814
Genus *Eotalpa* Sigé, Crochet & Insole, 1977

*Type species – Eotalpa anglica* Sigé, Crochet & Insole, 1977 (p. 141-157; 2 pls). Lower Headon Beds, Isle of Wight. Unique species of the genus.

**Plate 1.** Creechbarrow Limestone Formation. Two views of excavations in 2001 (above) and 2007 (below) showing the fossiliferous orange-buff coloured limestone marl approximately 75 cm deep, capped by layers of stony loam and with massive blocks of limestone at its base. Poole Harbour is just visible in the background.

***Eotalpa anglica*** **Sigé, Crochet & Insole, 1977**
Figure 1a-h

*Holotype* – Isolated M1 dex. (CL 1.54 CW 2.11) Sandown Museum, Isle of Wight, Geology (MIWG 5503). Headon Hill, Isle of Wight (Horizon HH2 of Bosma, 1974, pp. 23-25. Lignitic and green clay below the How Ledge Limestone). Headonian ( = Priabonian).

*Emended diagnosis* – A talpid of which the M1 has a W-shaped ectoloph with the commissures complete. Size smaller than Recent *Talpa europaea* Linnaeus, 1758 (see Sigé *et al*., 1977, p. 144). Upper molars with fully dilambdodont commissures and splitting of the mesostyle evident in unworn M1 and M2, scarcely or not evident in M3. M1 with transverse diameter greater than antero-posterior; M1 and M2 with prominent anteriorly projecting parastyle; M3 subtriangular with the parastyle variably developed. The p4 semi-molarised, with distinct separate metaconid and single, conical entoconid.
Lower molars with high, antero-posteriorly compressed trigonids; m1 and m2 with prominent entostylid continued buccally as a postcingulid; m3 lacking entostylid and all three molars without hypoconulid.

*Material* – HZM 1.37259 talonid m1-2 dex. TAL W 1.15 mm (Fig. 1g, h).

*Description and discussion* – HZM 1.37259 is a very small and gracile talonid of an m1-2 dex. falling well within the size range of *Eotalpa anglica* m1 and m2 from Hordle Rodent Bed (TAL W 0.96-1.25 mm; m = 1.12, n = 15). The type stratum population from HH2 may average slightly larger (TAL W 1.08-1.38 mm; m = 1.24 n = 4).
It is morphologically similar in all respects to the m1 and m2 of the species from Headon Hill and Hordle (see Fig. 1). The unworn entoconid and hypoconid are high and subequal, sharply pointed and connected by a narrow postcristid. The distal talonid wall is vertical and rather flat but there is a prominent conical entostylid, continued buccally as a postcingulid, declining towards the crown margin below the hypoconid externally.
Little remains of the talonid basin, but the cristid obliqua is narrow and the entoconid is prolonged mesially as an elevated pre-entoconid crest. The buccal margin of the hypoconid is strongly convex.
This specimen may indeed prove to be the oldest known talpid in the world since the isolated lower molar from Azillanet (Lutetian of Minervois) figured by Sigé, Crochet & Insole (1977; pl. 2, figs A-D) appears rather more marsupial in type, having a lingual hypoconulid connected to the hypoconid by an oblique crest. This morphological difference raises serious doubt regarding the possible talpid affinity of this tooth. The entostylid of *Eotalpa anglica* is always unconnected to the hypoconid and its postcingulid declines towards the base of the crown (Fig.1).
This unmistakably talpid talonid is the only evidence so far recovered of *Eotalpa anglica* in the Robiacian of England or elsewhere in the world. It is therefore a discovery of considerable interest, extending the known antiquity of the Talpidae by several million years and further strengthening the probable European ancestry of the family (Sigé *et al*., 1977, p. 141). Recovery of further, more complete material from Creechbarrow is highly desirable in order to confirm its specific identity.

Family Nyctitheriidae Simpson, 1928
Genus *Saturninia* Stehlin, 1940

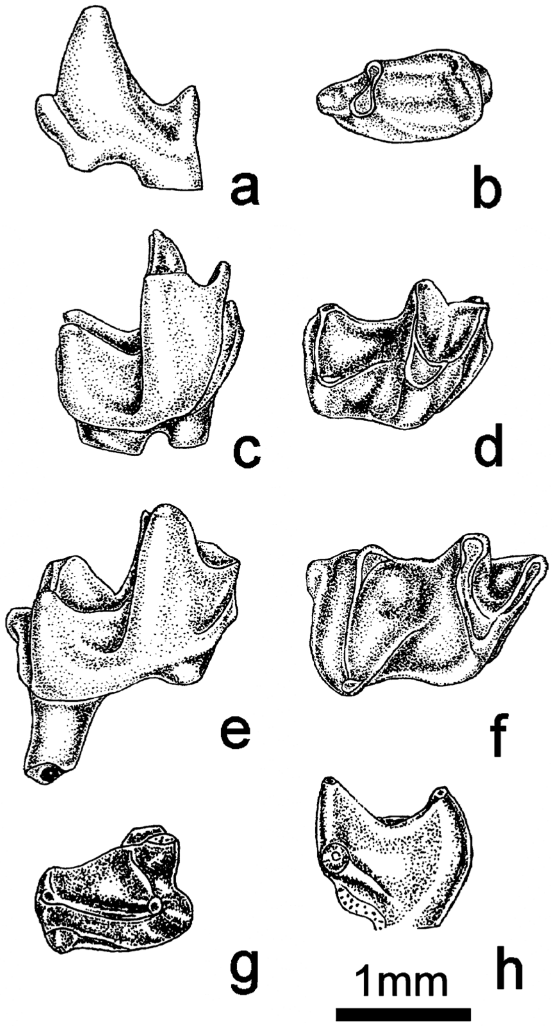



**Figure 1a-h**. Lower cheekteeth of *Eotalpa anglica* Sigé, Crochet & Insole, 1977; a, b: HZM 47.20844 p4 sin., Hordle Rodent Bed (Headonian); a: buccal view, b: occlusal view; c, d: HZM 13.24016 m1-2 dex., Hordle Rodent Bed; c: buccal view, d: occlusal view. **1e-f**. HZM 6.18999 m3 dex., Hordle Rodent Bed; e: buccal view, f: occlusal view. **1g-h**. HZM 1.37259 talonid m1-2 dex., Creechbarrow Limestone Formation. (Robiacian); g: occlusal view; h: distal view.

*Type species* – *Saturninia gracilis* Stehlin, 1940 (pp. 298-306; 5 figs). Gösgen (Kanal), Canton de Soleure, Switzerland.

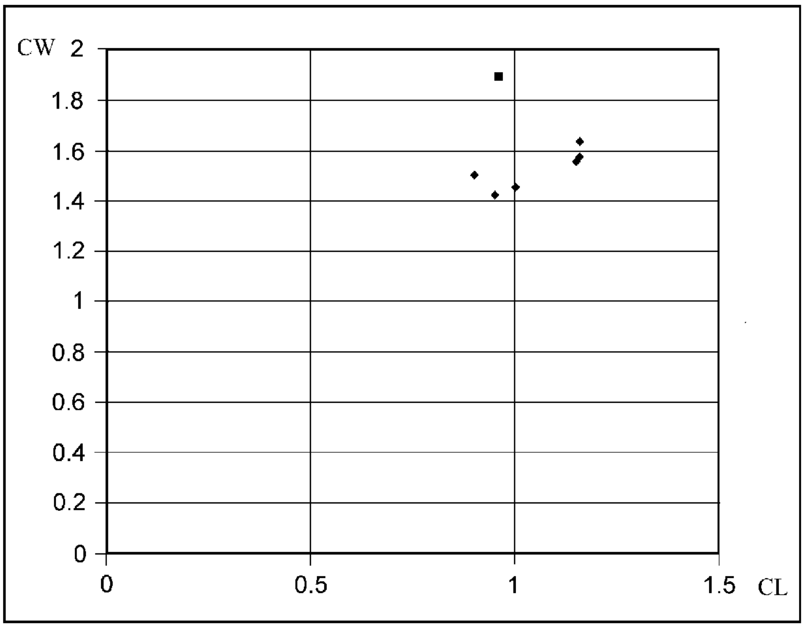
***Saturninia*** aff. ***mamertensis*** **Sigé, 1976**
Figures 2-4

1976 *Saturninia mamertensis* Sigé, p. 25, figs 17-26 [from Robiac (Robiac Nord), Gard, France].

*Holotype* – RBN 6033, fragment of right ramus, with p4-m3.

*Diagnosis* – See Sigé (1976, p. 25).

*Material* – HZM 11.34232 M1-2 dex. CL 0.96 CW 1.89 LLL 0.90 mm (Fig. 3a, b); HZM 1.31647 lingual lobe M1-2 dex. LLL 0.96 mm; HZM 4.31754 lingual lobe M1-2 dex. LLL 0.90 mm; HZM 24.38134 lingual lobe M1-2, LLL 0.93 mm; HZM 20.38334 lingual lobe M1-2 dex LLLa-p 0.96 mm; HZM 22.37964 trigonid p4 dex. TRI W 0.83 mm; HZM 19.37529 trigonid p4 dex. TRI W 0.80 mm; HZM 23.38025 trigonid p4 dex. TRI W 0.83 mm; HZM 16.34848 trigonid p4 sin. TRI W 0.83 mm; HZM 15.34652 trigonid p4 sin. TRI W 0.83 mm; HZM 22.38863 trigonid p4 sin. TRI W 0.74 mm; HZM 23.38903 trigonid p4 dex. TRI W 0.77 mm; HZM 18.36629 trigonid m1-3 sin. TRI W 1.09 mm; HZM 18.37499 trigonid m1-3 dex. TRI W 0.90 mm; HZM 21.37706 trigonid m1-3 sin. TRI W 1.02 mm; HZM 21.38616 trigonid m1-3 dex. TRI W 1.02 mm; HZM 17.35188 part trigonid m1-3 dex. TRI W 1.02 mm; HZM 5.31829 trigonid m1-3 sin. TRI W 1.09 mm; HZM 6.32004 trigonid m1-3 dex. TRI W 1.02 mm; HZM 7.32445 trigonid m1-3 dex. TRI W 0.96 mm; HZM 8.32768 trigonid m1-3 sin. TRI W 1.09 mm (Fig. 4a, b); HZM 20.37639 trigonid m1-3 dex. TRI W 0.99 mm; HZM 21.38616 trigonid m1-3 dex. TRI W 1.02 mm; HZM 14.34523 trigonid m1-3 dex. TRI W 0.99 mm; HZM 19.36945 talonid m1-2 sin. TAL W 0.90 mm; HZM 3.31796 talonid m1-2 sin. TAL W 0.90 mm (Fig. 4c, d); HZM 17.36399 talonid m3 sin. TAL W 0.80 mm.




◆ M1-2 *Saturninia mamertensis* (Robiac nord/sud)
■ M1-2 *Saturninia* aff. *mamertensis* (Creechbarrow)

**Figure 2**. M1-2 dimensions of *Saturninia mamertensis* Sigé, 1976 from Robiac and *S.* aff. *mamertensis* Sigé, 1976 from Creechbarrow.

*Description and discussion* – These specimens indicate the presence of a very small nyctithere, distinctly smaller than *Euronyctia grisollensis* (Sigé, 1976) or *Saturninia gracilis* Stehlin, 1940. HZM 11.34232 is a complete M1-2 dex. It is rather heavily worn and rolled, but a thin layer of enamel persists, as can be seen from the enamel ring round the tip of the paracone cusp. It differs strikingly from this element in both *Saturninia gracilis* and *Euronyctia grisollensis* on account of its pronounced transverse elongation and very narrow mesio-distal dimensions producing a length- width ratio of 1.97, rather in excess of this ratio in *Saturninia mamertensis* from Robiac to which the Creechbarrow form shows a number of marked similarities (see below). The paracone and metacone are close together, the centrocrista lacking any trace of dilambdodonty. Although the tip of the paracone is slightly worn it is clearly dominant, exceeding the metacone and the protocone in height.

A distinct paraconule forms a slight bulge on the mesial crown margin, but there is no trace of a metaconule on the postprotocrista. A very feeble precingular cusp is present and the hypocone is very small, the hypoconal lobe scarcely projecting behind the protocone. The postflexus is long and shallow, the ectoflexus scarcely evident. A relatively deep hollow is present between the pre- and postprotocone cristae. Cingula are not developed apart from a very slight indication on the disto-lingual side of the metacone.The metastyle is pointed and curved, projecting further than the short blunt parastyle.

Four other examples of the protocone lobe of M1-2 are present, showing significant variation from the complete specimen above. In each the protocone is high, but the hypocone is feebly developed and the hypoconal lobe is short, forming only a shallow emargination behind the protocone.

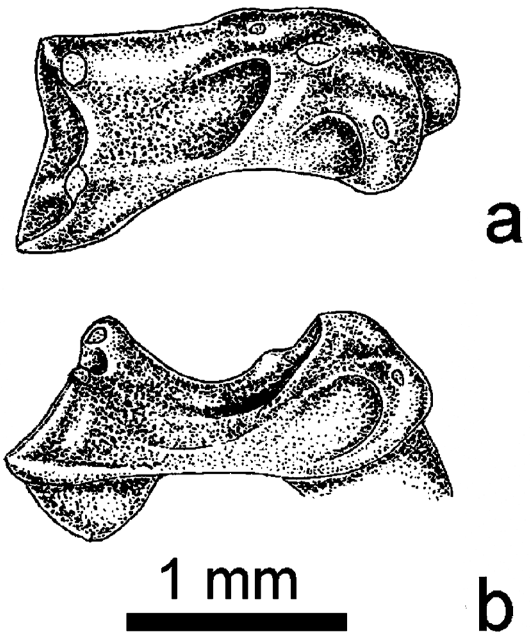



**Figure 3**. *Saturninia* aff. *mamertensis* Sigé, 1976; HZM 11.34232 M1-2 dex.; a: occlusal view; b: distal view.

In each case a distinct paraconule is present on the preprotocrista, better developed in HZM 4.31754, but there is no trace of a metaconule on the postprotocrista, which is preserved to a point well beyond the paraconule. The buccal part of both specimens is missing, including the paracone and metacone. In HZM 1.31647 a very narrow precingular cusp is present in front of the protocone, but there is no trace of this cusp in HZM 4.31754. Both these protocone lobes are very similar in size to the complete M1-2 described above and appear to belong to the same taxon. These specimens agree in most respects with Sigé's (1976, p. 28; figs 21, 22) description of S*aturninia mamertensis,* including the feeble hypocone and poorly developed or absent precingular cusp, and contrast strongly with *E. grisollensis* and *S. gracilis.* The intact M1-2 agrees more closely with the figured M2 than the M1 in the maxilla RBN 6053 figured by Sigé, 1976 (fig. 21) but is even more transversely elongated and notably exceeds its width (CL 0.90 CW 1.50 Sigé, tab. 13).
Seven specimens are considered to be trigonids of p4, owing to the close proximity of the protoconid and metaconid. The best preserved, HZM 23.38025, has a distinct antero-buccal cingulum; the small paraconid is upturned and the trigonid is less compressed than those of m1-3. Twelve m1-3 trigonids are present of which HZM 5.31829 (m1-3 sin.) and HZM 8.32768 (m1-3 sin). are best preserved and referred on account of their small size and marked mesio-distal compression. The mesio-buccal cingulum is strong and the low paraconid directed strongly buccally. Only two talonids of m1-2 have been recovered, with low central hypoconulids. HZM 17.36399 is a talonid of m3 sin. tentatively referred here on account of its small size and prominent hypoconulid. HZM 3.31796 and HZM 19.36945 are talonids of m1-2 sin. compatible in size with the trigonids described above. The hypoconulid is central and low, the hypoconid larger and higher than the entoconid. The postero-labial cingulum is absent, which is often the case in *Saturninia mamertensis* (compare Sigé, 1976, p. 27). Although the available material is scanty and mostly fragmentary, the upper and lower molar specimens described here resemble in size and most morphological features the very small species *Saturninia mamertensis* described from Robiac Nord. The diagnostic features listed by Sigé (1976, p. 25) include the very small size, absent metaconule, feeble or absent precingular cusp of the non-dilambdodont M1-2; and mesio-distally compressed high trigonid of m1-2, with feeble or absent postero-labial cingulum.

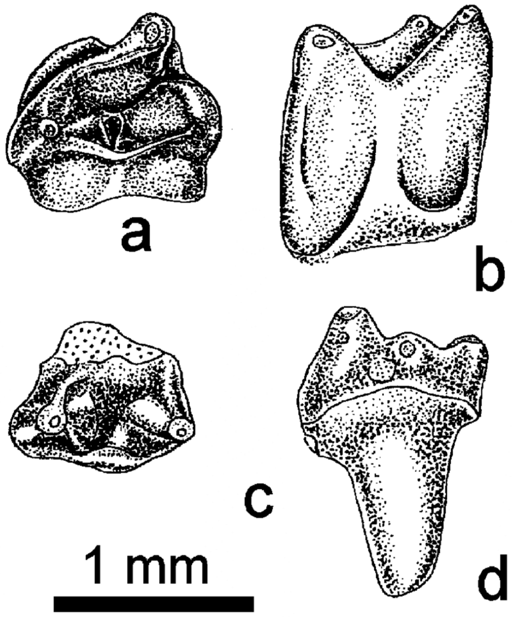



**Figure 4.** *Saturninia* aff. *mamertensis* Sigé, 1976 ; a, b: HZM 8.32768 trigonid m1-3 sin.; a: occlusal view; b: distal view; c, d: HZM 3.31796 talonid m1-2 sin.; c: occlusal view; d: distal view.

Some differences are, however, present in the complete Creechbarrow M1-2, which is very transversely elongated and narrow (Fig. 3). These differences may lead to consideration of a new specific identity for it, although it is most probably a closely related, perhaps descendant species, evolved in isolation in the British Eocene island.

Genus *Cryptotopos* Crochet, 1974 (*sensu* Hooker & Weidmann, 2000).

*Type species – Cryptotopos beatus* Crochet, 1974 (Quercy Phosphorites).

*Included species and emended diagnosis –* See Hooker & Weidmann (2000, p. 64).

***Cryptotopos hartenbergeri* (Sigé, 1976)**
Figures 5-7; Plate 2

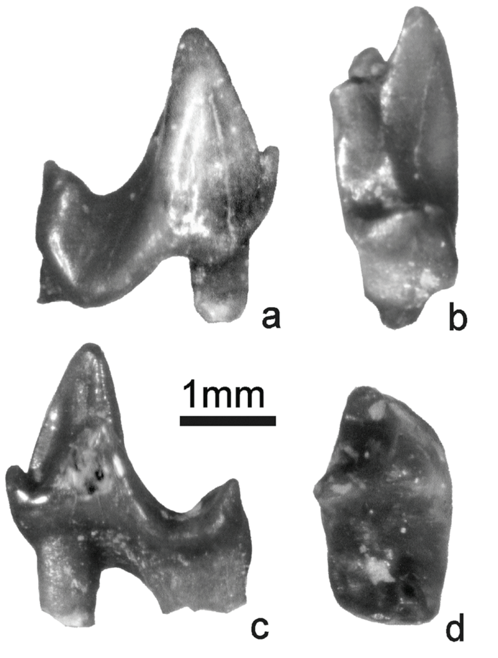



**Plate 2.** *Cryptotopos hartenbergeri* (Sigé, 1976); HZM 10. 35883 p4 dex.; a: buccal view; b: distal view; c: lingual view; d: occlusal view.

1976 *Saturninia hartenbergeri* Sigé, p. 38; figs 41-54; tabs 21, 22.
1968 *Saturninia* sp. 3 – Hartenberger *et al*., p. 22.
1969 *Saturninia* sp. 1 – Sudre, pp. 108, 109.
1986 *Scraeva* sp. indet. – Hooker, pp. 240-241, text-fig. 15A-J.

*Holotype* – RBS 130. Fragment of right mandibular ramus with c, p2 - m3 *in situ*. Robiac Sud, France (Sigé, 1976, fig. 42a-c).

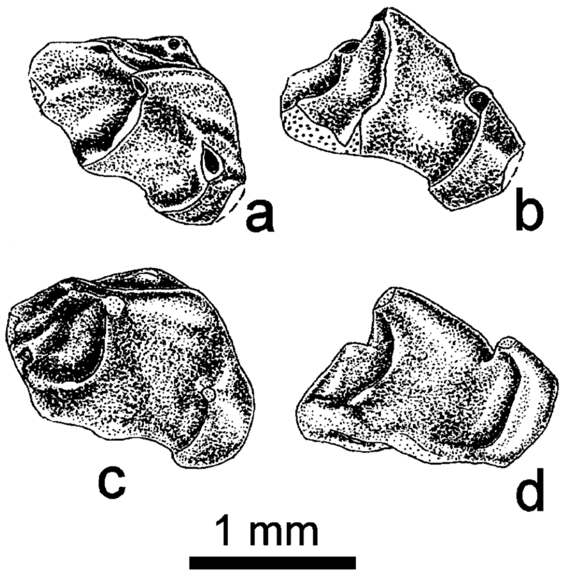



**Figure 5a-d**. *Cryptotopos hartenbergeri* (Sigé, 1976); lingual lobes of M1-2 dex.; a, b: HZM 7.35326; a: occlusal view; b: distal view; c, d: HZM 6.33938; c: occlusal view; d: distal view.

*Material* – HZM 21.377813 P4 sin. CL 2.21+ CW 2.88 mm; HZM 18.37592 P4 sin. CL 1.73 (e) CW 1.47 mm; HZM 14.36526 lingual lobe M1-2 sin. LLL 1.15 mm; HZM 5.31025 lingual lobe M1-2 sin. LLL 1.28 mm; HZM 6.33938 lingual lobe M1-2 dex. LLL 1.28 mm (Fig. 5c, d); HZM 4.32468 lingual lobe M1-2 sin. LLL 1.18 mm; HZM 8.33763 lingual lobe M1-2 sin. LLL 1.22 mm; HZM 3.32060 lingual lobe M1-2 sin. LLL 1.15 mm; HZM 7.35326 lingual lobe M1-2 dex. LLL 1.15 mm (Fig. 5a, b); HZM 9.35825 part lingual lobe M1-2 sin; HZM 20.377812 part p4 dex. TAL W 0.77 mm; HZM 1.35405 p4 dex. CL 1.54 TRI W 0.80 TAL W 0.86 mm (Fig. 6a-c); HZM 10.35883 p4 dex. CL 1.60 TRI W 0.90 TAL W 0.80 mm (Fig. 6d-f); HZM 19.37768 trigonid p4 dex. TRI W 0.83 mm; HZM 16.36846 trigonid p4 dex. TRI W 0.77 mm; HZM 13.36230 trigonid p4 sin. TRI W 0.90 mm (Fig. 7a-c); HZM 15.36527 trigonid p4 sin. TRI W 0.80 mm; HZM 12.34463 trigonid ?p4 sin. TRI W 0.86 mm; HZM 12.38292 dp4 sin. CL 1.66 TRI W 0.77 TAL W 0.70 mm; HZM 13. 34483 trigonid m1-2 dex. TRI W 1.02 mm; HZM 2.33830 m3 sin. CL 1.22 TRI W 0.90 TAL W 0.64 mm (Fig. 6g-i).

HZM 21.377813 and 18.37592 are P4's tentatively referred to this species. Both are damaged but the former has a notably distinct hypocone.

*Description and discussion* – **M1-2**: The eight lingual lobes of M1-2 listed above consistently exhibit the characteristic morphology of *Cryptotopos* as redefined by Hooker & Weidmann (2000, p. 64) in their emended diagnosis of the genus. These features include: precingulum well developed, usually with distinct protostyle; large rounded talon basally tilted with distinct hypocone; paraconule and metaconule strong; premetaconule crista well developed. Unfortunately no complete M1-2 has yet been found at Creechbarrow with the buccal cusps, styles and centrocrista. The size of these fragments is definitely smaller than *C. beatus* and allowing for the slightly greater buccal than lingual length of M1-2 in this genus the specimens seem very compatible with *C. hartenbergeri.*

**p4:** HZM 1.35405 is a p4 dex. which has been compared with a cast of the holotype, original RBS130, right mandibular ramus with c, p4 – m3 *in situ* and is considered referable to this taxon. The tooth is complete apart from missing cusp tips of the protoconid and metaconid. Its size corresponds with the upper limit of a series from Robiac listed by Sigé (1976, tab. 21). The trigonid and talonid are of equal width, the protoconid is dominant and the paraconid is small and low as in the holotype. The cristid obliqua does not ascend the posterior trigonid wall. The talonid cusps are distinct with the hypoconid closer to the median hypoconulid than the slightly reduced entoconid. The anterobuccal cingulum is distinct, the posterobuccal cingulum absent. HZM 10.35883 is a second example of p4 dex., better preserved with only the tip of the metaconid missing. It exhibits similar variation to that described by Sigé (1976, p. 40) in the French material. In this specimen, marginally larger than HZM 1.35405, the entoconid is completely lacking and both the anterobuccal and posterobuccal cingula are absent. The unworn protoconid is strikingly higher than those of p4 – m2 trigonids here referred to *S.* aff. *mamertensis.*

HZM 13.36230 (Fig. 7a-c) is a perfectly preserved trigonid of p4 sin. With the protoconid clearly higher than the metaconid, the paraconid low but distinct. The mesiobuccal cingulum is poorly developed, the cristid obliqua attached low down on the high, narrow distal wall. Four other specimens of p4 (HZM 20.377812 distal part of p4 dex., and trigonids HZM 16.36846, HZM 12.34463, HZM 19.37768 and HZM 15.36527) are tentatively referred here. Isolated trigonids are often broken off at different levels of crown height and cusp tips are frequently missing. Confusion with the similar sized *S. mamertensis* is therefore very possible and it seems inevitable that some mistaken assignments will be made.

**m3**: HZM 2.33830 (Fig. 6g-i) is a complete m3 sin. conforming in size with the series of this element reported by Sigé (1976, tab. 21) and also in its distinctive morphology with the holotype m3. The trigonid is very compressed mesiodistally; the paraconid appears virtually absent and the trigonid basin reduced to a narrow transverse fold. The protoconid and metaconid have their cusps worn but the protoconid is slightly dominant. The talonid is strikingly long and narrow relative to the trigonid; its cusps are worn, but the hypoconid is clearly larger than the entoconid and the hypoconulid. The cristid obliqua does not ascend the posterior trigonid wall; it is distinctly notched opposite the narrow waist of the tooth. The antero-external cingulum is narrow but distinct. Sigé (1976, p. 41) comments on the variability of this cingulum, stating that it may be more or less developed. The rather less prominent hypoconulid in the Creechbarrow specimen seems almost certainly due to its rather worn condition.

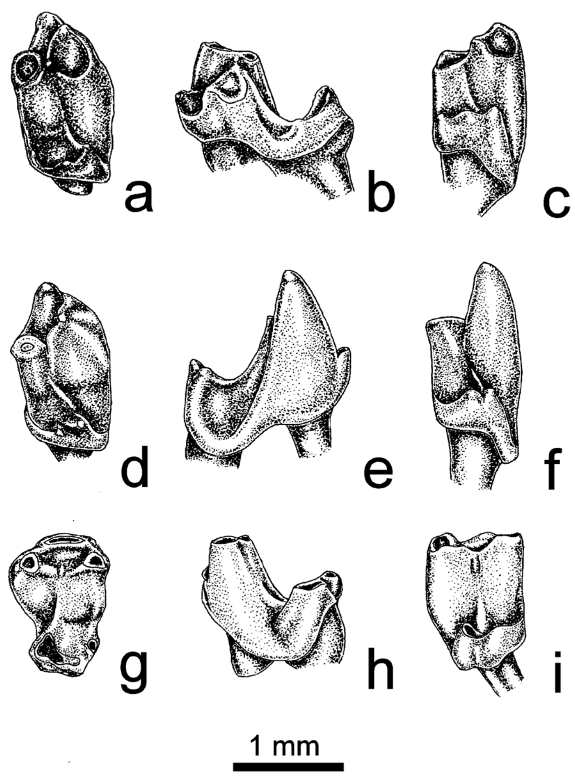



**Figure 6a-i.** *Cryptotopos hartenbergeri* (Sigé, 1976); a-c: HZM 1.35405 p4 dex.; a: occlusal view; b: lingual view; c: distal view; d-f: HZM 10.35883 p4 dex.; d: occlusal view; e: buccal view; f: distal view: g-i: HZM 2.33830 m3 sin.; g: occlusal view; h: buccal view; i: distal view.

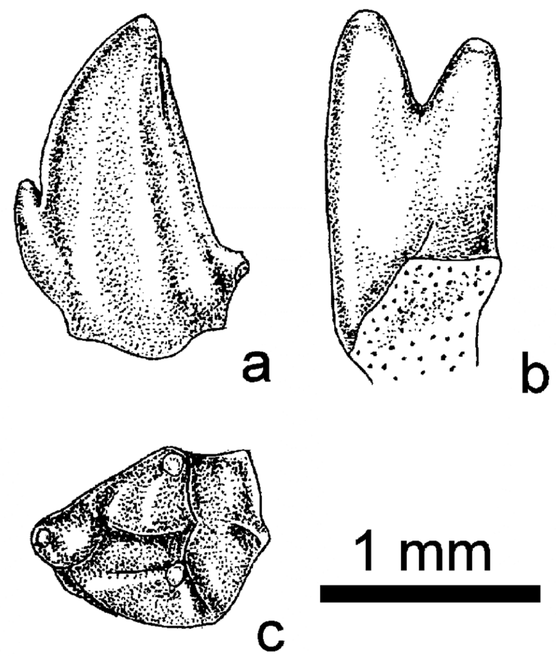



**Figure 7.** *Cryptotopos hartenbergeri* (Sigé, 1976); HZM 13.36230 trigonid p4 sin.; a: buccal view; b: distal view; c: occlusal view.

Two isolated trigonids (HZM 12.34463 ?p4 sin. and HZM 13.34483 m1-3 dex.) are tentatively referred here on account of their high protoconids. It may be noted that the CL and CW of *S. mamertensis* p4 – m3 fall into a similar size range as those of *C. hartenbergeri* (see Sigé, 1976, tabs 13, 21). The crown heights of the unworn protoconid and metaconid seem likely to be a reliable distinguishing character.

HZM 12.38292 is considered to be a dp4 sin. because of its very narrow crown and minute, low paraconid. The talonid is oblique, with the entoconid situated mesially. The tip of the metaconid is missing. It is tentatively referred here.

Following Hooker & Weidmann's (2000, p. 64) reinstatement and redefinition of this genus it has become clear that the fragmentary teeth from Creechbarrow previously referred by Hooker (1986, p. 240; fig.15A-J) to *Scraeva* sp. indet. are in fact referable to *Cryptotopos.* The new Creechbarrow material, including complete p4's and m3 and the series of lingual lobes of broken M1-2's has enabled a firm identification of this taxon as *Cryptotopos hartenbergeri*.

Order Primates Linnaeus, 1758
Suborder Strepsirhini Geoffroy St. Hilaire, 1812
Family Adapidae Trouessart, 1879 (*sensu* Hill, 1953)
Subfamily Adapinae Trouessart, 1879 (*sensu* Hill, 1953)
Genus *Adapis* Cuvier, 1822

*Type species – Adapis parisiensis* de Blainville, 1849.

***Adapis laharpi* (Pictet & Humbert, 1869)**
Figures 8a-c, 9

- 1869 *Lophiotherium Laharpi* Pictet & Humbert, pp. 166, 167, pl. 23, fig. 6a-e.
- 1869 *Lophiotherium Laharpii* Pictet & Humbert – Harpe, p. 466.
- 1873 *Lophiotherium Laharpii* Pictet & Humbert – Major, pp. 122, 124; pl. 6.
- 1912 *Adapis parisiensis* Cuvier (*sensu* Stehlin, pp. 1236, 1237; pl. 22, fig. 15).
- 1977 *Adapis laharpei* (Pictet & Humbert) – Gingerich, pp. 71, 77, fig. 8.
- 1979 *Adapis parisiensis* Cuvier (*sensu* Szalay & Delson, p. 139).
- 1984 *Cryptadapis*? *laharpei* Pictet & Humbert (*sensu* Godinot, p. 1292).
- 2000 *Adapis laharpi* (Pictet & Humbert) – Hooker & Weidmann, pp. 68-69; fig. 42.

*Holotype* – Left ramus fragment with m1–m3 (MGL 40455: LM 1261a) from Eclépens Gare, Switzerland, until now the only specimen representing this species, since Stehlin's M1-2 fragment (LM 1262) could not be found and remains unillustrated (Hooker & Weidmann, 2000, p. 68).

*Diagnosis* – See Hooker & Weidmann (2000, p. 68). The salient points are discussed below in comparison with the new specimen from Creechbarrow.

*Material* – HZM 1.34240 ?m2 dex. CL 5.89, TRI W 3.07, TAL W 3.46 mm (Fig. 8a-c ).

*Description and discussion* – The elongated form of HZM 1.34240 compares well with a cast of the holotype jaw fragment (MGL 40455) in the collection of NHMUK. Its measurements differ slightly, conforming better with the holotype m2 than with the m1. It is considered most likely to be an m2. Like the holotype the tooth is notably low-crowned, with the cusp tips rather more worn. Preservation of some parts of the crown in the Creechbarrow specimen is poor, the buccal and lingual aspects of the cristid obliqua with particularly badly corroded enamel.

The specimen has a more evenly rounded crown mesially, lacking the distinct mesial projection of the trigonid present in the holotype, as noted in the emended diagnosis of Hooker & Weidmann (2000, p. 68). The paracristid is, however, quite strongly curved at its lingual extremity as in the holotype. The paraconid appears to be relatively larger and more directly in front of the protoconid in the Creechbarrow specimen, but the rather advanced wear renders comparison difficult. The metaconid is similarly close to the lingual crown margin and has a very similar prolonged, straight postmetacristid. This terminates close to the sloping base of the entoconid, forming a distinct notch. A low preentoconid cristid is present, almost obliterated by wear. No metastylid is developed on the postmetacristid. The larger hypoconid is situated distinctly mesial to the entoconid. No trace of a hypoconulid can be discerned, although enamel erosion could have eliminated a small cusp.

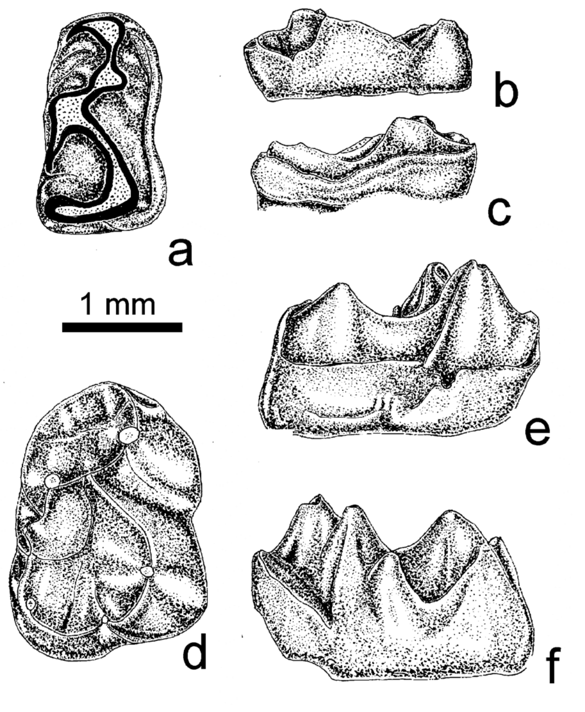



**Figure 8a-c**: *Adapis laharpi* (Pictet & Humbert, 1869), HZM 1.34240 ?m2 dex.; a: occlusal view; b: lingual view; c: buccal view. **8d-f**: *Leptadapis magnus* Filhol, 1874, HZM 33.25406 m1-2 dex.; d: occlusal view; e: lingual view; f: buccal view, Hordle Rodent Bed, Hordle, Hampshire.

The cristid obliqua joins the protocristid distinctly lingual to the midline and close to the metaconid, heavy wear of the latter cusp rendering comparison difficult.
As in the holotype a distinct buccal cingulum extends from the paraconid along the whole buccal margin of the crown, becoming indistinct behind the hypoconid, where there is significant enamel erosion, but a narrow postcingulid was apparently present. No cingulum is present on the lingual border and the pre-entoconid cristid makes direct contact with the postmetacristid.
The essentially similar morphology and proportions of the Creechbarrow m2 to the holotype render it unlikely that the elongation of the molars is due to diagenetic compression (Stehlin, 1912) and the presence of other distinctive diagnostic characters is confirmed. Measurements of the Creechbarrow m2 agree quite closely with those of the m2 of the holotype [CL 6.2 TRI W 3.0 TAL W 3.2 mm (Hooker & Weidmann, 2000, tab. 13)]. Although still little known, the taxon cannot simply be dismissed as a synonym of *Adapis parisiensis* (Cuvier, 1821 – see Szalay & Delson 1979, p. 139). Possible confusion with a dp4 of *Leptadapis magnus* Filhol, 1874 (Fig. 8d-f) has to be borne in mind, but this element does not appear to be well known.

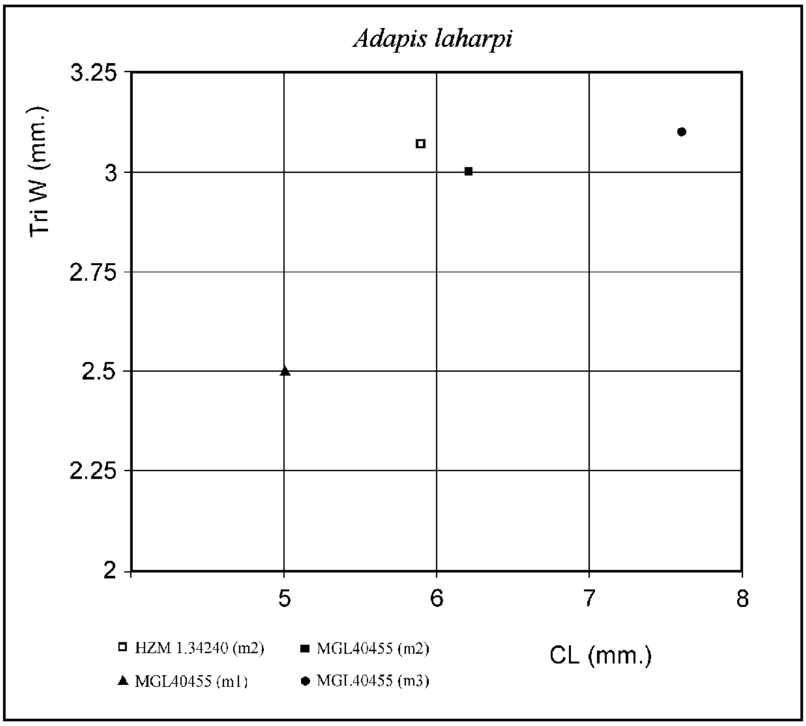



**Figure 9.** *Adapis laharpi* (Pictet & Humbert, 1869). Dimensions of lower molars in mm. Trigonid width (TRI W) plotted against crown length (CL).

Hooker & Weidmann (2000, p. 68-69) discuss the uncertain affinities of this little known species within the Adapinae. This is only the second specimen to be referred to the taxon. Clearly further material is required, especially upper molars. Meanwhile the Creechbarrow specimen represents the first from the British Eocene.

Order Rodentia Bowdich, 1821
Infraorder Protrogomorpha von Zittel, 1893
Family Ischyromyidae Alston, 1876(= Paramyidae Miller & Gidley, 1918)
Subfamily Pseudoparamyinae Michaux, 1964
Genus *Plesiarctomys* Bravard, 1850

*Type species – Plesiarctomys gervaisii* Bravard, 1850.

***Plesiarctomys curranti* Hooker, 1986**
Figures 10b, 11

1986 *Plesiarctomys curranti* Hooker, p. 283.
1977 *Plesiarctomys* sp. 2 – Hooker, p. 141.
1980 *Plesiarctomys* sp. 2 - Hooker & Insole, p. 39.

*Holotype* – Right m1, M37188 (NHMUK), Hooker (1986, pl. 13, fig. 6; text-figs 29, 30A). Creechbarrow Limestone Formation, Creechbarrow.
*Diagnosis* – see Hooker (1986: 284).

*Material* – HZM 3.31221 P4 dex. CL 3.84 CW 4.58 mm (Fig. 11c, d); HZM 7.36873 M1-2 dex. (?M2) CL 3.58 CW 4.22 mm; HZM 12.38060 M1-2 sin. (?M2) CL 3.39 CW 3.90 mm; HZM 8.37210 ? mesial part m1-2 sin. AW 3.65 mm; HZM 5.34824 M3 sin. CL 3.56 CW 3.71 mm (Fig.11a, b); HZM 13.39270 M3 dex. CL 3.85 CW 3.78 mm; HZM 85.33919 p4 dex. CL 2.82 CW 2.53 mm; HZM 10.37700 p4 dex. CL 3.07 CW 2.43 mm; HZM 6.36838 m2 sin. CL 3.45 CW 3.20 mm (Fig.10b).

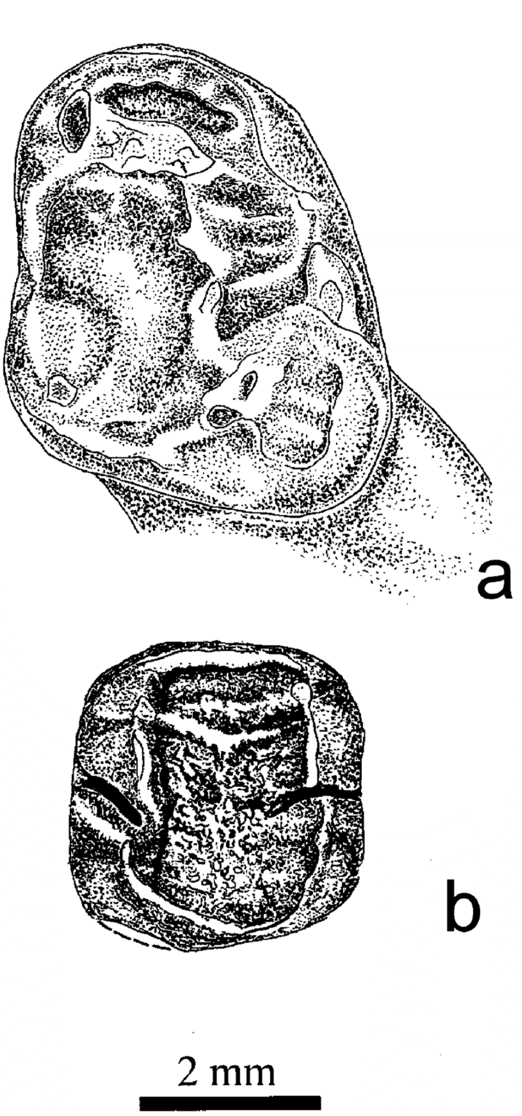



**Figure 10a-b.** Lower cheekteeth of *Plesiarctomys* from the Creechbarrow Limestone Fm.; a: *Plesiarctomys huerzeleri* Wood, 1970. HZM 1.35941 dp4 dex.; occlusal view; b: *Plesiarctomys curranti* Hooker, 1986. HZM 6.36838 m2 sin.; occlusal view.

*Description and discussion* – HZM 3.31221 P4 dex. is well preserved and shows only light to moderate wear of the principal cusps. It is a robust tooth, falling into the same size range as the known upper molars of the species described by Hooker (1986, text-fig. 29). The ovoid outline of the crown differs from the squarish or subrectangular M1-2 and quite strikingly from the subtriangular M3 illustrated in Hooker's (1986, pl.13, fig. 3) original description. The cusps are notably bunodont, the protocone forming part of a long arcuate endoloph crest, on which a hypocone cannot be distinguished. The smooth and rounded lingual slope from the endoloph is fissured by a linear area of enamel damage. The paracone and metacone are subequal and although the cusp apices are flattened by moderate wear, they appear to have been subequal in height. A striking feature of this tooth is the large size of the metaconule, clearly dominating the much smaller paraconule and encroaching into the narrowed protofossa; it is separated from the metacone and endoloph by narrow fissures. Both the conules are obliquely elongated anteroposteriorly. The anterior and posterior cingula form broad shelves; the buccal cingulum is a narrow margin without any distinct mesostyle. The tooth is three-rooted, the internal root dominant. The enamel is finely rugose, with a number of small pits in the protofossa and cingular shelves, which may be partly traumatic. HZM 7.36873 is a very worn M1-2 dex. (?M2) of which the metacone is slightly damaged and enamel extensively denuded. HZM 12.38060 is a heavily worn M1-2 sin. with only remnants of the protocone and hypocone remaining on the endoloph; the basal outline of a large metaconule can be discerned on the metaloph, the crown structure is otherwise erased by wear.

HZM 5.34824 is a complete M3 sin. The paracone is the only unworn principal cusp, the metacone clearly reduced and smaller. The metaloph is slender, with two low and rounded metaconules extruding, the lingual one larger. The protoloph is heavily excavated by wear, so that the size of the protoconule cannot be determined. The mesostyle is long and low and there is no mesoloph in the finely wrinkled crown basin. The tooth is readily distinguished from the M3 of *Patriarchamys batesi* Harrison, 2006 by its robust, globose appearance and less elongated shape.

HZM 13.39270 is a more heavily worn M3 dex. with little traces of the crests and conules remaining. The paracone and metacone are reduced to narrow ridge-like remnants buccally, with a small projecting mesostyle. A shallow indentation marks the lingual sinus and in this specimen there is a narrow buccal cingulum, bordering the paracone, lacking in HZM 5.34824. This is clearly variable and not a diagnostic feature of *P. curranti* as suggested by Hooker (1986, p. 287).

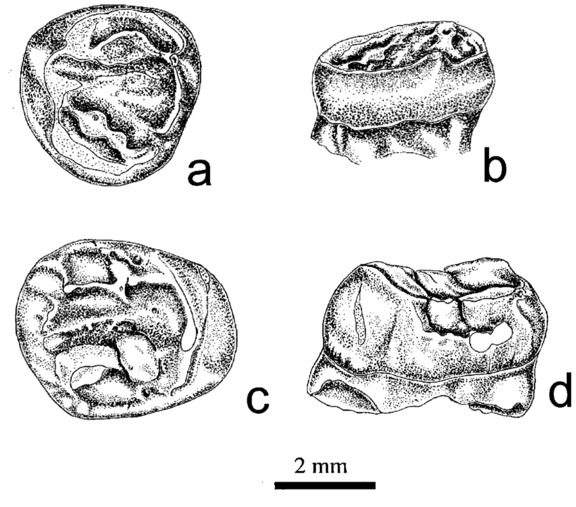



**Figure 11a-d.** Cheekteeth of *Plesiarctomys curranti* Hooker, 1986 from the Creechbarrow Limestone Formation; a, b: HZM 5.34824 M3 sin.; a: occlusal view; b: buccal view; c, d: HZM 3.31221 P4 dex.; c: occlusal view; d: distal view.

Two examples of the dp4 dex. HZM 10.37700 and HZM 85.33919 are both slightly damaged mesially and the hypolophid of each is lacking; the crown basin of HZM 85.33919 is finely wrinkled and both are bluntly triangular in outline; the ectolophid of HZM 85.33919 is complete, that of HZM 10.37700 was probably complete before wear.

HZM 6.36838 is the second known m2 of the species. It is well preserved apart from minor damage to the distobuccal and distolingual crown margins. It is unworn. The metaconid is the highest of the four well-spaced cusps. The anterolophid is strong, the metalophid irregularly divided into two parts of which the distal metalophid 2 is slightly stronger. There is no hypolophid and the posterolophid is narrow and lacks any hypoconulid. The ectolophid is complete, the mesoconid scarcely detectable, as in Hooker's (1986, pl. 13; fig. 7) M35450. A deep fissure lingually separates the postmetacristid from the entoconid. The talonid basin is extensively covered by fine reticulate wrinkling of the enamel. The sinusid is deep and narrower than M35450, which appears to have a single metalophid (Hooker, 1986, pl. 13; fig. 7). The cheekteeth of *Plesiarctomys* are often heavily worn and difficult to interpret, particularly when damaged. They are readily recognisable, however, by the combination of robust size, low cusps, and other details noted in Hooker's (1986, p. 284) diagnosis.

***Plesiarctomys huerzeleri*** **Wood, 1970**
Figure 10a

1970 *Plesiarctomys huerzeleri* Wood, pp. 255-257, figs 5-6.
1977 *Plesiarctomys* sp.1 – Hooker, p. 141.
1980 *Plesiarctomys* sp.1 – Hooker & Insole, p. 39.
1986 *Plesiarctomys hurzeleri* Wood, 1970 – Hooker, pp. 288-290; pl.14, figs 1-3.
2000 *Plesiarctomys gervaisii* Bravard, 1850 and *P. huerzeleri* Wood, 1970 – Hooker & Weidmann, p. 24.

*Holotype* – Left mandibular ramus with m1 – m2 (FSL 4012), Lower Calcaire de Fons, Robiac, Gard, France. Robiacian.

*Range and emended diagnosis* – See Hooker (1986, p. 288).

*Material* – HZM 1.35941 dp4 dex. CL 4.69 CW 3.90 mm (Fig.10a).

*Description and discussion* – HZM 1.35941 is considered to be a dp4 on account of its high length/ distal width ratio of 1.2 and the complete ectolophid, both features of this element noted by Hooker (1986, p. 285) in the dp4 of *P. curranti*. The only previously known dp4 of *P. curranti* (M35764 Hooker, 1986, pl. 13, fig. 4) is substantially smaller. The tooth is only moderately worn and quite well preserved. The metaconid is the largest trigonid cusp, with a distinct metastylid extending from it along the lingual border to meet the well developed entoconid at a sharp notch. The protoconid is reduced, extending as an oblique transverse crest from the metaconid, without any distinct cusp.
The hypoconid is the dominant, relatively massive cusp, the ectolophid extending mesially from it, bearing a worn mesoconid. The latter has a low buccal crest, which does not, however, extend to the buccal crown margin, which is occupied by a prominent ectostylid.
The hypoconulid is small, represented by a nodular thickening of the postcristid, close to the hypoconid and merging with it. There is no hypolophid; the talonid basin contains some irregular nodules and wrinkles. The anterior cingulid is thickened and defined from the protocristid by a well marked groove.Hooker (1986: 288-290) considered size to be the only valid difference between this and the earlier named *P. gervaisii* Bravard, 1850, which Wood (1970) had maintained as distinct. *P. gervaisii* is a stratigraphically later Ludian form.
Hooker & Weidmann (2000, pp. 24-25) have reviewed this problem and show (p. 26, fig. 17) the size variation of different elements of the two species from different localities. It is noteworthy that HZM 1.35941) plots close to the three P4's from Eclepens Gare ?, Quercy and La Debruge and far from the large P4 from Eclepens A commented upon by Hooker & Weidmann (2000, p. 25), which does not conform to the time-linked size increase.
These authors concluded that *P gervaisii* and *P. huerzeleri* are almost certainly part of a single evolving lineage and that *P. huerzeleri* should probably be reduced to the rank of a stratigraphical subspecies. It is significant therefore that *P. curranti* and *P. huerzeleri* both occur in the Creechbarrow Limestone Formation, but *P. gervaisii* does not.

***Plesiarctomys*** sp. indet.

*Material* – HZM 1.31219 incisor fragment; HZM 2.31220 incisor fragment; HZM 3.32269 incisor fragment; HZM 4.32302 incisor fragment; HZM 5.32734 incisor fragment; HZM 8.33441 upper incisor fragment; HZM 9.34213 part lower incisor; HZM 11.36149 lower incisor tip; HZM 12.36231 incisor tip; HZM 11.37925 incisor fragment; HZM 13.37019 incisor fragment; HZM 9.34609 incisor fragment; HZM 14.38757 incisor fragment.

*Remarks* – These specimens include two pairs of incisor fragments, which in each case may have originated from the same tooth, although they do not fit each other. They are, however, compatible in size and shape and the teeth have often split longitudinally through the pulp cavity, leaving only one side of the surface. They are readily distinguishable from those of *Sciuroides rissonei* Hooker, 1986 by their much larger size, and from those of *Ailuravus* by their rectangular mesio-lingual angle and less rounded cross section (Hooker, 1986; text-fig. 30C-E, J-K).
Order Creodonta Cope, 1875

Family Hyaenodontidae Leidy, 1869
Subfamily Proviverrinae Matthew, 1909
Genus *Allopterodon* Ginsburg *in* Ginsburg *et al*., 1977

*Type species* – *Prodissopsalis phonax* van Valen, 1965b.

***Allopterodon minor* (Filhol, 1877) *sensu* Lange-Badré & Mathis, 1992**
Figure 12

*Material* – HZM 1.36450 buccal fragment M1 sin. CL [parastyle to metacone 3.84 mm. Parastyle to metastyle 4.48 mm (Fig. 12a-b)].

*Description and discussion* – In this specimen, the metacone and metastyle are complete as well as the parastyle. The paracone is missing, as are the protocone lobe and conules. In lingual view the metacone is conical and high, separated by a deep notch from the sharp, blade-like metastylar wing. The cutting edge of the metastylar blade is almost horizontal. The basal area of the paracone is almost equal to that of the metacone. The parastyle projects at a right angle to the metastyle. A feeble cingulum between the parastyle and metastyle is partly eroded. A small part of the metaconule is preserved mesial to the metacone. The parastyle is crested buccally. The paracone and metacone are evidently situated close together at their contiguous bases.

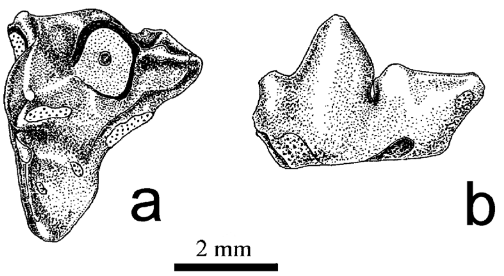



**Figure 12a-b.** *Allopterodon minor* (Filhol, 1877); HZM 1.36450 buccal part of M1 sin.; a: occlusal view; b: buccal view.

This M1 fragment closely resembles a similar broken M1 (MGL40936) described from Mormont (Eclépens, probably fissure B) by Hooker & Weidmann (2000, p. 75, fig. 47c, d) associated with an intact M2 (MGL 47337, probably from the same fissure. Although no useful measurements could be taken from the incomplete Mormont M1, the M2 is 4.4 mm long measured parallel to a line drawn between the paracone and metacone and 7.5 mm in maximum width measured at right angles to the length. The length of the Creechbarrow specimen measured in the same way is 3.84 mm so that its size is clearly compatible with the Mormont specimen.
Apart from Mormont, this little known creodont is known from Le Quercy [MP 16 and 17 sites of Lavergne, Salème, Les Clapiès, Le Bretou, Malpérié and La Bouffie (Lange-Badré & Mathis, 1992)]. It is also known from Robiac (Mathis, 1985) as *Prototomus* ? aff. *minor*.
Lange-Badré & Mathis (1992, p. 172) transferred this taxon from *Prototomus* to *Allopterodon.* The Creechbarrow specimen extends its range to the British Robiacian, where it appears to be exceedingly rare.

Order Carnivora Bowdich, 1821

Family Miacidae Cope, 1880
Genus *Paramiacis* Mathis, 1985

*Type species* – *Paramiacis exilis* (Filhol, 1876) (see Mathis, 1985, p. 313; Mathis, 1987, p. 316; Teilhard de Chardin, 1888, p. 112, fig. 2B).

*Included species* – *Paramiacis teilhardi* Mathis, 1987.

*Generic diagnosis* – See Mathis (1987, p. 314).

***Paramiacis exilis* (Filhol, 1876)**
Figures 14, 15d-f, 16

1876 *Cynodictis exilis* Filhol, p. 139; figs 97-101.
1888 ? *Miacis exilis* (Filhol, 1876) – Teilhard de Chardin, pp. 112-113; pl. 1, figs 1, 2, 5, 6.
1964 *Miacis exilis* (Filhol, 1876) – Guth, pp. 359-365; fig. 1, pls xv, xvi.
1977 Miacidae indet. – Hooker, p. 141.
1980 Miacidae indet. – Hooker & Insole, p. 41.
1986 ? *Miacis* sp. indet. – Hooker, p. 336; text-fig. 41A-U.

*Diagnosis* – See Mathis (1987, p. 314).

*Lectotype* – Left mandibular ramus with p2–m3 *in situ.* Qu 8752 Muséum national d'Histoire naturelle, Paris, designated by Mathis (1987, p. 316, fig. 1a, b.), figured by Teilhard de Chardin (1915, fig. 2B).

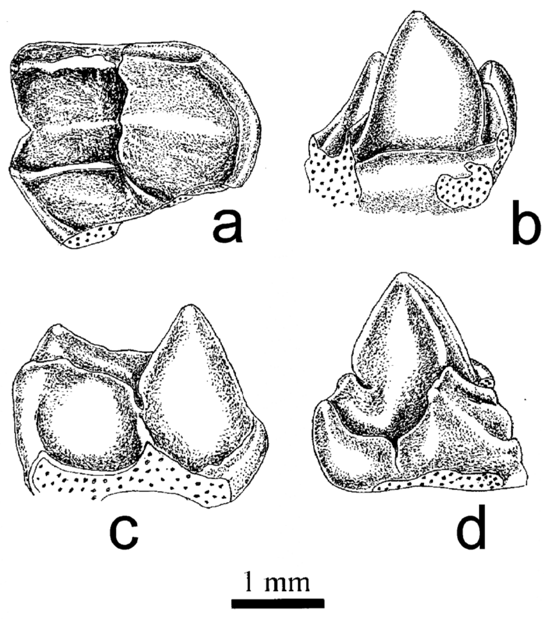



**Figure 13a-d**. *Paramiacis teilhardi* Mathis, 1987; HZM 3.38849 trigonid m2 dex.; a: occlusal view; b: buccal view; c: distal view; d: lingual view.

*Stratigraphic range* – Early Robiacian to early Ludian (Egerkingen, Switzerland to Robiac, France). Both species of *Paramiacis* are here considered to occur at Creechbarrow. Few specimens of isolated teeth, however, can be confidently referred to each as listed below. The remainder are treated as *Paramiacis* sp. indet. The description and discussion section below embraces all the Creechbarrow material referred to the genus.

*Material of Paramiacis exilis* – HZM 13.36847 lingual fragment M1-2 dex. CL (at protocone) 2.05 mm; HZM 12.36656 lingual fragment M1-2 dex. CL (at protocone) 2.18 mm (Fig. 14a); HZM 5.32740 trigonid m1 dex. TRI W 2.69 TRI L 2.75 mm (Fig. 15d-f); HZM 9.34053 trigonid m1 sin. TRI W 2.82 TRI L 2.50 mm; HZM 11.34417 trigonid m1 dex. TRI W 2.82 TRI L 2.69 mm; HZM 3.31333 m2 dex. CL 2.88 TRI W 1.82 TAL W 2.02 mm (Fig. 14b-d); HZM 3.38849 trigonid m2 dex. TRI W 2.56 mm (Fig. 13a-d).

***Paramiacis teilhardi* Mathis, 1987**

Figure 13, 15a-c

1915 *Miacis exilis* (Filhol) forme A - Teilhard de Chardin, pp. 112-113, fig. 2A; pl. 1, fig. 5.
1964 *Miacis exilis* (Filhol) – Guth, p. 359-365; pl. 16 (*partim*).
1985 *Paramiacis exilis* (Filhol) forme A – Mathis, p. 324; figs 7, 11-14, 16-17.
1987 *Paramiacis teilhardi* Mathis, p. 316; figs 2, 5, 8; tab. 4.

*Diagnosis* – See Mathis (1987, p. 316).

*Holotype* – Left mandibular ramus with alv. p1, p3; p2, p4, m1- m3 *in situ.* Natural History Museum, Montauban (France). Teilhard de Chardin (1915, fig. 2A), Mathis (1987, fig. 2a, b).

*Type locality* – Phosphorites du Quercy.

*Stratigraphic range* – Robiacian to early Ludian (Robiac to Perrière, France).

*Material* – HZM 1.35504 trigonid m1 sin. TRI W 3.52 TRI L 3.20 mm (Fig. 15a-c); HZM 2.30732 part trigonid m1 dex. (two fragments restored) TRI L 3.52 mm (Fig. 16f); HZM 3.38849 trigonid m2 dex. TRI W 2.56 mm (Fig. 13a-d).

***Paramiacis* spp. indet.**

*Material* – HZM 12.36909 I1 or 2 CL 1.60 CW 1.41 mm; HZM 11.36470 ?I3 CL 1.41 CW 1.25 mm; HZM 1.30592 I1 or 2 CL 1.47 CW 1.41 mm; HZM 8.33843 I1 or 2 CL 1.60 CW 1.38 mm; HZM 6.32831 ?I3 sin. CL 1.47 CW 1.54 mm; HZM 13.35511 ?I3 CW 1.44; HZM 12.35260 I3 sin.?CL 1.60 CW 1.34 mm; HZM 10.34054 I1 or 2 CW 1.47 mm; HZM 4.31539 ?upper canine tip and part shaft CL 2.18 (e) CH 4.86 mm (e). (Fig. 16a).

*Description and discussion* – Eight incisors are referred to this genus. Three tooth types are recognisable: tall and unicuspid, with laterally compressed root (HZM 10.34054, HZM 8.33843); bicuspid with prominent distal lobe (HZM 1.30592 and HZM 12.36909) and incisors with a triangular crown and a single prominent cusp situated near the straight ? internal margin and a deep hollow alongside the cusp, the rim of the crown thickened and triangular (HZM 6.32831, HZM 11.36470, HZM 13.35511 & HZM 12.35260). The last four seem likely to be outer incisors, possibly I3's. They are smaller than the others which may be I1 or I2. It is clearly not possible at present to assign these isolated incisors to either species. According to Guth (1964, p. 360) the third upper incisor of the type skull is stronger and longer than I2 and I3, which are the same size. HZM 12.36656 is a lingual fragment of M1-2 dex. It is marginally larger than HZM 1.19546, an intact M1 dex. from the lignitic clay below the How Ledge, Headon Hill, Isle of Wight. It is low crowned, but much less worn than the intact specimen. The paraconule is preserved and separated from the preprotocrista by a distinct notch. The metaconule is less prominent. The enamel is pitted and rough close to the broad lingual cingulum. The lingual lobe measures 2.18 mm a–p at the protocone and the specimen is not considered large enough to represent *P. teilhardi*. No hypocone is present in this specimen, evidently a variable feature (Mathis, 1987, p. 316); the mesial and distal cingula are strong.

HZM 13.36847 is a second very similar lingual fragment of M1-2 dex. of very similar size and consisting of the same preserved elements. The absence of any hypocone may help to identify these lingual fragments as M1 or M2, although the hypocone is not always present in M1 and they may not be so easily distinguishable from M3. The M2 is deceptively variable (Mathis, 1987, p. 320). It is noteworthy that both these lingual fragments of M1-2 are very slightly larger than the intact specimen from Headon Hill, which is considered to be an M1.

HZM 4.31539 (Fig. 16a) is a canine tip and incomplete shaft, the curvature of which is rather more suggestive of an upper than a lower canine. It was found in association with the trigonid fragment of an m1 dex. (HZM 2.30732 *P. teilhardi*; Fig. 16f) and is tentatively referred to *Paramiacis.* The latter specimen is composed of two restored fragments here interpreted as the metaconid and part paraconid of a right m1, from which almost all the talonid and protoconid have broken away. The tooth was much larger than the m2 described below; the paraconid and metaconid are subequal in height. The posterior face of the metaconid rises steeply from the talonid, of which only a small fragment remains at its base lingually. HZM 1.35504 (Fig. 15a-c) is a well preserved trigonid of m1 sin. Its robust size slightly exceeds the figures given by Mathis (1987, tab 3) for *P. teilhardi*, to which taxon it is here referred (see the following paragraph). HZM 5.32740 is a smaller and intact trigonid of m1 dex. It is very similar in size and morphology to the m1 trigonid described by Hooker (1986, text-fig. 41A-C), with damaged metaconid. The protoconid dominates the subequal paraconid and metaconid. The paraconid is similarly keeled anteriorly, the posterior trigonid wall is vertical with the cristid obliqua attached low down beneath the protoconid-metaconid notch; the anterobuccal cingulum is short.

HZM 9.34053 is another very similar m1 trigonid, differing only in slightly different length-width proportions, consistent with individual variation. The m2 dex. (HZM 3.31333; Fig.14b-d) is intact and better preserved although with denuded enamel. It has two transverse roots, the posterior one much more robust. The trigonid is antero-posteriorly compressed, but with a broadly ovoid and smooth trigonid basin, the cusps subequal in height and sharply pointed. The large talonid is characteristically oblique with a marked buccal curvature and high lingual crest, on which no trace of an entoconid or hypoconulid is present; the talonid basin is smooth and concave. A low hypoconid forms a sharp angulation at the projecting disto-buccal corner of the talonid. A low cristid obliqua extends from the hypoconid to a point near the median base of the distal trigonid wall. There is no trace of a cingulum on the lingual aspect of the crown and only a faint indication buccally below the talonid, continuing anteriorly as a narrow ledge towards the base of the protoconid. Details of the cingulum may be obscured by enamel loss.The species *Cynodictis exilis* Filhol, 1876 was further described by Teilhard (1915). Guth (1964) made a new detailed study of the skull and associated mandible after extraction from matrix. Variation in size of the six rami from the Phosphorites du Quercy had led Teilhard (1915) to distinguish two forms, larger (A) and smaller (B). Guth believed these to be well within the range of individual variation in a single species and was able to describe in detail and figure the upper dentition, except for the canine and M3 as well as the lower dentition except for the incisors. Mathis (1985, p. 313) erected the new genus *Paramiacis* and transferred *Cynodictis exilis* Filhol, 1876 to it as type species. Mathis later (1987, p. 316) described a larger species from the French upper Eocene of Quercy as *Paramiacis teilhardi* (= Form A of Teilhard).

The holotype of *P. teilhardi* was designated by Mathis (1987, p. 317) as a left ramus in the Montauban Museum with p2, p4 and m1 – m3 *in situ*. The lectotype of *P. exilis* was at the same time designated as the left ramus from Quercy (QU 8752 Muséum national d'Histoire naturelle, Paris). Remains of miacid carnivores from Creechbarrow were first noted by Hooker (1977) and Hooker & Insole (1980). Hooker (1986, pp. 336-338; text-fig. 41) described isolated teeth, including an intact right P2, two fragmentary P4's a fragmentary right p4, three broken left m1 trigonids and a damaged left m2. He considered these teeth to represent a form very similar in size to *Miacis exilis* (= *Paramiacis exilis)*, but noted some differences which may or may not prove to be individual. The intact m2 here described is therefore of particular importance in comparison with the material studied by Guth (1964, p. 62) and Mathis (1987). Its size is almost identical to that given for 'Form B', and is only very slightly larger than the m2 in a cast of the lectotype of *Paramiacis exilis* in the Natural History Museum collection, London, from Quercy (original No Qu 8752). Its measurements certainly fall within the range of four specimens of m2 from La Bouffie given by Mathis (1987, p. 322, tab. 3 ). However, the enamel of the Creechbarrow specimen has been eroded, so that it could have been significantly larger.

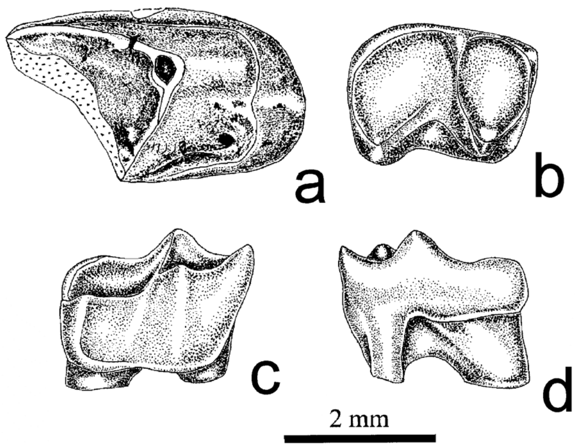



**Figure 14a-d**. *Paramiacis exilis* (Filhol, 1876); a: HZM 12.36656 lingual fragment M1 dex.; b-d: HZM 3.31333 m2 dex.; b: occlusal view; c: buccal view; d: lingual view.

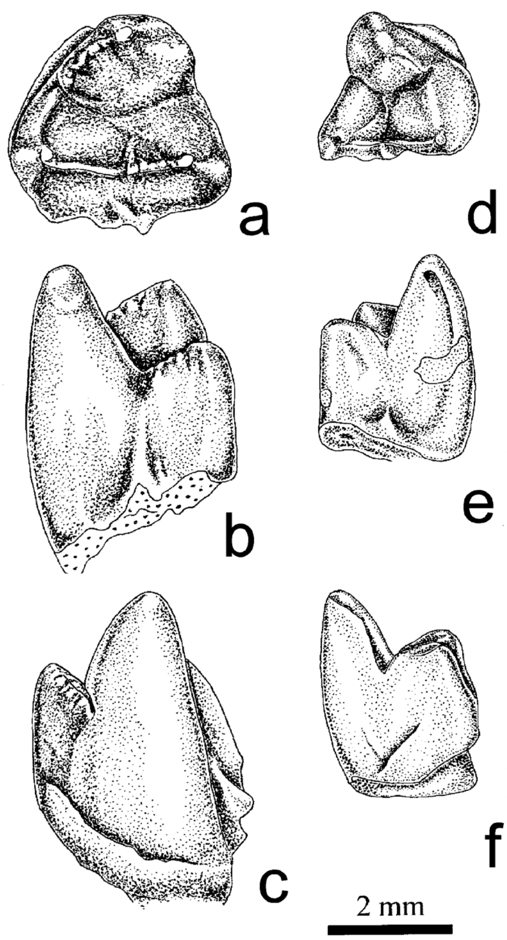



**Figure 15a-c**. *Paramiacis teilhardi* Mathis, 1987; HZM 1.35504 trigonid m1 sin.; a: occlusal view; b: distal view; c: buccal view. **d-f**: *Paramiacis exilis* (Filhol, 1876); HZM 5.32740 trigonid m1 dex.; d: occlusal view; e: distal view; f: buccal view.

It is referred here to *P. exilis* with reasonable confidence. The damaged m2 [(M37569) studied by Hooker (1986, p. 338)] gave estimated dimensions almost identical with 'Form A'. The morphology of HZM 3.31333 appears identical to the m2 of the cast of the lectotype. The three m1 trigonids described here (HZM 5.32740, HZM 9.34053 and 11.34471) are similar in size to Hooker's M37568, the four known Creechbarrow m1's thus having a TRI W of 2.69, 2.70, 2.82 and 2.82 mm, respectively. Mathis (1987, tab. 3) gives a range of 2.3–2.9 mm TRI W for sixteen specimens referred to *P. exilis* from the French sites of Le Bretou, La Bouffie, Lavergne and Perrière. By contrast his figures for *P. teilhardi* TRI W are 2.9-3.3 mm for six specimens from La Bouffie and Lavergne, thus slightly exceeded by the two specimens here referred to *P. teilhardi* from Creechbarrow. A small and a large m2 specimen are represented in this material as described above. It can now therefore be considered reasonably certain that both *Paramiacis exilis* and *P. teilhardi* occur at Creechbarrow, the size variation being very similar to the more extensive continental material studied by Mathis. The size difference between isolated teeth of the two species is, however, narrow (Mathis, 1987, tabs II-V; figs 9, 10), which renders determination of isolated teeth particularly difficult, especially when incomplete. More intact material is clearly required to resolve this complex problem.

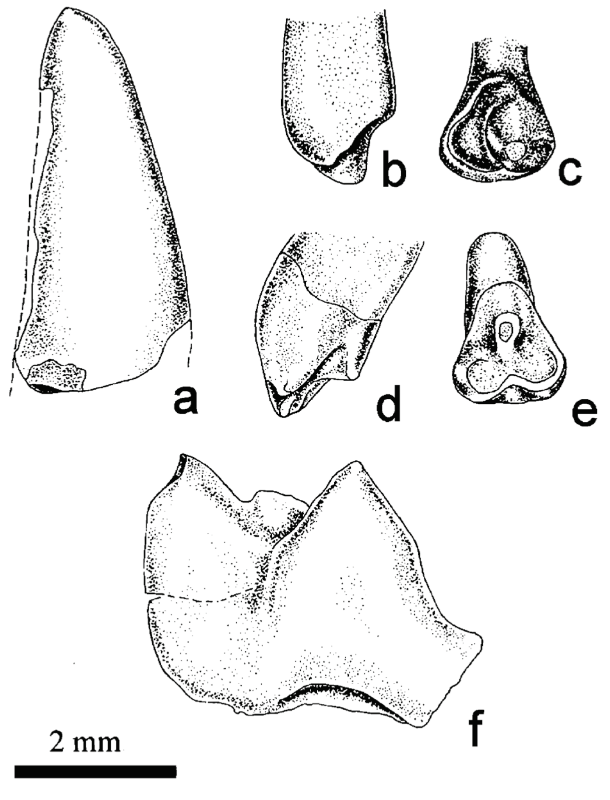



**Figure 16a-e:** *Paramiacis* spp. a: HZM 4.31539 ?upper canine tip and part shaft. b, c: HZM 6.32831 ?I3 - b: labial view; c: occlusal view. d, e: HZM 1.30592 I1 or I2; d: labial view; e: occlusal view. f: *Paramiacis teilhardi* Mathis, 1987, HZM 2.30732 part trigonid m1 dex., lingual view.

The possibility that sexual dimorphism in size like that occurring in Recent mustelids could have occurred in Eocene miacids must also be borne in mind.
Mathis (1987, p. 313) has, however, discounted the possibility of sexual dimorphism as an explanation of the size variation pointing out that the larger species is absent from Le Bretou and that there are dental differences between the two species.

Order Condylarthra Cope, 1881
Family Paroxyclaenidae Weitzel, 1933
Genus *Paravulpavoides* Harrison, 2009

*Type species – Vulpavoides cooperi* Hooker, 1986.

***Paravulpavoides cooperi* (Hooker, 1986)**
Figure 17

1977 *Russellites* sp. – Hooker, p. 141.
1980 *Pugiodens* sp. – Hooker& Insole, p. 42.
1986 *Vulpavoides cooperi* Hooker, p. 340; text-figs 42A-D, 42I-K.
2009 *Paravulpavoides cooperi* (Hooker, 1986) (*sensu* Harrison, 2009).

*Holotype* – Right M1, NHMUK M 37570 (Hooker, 1986, text-fig. 42A-D).

*Type locality* – Creechbarrow, Dorset, England SY8240 9215. Creechbarrow Limestone Formation, Robiacian (ELMA MP 16).

*Material* – HZM 10.38796 buccal part p2 dex. CL 3.33 mm (e) CW - (Fig. 17d-e); HZM 11.39051 m3 dex. CL 3.46 TRI W 2.50 TAL W 2.18 mm (Fig.17a-c).

*Additional material* – See Harrison (2009).

*Description and discussion* – HZM 10.38796 is the buccal part of a right lower premolar. The intact buccal aspect of the crown is very bulbous, establishing its paroxyclaenid affinity. It is sharply crested mesially and lacks any trace of a buccal cingulum. Although there is no trace of a metaconid, the former presence of a small one cannot be excluded, due to the substantial lingual damage. The cusp is slightly worn. There is a poorly developed talonid, slightly hollowed out buccally in a similar manner to the p3, HZM 8.37499 (Harrison, 2009; text-fig. 2c), but lacking the distal crest rising to the metaconid present in the p3 and with the low buccal talonid cusp even less evident.
These morphological features, combined with the size, which is intermediate between the small p1-2 (HZM 7.35425) and the p3 (HZM 8.37498) (see Harrison, 2009), leave no doubt that this represents the previously unseen p2. It may now be considered certain that HZM 7.35425, descried and figured by Harrison (2009, fig. 2a) is in fact a p1.
HZM 11.39051 is an m3 dex. also an element that was previously unknown. It is slightly smaller than the m2 (HZM 5.34877) described and figured by Harrison (2009, text-fig.

5) and differs in some important morphological features. The talonid is considerably less reduced in length, although equally narrow and is approximately the same length as the trigonid. The paraconid is considerably more reduced than that of the m2, forming merely a slightly thickened lingual rim to the trigonid basin. The mesial border of the trigonid crown is smoothly rounded, altogether lacking the incipient protoconulid present in the m2. The cusps of the talonid are low and with the entoconid distinctly smaller than that of the m2, the hypoconulid similarly minute and situated close to the hypoconid. The shallow talonid basin is notably more elongate than that of the m2 and enclosed by a poorly defined pre-entoconid cristid and cristid obliqua. Only a single root is present, grooved centrally on both aspects.

*Remarks* – The addition of p2 and m3 means that the post-canine mandibular dentition of this rare paroxyclaenid is now completely known, although some elements are damaged. It is noteworthy that each of the lower molars is morphologically different, with progressive reduction of the paraconid, thus adding significantly to the distinctive dental profile of the genus (Harrison, 2009). The relatively unreduced talonid of the m3 conforms with the similarly unreduced M3 with prominent protocone and paracone described by Harrison (2009, fig. 1b). These findings permit a significant emendation of the generic and specific diagnosis, as below. The incisors, canines, upper premolars and M2 remain, however, unknown.

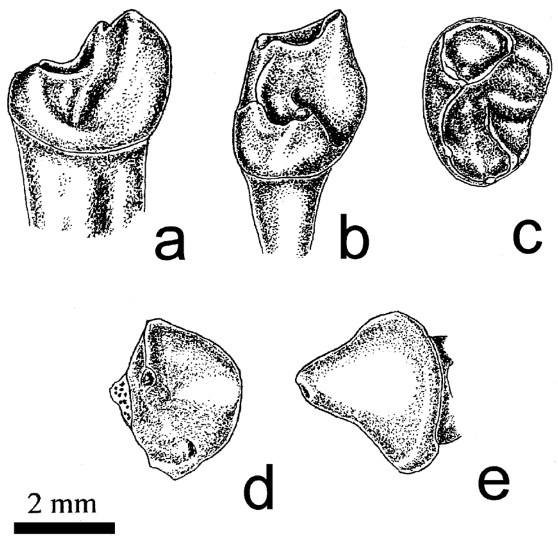



**Figure 17a-e**. *Paravulpavoides cooperi* (Hooker, 1986); a-c: HZM 11.39051 m3 dex.; a: buccal view; b: oblique distal view; c: occlusal view.; d, e: buccal part p2 dex. HZM 10.38796; d: occlusal view; e: buccal view.

*Emended specific diagnosis* – M1 small (CL 3.0-3.1 CW 5.1-5.2 mm).

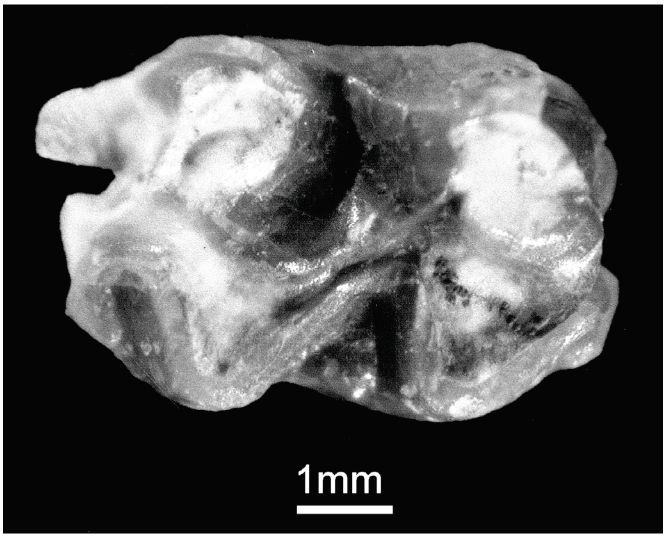



**Plate 3**. *Dichobune robertiana* Gervais, 1848-1852; HZM 1.33150 m3 dex. (hypoconulid missing). Light macrograph.

*Vulpavoides germanica* Matthes, 1952, *V. vanvaleni* Russell & Godinot, 1988 and *V. simplicidens* van Valen, 1965a are larger. M1 relatively short and broad with no paraconule, metaconule weak to absent, paracone and metacone close together, ectoflexus weak. M3 and m3 not greatly reduced, former with prominent protocone and paracone, latter with talonid longer than that of m2. The combined lengths of p3 and p4 are close to those of m1 and m2 combined. The p3 and p4 are semimolariform, both with discrete cuspate metaconids and absent paraconids; m1 and m2 with incipient protoconulid; m3 single rooted. For differential diagnosis see Harrison (2009).

Order Artiodactyla Owen, 1848
Family Dichobunidae Gill, 1872 (*sensu* Sudre 1978)
Genus *Dichobune* Cuvier, 1822

*Type species* – *Dichobune leporina* Cuvier, 1822.

***Dichobune robertiana* Gervais, 1848-1852**
Figure 18a-c; Plate 3

1848-52 *Dichobune robertianum* Gervais, p. 199, pl. 35, fig. 13 [Calcaire Grossier (Lutetian)].
1906 *Dichobune* cf. *robertiana* – Stehlin, p. 670; pl. 12 (Egerkingen).
1972 *Dichobune robertiana* – Sudre, p. 118 [Lissieu, Rhône; middle Eocene (Auversian)].

*Holotype* – Left mandibular ramus with seven cheekteeth (p1–m3) *in situ.* See Gervais (1848–1852, pl. 35; fig. 13). Specimen lost (Sudre, 1978, p. 21).

*Material* – HZM 1.33150 m3 dex. CL 6.7 (e) CW 4.22 mm (hypoconulid missing, Fig. 18a-c, Pl. 3).

*Description and discussion* – HZM 1.33150 is a right m3 of a small artiodactyl, from which the hypoconulid lobe, together with the posterior part of the entoconid has been broken off. The general aspect of the tooth is primitive and low-crowned, with the four principal cusps moderately worn and forming two subequal pairs. The two internal cusps, originally conical, are worn down to a rounded shape, each external cusp rather v–shaped.

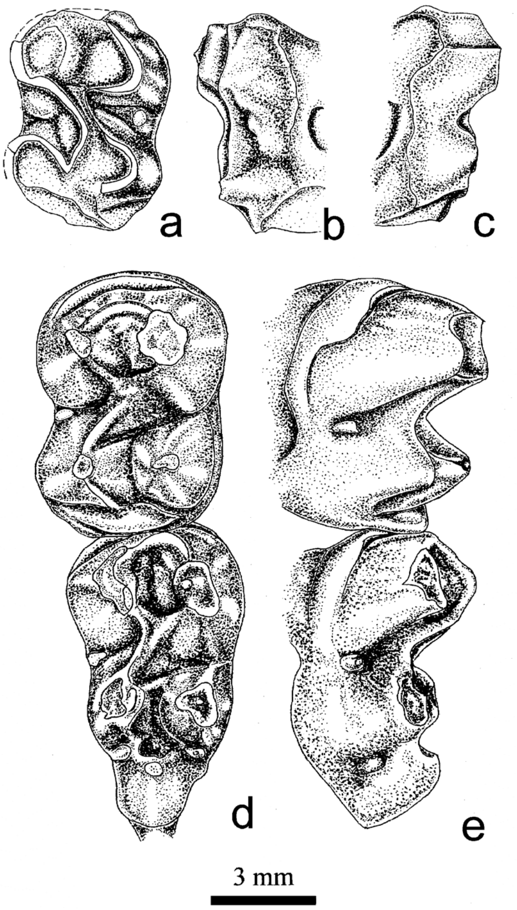



**Figure 18a-c.** *Dichobune robertiana* Gervais, 1848-1852; HZM 1.33150 m3 dex.; a: occlusal view; b: buccal view; c, lingual view; **d-e.** *Dichobune leporina* Cuvier 1822; M1499 (Caylux) m2-m3 sin.; d: occlusal view; e: buccal view.

The protoconid and metaconid are slightly higher than the posterior pair (hypoconid and entoconid). The metaconid is as large as the protoconid and clearly rounded, although its enamel surround is damaged and incomplete. The cristid obliqua connects the hypoconid to the mid-point between the metaconid and protoconid. A low, rounded ectostylid is situated near the buccal margin between the protoconid and hypoconid. The anterior cingulum, originally bluntly rounded as usual in the genus, is only preserved at its buccal extremity just internal to the protoconid cusp.

This m3, although damaged, conforms to the classical descriptions of the lower molars of this genus (Viret, 1961, p. 894; Sudre, 1978, p. 25). It is distinctly larger than the right m3 of *Hyperdichobune* sp.1 from Creechbarrow (NHMUK M 36815) recorded by Hooker (1986, tab. 29; pl. 28, fig. 11) TRI W 3.0 TAL W 2.6 mm. The seven cheekteeth of the holotype ramus measured 39 mm (Gervais, 1848-1852, p. 199) compared with 49 mm in a specimen of *D. leporinum* given by the same author. No other measurements of the lost holotype are available.
Comparison with a left ramus of the type species of the genus, *Dichobune leporina* Cuvier 1822 (Fig. 18d-e), with m2, m3 *in situ* (NHMUK M 1499) originating from the 'Phosphorites', Caylux, Tarn et Garonne (France), shows that the Creechbarrow m3 is very similar morphologically, including the presence of a small ectostylid. A hypolophid is, however, present in the Caylux specimen and the tooth is substantially larger. The smaller size of the Creechbarrow tooth is confirmed by comparison with measurements of m3's of *D. leporina* given by Sudre (1978, tab. 2) from Quercy (old collections) ACQ1 8.1 x 5.1 mm; ACQ2 7 x 5 mm; Aubrelong 1 ABL1 2983 9.5 x 6.2 mm and Bembridge (NHMUK M 29475) 11.3 x 7 mm. Comparison with Stehlin's (1906; p. 4, pl. 12, fig. 27) left ramus of *Dichobune* cf. *robertiana* with m2, m3 *in situ* shows a close correspondence in size and morphology with the Creechbarrow specimen. Stehlin (1906) in fact gave measurements of two figured m3's of his Egerkingen material of *D.* cf. *robertiana* (Eg 510 m3 length 7 mm; Eg 544 m3 length 7.5 width 4.5 mm. Sudre (1972, tab. 1) gave measurements of two m3's of this species from Lissieu (2585. m3 sin. CL 6.6 CW 4.1 mm; 3. m3 dex. CL 7.8 CW 5.0 mm), commenting that the Lissieu specimens are in general slightly larger than the Egerkingen material. The m3 sin. specimen from Lissieu seems almost identical in size to the Creechbarrow m3 and allowing for the estimation of CL in the latter it seems reasonable to conclude that all may be referable to the same species. Sudre (1978, p. 30) described *Dichobune sigei* from Lavergne (Quercy), a Bartonian site (*fide* J.J.Hooker, pers.comm.). This species is known only from the single upper molar holotype, which is smaller than *D.* cf. *robertiana* from Egerkingen. Until more material of the molars of these rare and primitive small artiodactyls become available it seems reasonable to refer the specimen from Creechbarrow to the latter taxon, which it closely resembles. It is the first occurrence of it in the British Eocene.

Family Choeropotamidae Owen, 1845 *sensu* Hooker & Weidmann (2000)

Genus *Amphirhagatherium* Depéret, 1908 *sensu* Hooker & Thomas (2001)

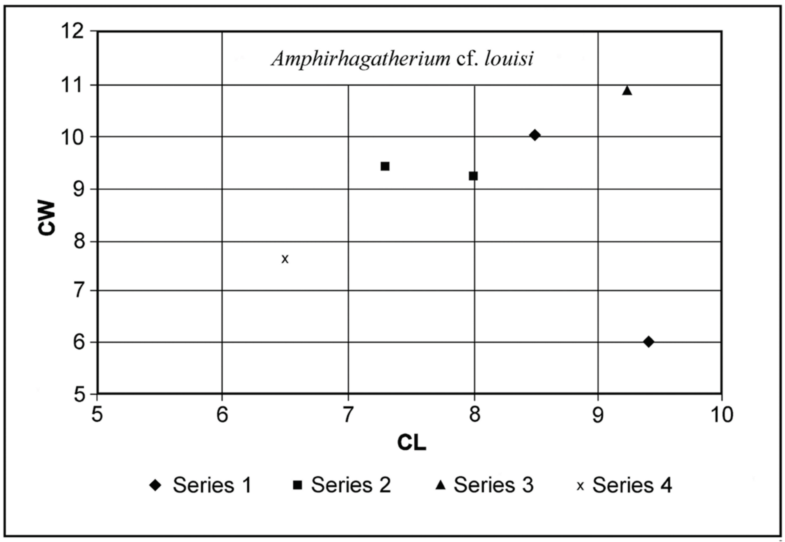
*Type species* – *Amphirhagatherium fronstettense* (Kowalevsky, 1874) (*sensu* Depéret (1908).

***Amphirhagatherium louisi*** **(Sudre, 1978)** *sensu* **Hooker & Thomas (2001)**
Figures 19, 20

1978 *Anthracobunodon louisi* Sudre, p. 94; pl. texte 10, figs 1-4; pl. 4; figs 3, 7, 8; pl. 5, figs 4, 5; tab.8 [Grisolles, Aisne, France. Marinesian (Calcaire de St. Ouen)].

*Holotype* – Maxilla with left P2 (damaged), P3-M3 and right P3-M3 (GRI 661). P. Louis collection.

*Material* – HZM 1.32665 M3 dex. [two fragments restored, CL 9.24 (e) CW 10.92 mm (e) (Fig. 20].




◆ *Amphirhagatherium louisi*. Grisolles. M3.
■ *Amphirhagatherium louisi*. Grisolles. Holotype. M3 *dex*. et *sin*.
▲ *Amphirhagatherium louisi*. Creechbarrow. M3 (estimated).
× *Anthracobunodon weigelti*. Geiseltal. M3 (after Sudre, 1978; Tab. 8).

**Figure 19**. *Amphirhagatherium louisi* (Sudre, 1978) and *Anthracobunodon weigelti* (Heller, 1934). Dimensions of cheekteeth in mm.

*Diagnosis* – See Sudre (1978, p. 94). For emended generic diagnosis and species list see Hooker & Thomas (2001, p. 830).

*Description and discussion* – HZM 1.32665 is an incomplete right upper molar lacking the paracone and distal part of the paraconule. It is very brachyodont. The absence of any interstitial wear facet along its distal border indicates that it is an M3. The bulbous mesostyle is massive and forms a prominent protrusion on the buccal margin characteristic of some of the more derived species of this genus (Hooker & Thomas, 2001, p. 830). Its cusp is lower than the metacone in buccal view. Cingula are strongly developed and papillose around the distal and distobuccal aspects of the metacone and metaconule. A prominent row of enlarged papillae extends from the metastylar crest of the metacone towards the buccal aspect of the metaconule. There is no cingulum on the buccal aspect of the mesostyle or the lingual side of the protocone, but a strong anterior cingular shelf is situated on the mesial aspect of the protocone. Hooker & Weidmann (2000) have synonymized the family Haplobunodontidae Pilgrim, 1941 with Choeropotamidae Owen, 1845.

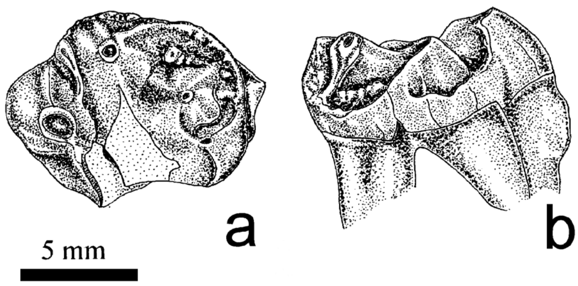



**Figure 20a-b**. *Amphirhagatherium louisi* (Sudre, 1978) ; HZM 1.32665 M3 dex.; a: occlusal view; b: distal view.

Hooker & Thomas, 2001 have transferred *Anthracobunodon louisi* Sudre, 1978 together with the other species of *Anthracobunodon* Heller, 1934 to the genus *Amphirhagatherium*, showing that these form a monophyletic group, while *Anthracobunodon* is paraphyletic.
This specimen differs from species of *Haplobunodon* Depéret, 1908 and in particular from *Haplobunodon venatorum* Hooker, 1986 described from Creechbarrow because

of its relatively massive mesostyle and papillose cingula. Comparison with a cast of the holotype shows the presence of a similar prominent row of papillae on the distal cingulum behind the metastyle present both in M2 and M3. Although incomplete the specimen agrees with Sudre's (1978, pp. 95-96) description of *A. louisi*. It clearly differs from *Haplobunodon venatorum*. Hooker (1986, pl. 33) has shown that this has distinctly smaller upper molar mesostyles and less papillose cingula. Its dimensions are close to those of the M3 of specimens from Grisolles (GRI 667 CL 8.5 CW 10 mm and GRI 335 CL 9.4 CW 6.0 mm) and those of the holotype (GRI 661 CL 7.3, 8.0 CW 9.4, 9.2 mm). Sudre (1978, tab. 8) compared these measurements with a single M3 of *Anthracobunodon weigelti* Heller, 1934 (= *Amphirhagatherium weigelti*; Fig. 19) from the Geiseltal, which is evidently smaller (M3 CL 6.5 CW 7.6 mm). It is also slightly smaller than the right M3 of the holotype of *A. edwardsi* (M25076 CL9.5 CW 12.0 mm), described by Hooker & Thomas (2001) from the Hatherwood Limestone Member, Headon Hill, Isle of Wight. This species also has a bulbous mesostyle and nests with *A. fronstettense* (Kowalevsky, 1874) *sensu* Depéret, 1908 close to *A. louisi* in phylogenetic analysis (Hooker & Thomas, 2001, text-figs 3, 7) but both are separated from it by their unique deeply notched upper molar preprotocrista and other dental differences listed by Hooker & Thomas (2001, p. 845). It is unfortunate that the Creechbarrow M3 is incomplete, lacking the paraconule and premetaconule crista.

This genus has hitherto been rarely recorded from the British Eocene and it is of some interest that it occurs together with *Haplobunodon venatorum* at Creechbarrow. Its degree of affinity with *Amphirhagatherium louisi* remains uncertain until more material becomes available.

## Summary

This paper records nine additional mammalian taxa to the known late middle Eocene (Robiacian) fauna of Creechbarrow. The addition of *Eotalpa anglica*, represented by a single, very characteristic, lower molar talonid, is considered to be the earliest known talpid fossil in the world. *Saturninia* aff. *mamertensis* and *Cryptotopos hartenbergeri* are also additional insectivores to the fauna. A single specimen of *Adapis laharpi* described here is the second known specimen of this rare primate.

Two species of artiodactyl, *Dichobune robertiana* and *Amphirhagatherium louisi*, each represented by a single specimen, are also new additions to the fauna. *Allopterodon minor*, a creodont carnivore, is also represented and two miacid carnivores, *Paramiacis exilis* and *Paramiacis teilhardi*, are confirmed.

These additional taxa are consistent with the Robiacian age of the fauna, significantly expanding knowledge of its composition.

## Acknowledgments

The authors are much indebted to E.C.C. International and Imerys Minerals Ltd for permission to carry out this research on their land. J.J. Hooker has given invaluable help and advice with identification and also provided access to comparative material in the Natural History Museum, London. The excavation in the field has been undertaken by staff and helpers of the Harrison Institute, Sevenoaks (UK). Special thanks are due to Alison, Robert and Andrew Ward, Lorna MacGregor, June Cree, Pippa Capon, P.G. White, Tom Writer and J. Stephen, who all gave time and effort to help with the arduous field work. Our students, Bounsavane Douanboubpha, Phouthone Kingsada, and Kin Maung Swe also assisted. The authors are most grateful to Loïc Costeur (Naturhistorisches Museum Basel, Switzerland) and Ainara Badiola Kortabitarte (Universidad del País Vasco UPV/EHU, Bilbao, Spain) for their very useful suggestions on review.

## References

Alston, E.R. 1876. On the classification of the order Glires. *Proceedings of the Zoological Society of London* (1876): 61-98.

Blainville, H.M.D. de 1864 (1839-64). *Ostéographie, ou description iconographique composée du squelette et du système dentaire des mammifères récents et fossiles pour servir de base à la zoologie ou à la géologie*. Paris (Bertrand): 8 vols.

Bosma, A.A. 1974. Rodent biostratigraphy of the Eocene-Oligocene transitional strata of the Isle of Wight. *Utrecht Micropalaeontological Bulletins. Special Publication* 1: 1-113.

Bowdich, T.E. 1821. *An analysis of the natural classifications of Mammalia, for the use of students and travellers*. Paris (Smith): 115 pp.

Bravard, A. 1850. Notes sur les ossements fossiles de Débruge. *In*: Gervais, P. *Zoologie et paléontologie françaises. Nouvelles recherches sur les animaux vertébrés dont on trouve les ossements enfouis dans le sol de la France et sur leurs comparaisons avec les espèces propres aux autres régions du globe*, 2. Explication des planches et divers mémoires. Paris (Bertrand): expl. pls 46-48: 2-3 (see Gervais, 1852).

Cope, E.D. 1875. On the supposed Carnivora of the Eocene of the Rocky Mountains. *Proceedings of the Academy of Natatural Sciences of Philadelphia* 27: 444-448.

Cope, E.D. 1880. On the genera of the Creodonta. *Proceedings of the American Philosophical Society of Philadelphia* 19: 76-82.

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

Crochet, J.-Y. 1974. Les insectivores des Phosphorites du Quercy. *Palaeovertebrata* 6: 109-159.

Cuvier, G. 1821. *Discours sur la théorie de la terre, servant d'introduction aux recherches sur les ossements fossiles*. Paris. 105 pp.

Cuvier, G. 1822. *Recherches sur les ossemens fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces,* 2-3 (new edition). Paris (G. Dufour & E. d'Ocagne): 648 pp. (2), 412 pp. (3).

Depéret, C. 1908. L'histoire géologique et la phylogénie des anthracothériidés. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences de Paris* 146: 158-162.

Filhol, H. 1874. Nouvelles observations sur les mammifères des gisements de phosphate de chaux (lémuriens et pachylémuriens). *Annales des Sciences Géologiques* 5: 1-36, pls 7-8.

Filhol, H. 1876-1877. Recherches sur les phosphorites du Quercy.

Etudes des fossiles qu'on y rencontre et spécialement des mammifères, 1-2. *Annales des Sciences Géologiques* 7: 1-220 (1, 1876), 8: 1-340 (2, 1877). Also: *Bibliothèque de l'Ecole des hautes Etudes de Paris*, *section des sciences naturelles* 16: 1-338.

Fischer von Waldheim, G. 1813-1814. *Zoognosia tabulis synopticis illustrata*, 1-3. Moscow (Nicolai Sergeidis Vsevolzsky): 3-1814.

Geoffroy St. Hilaire, E. 1812. Tableaux des quadrumanes, 1. Ord. Quadrumanes. *Annales du Muséum National d'Histoire naturelle, Paris* 19: 85-122.

Gervais, P. 1852 (1848-52). *Zoologie et paléontologie française (animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France*, 1-3 (1st edition). Paris (Bertrand): 271 pp. (1), explanation of plates (2); atlas, 80 pls (3).

Gill, T. 1872. Arrangement of the families of mammals. With analytical tables. *Smithsonian miscellaneous Collections* 11(230)(1): vi + 98 pp.

Gingerich, P.D. 1977. New species of Eocene primates and the phylogeny of European Adapidae. *Folia Primatologica* 28: 60-80.

Ginsburg, L., Arques, J., Broin, F. de, Le Calvez, Y., Mouton, J., Obert, D., Privé-Gill, C. & Roucan, J.-P. 1977. Découverte d'une faune de mammifères dans le Lutétien supérieur de la Défense, à Puteaux, près Paris (Hauts-de-Seine). *Compte rendu sommaire des Séances de la Société géologique de France* (1977)6: 311-313.

Godinot, M. 1984. Un nouveau genre remoignant de la diversité des adapinés (Primates, Adapidae) à l'Eocène terminal. *Compte Rendu Hebdomadaire des Sciences de l'Academie des Sciences, Paris* 299(18): 1291-1296.

Guth, C. 1964. A propos de *Miacis exilis* des Phophorites du Quercy. *Mammalia* 28: 359-365.

Haeckel, E. 1866. *Generelle Morphologie der Organismen. Allgemeine Entwicklungsgeschichte der Organismen. Kritische Grundzüge der mechanischen Wissenschaft von den entstehenden Formen der Organismen, begründet durch die Descendenz-Theori*, 1-2. Berlin (Georg Reiner): clx + 462 pp.

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.

Harrison, D.L. 2006. A new genus and species of 'paramyid' rodent (Rodentia: Ischyromyidae) from the Creechbarrow Limestone Formation (late middle Eocene) of Dorset, England. *Cainozoic Research* 4: 51-60.

Harrison, D.L. 2009. A new genus of paroxyclaenid (Mammalia: Condylarthra: Paroxyclaenidae: *Paravulpavoides)* from the upper middle Eocene of Creechbarrow, Dorset, S. England. *Cainozoic Research* 6: 25-35.

Harrison, D.L. & Hooker, J.J. 2010. Late middle Eocene bats from the Creechbarrow Limestone Formation, Dorset, southern England with description of a new species of *Archaeonycteris* (Chiroptera: Archaeonycteridae). *Acta Chiropterologica* 12: 1-18.

Hartenberger, J.-L., Sigé, B. & Sudre, J. 1968. Nouveaux gisements de vertébrés dans l'Éocène continentale de Minervois. *Compte rendu sommaire des Séances de la Société géologique de France* (1968)1: 22-23.

Heller, F. 1934. *Anthracobunodon weigelti* n.g., n. sp., ein Artiodactyle aus dem Mitteleozän des Geiseltales bei Halle a. S. *Paläontologische Zeitschrift* 16: 247-263.

Hill, W.C.O. 1953-55. *Primates: Comparative anatomy and taxonomy* 1. *Strepsirhini*. 2, *Haplorhini*. Edinburgh (University Press): xxiii + 798 pp (1, 1953); 347 pp (2, 1955).

Hooker, J.J. 1977. The Creechbarrow Limestone - its biota and correlation. *Tertiary Research* 1: 139-145.

Hooker J.J. 1986. Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin. *Bulletin of the British Museum (Natural History) (Geology)* 39:191-478.

Hooker, J.J. & Insole, A.N. 1980. The distribution of mammals in the English Palaeogene. *In*: Hooker, J.J., Moody, R.T.J, Walker, C.A. & Ward, D.J. (eds). The distribution of cartilaginous fish, turtles, birds and mammals in the British Palaeogene. *Tertiary Research* 3: 31-45.

Hooker, J.J. & Thomas, K.M. 2001. A new species of *Amphirhagatherium* (Choeropotamidae, Artiodactyla, Mammalia) from the late Eocene Headon Hill Formation of southern England and phylogeny of endemic European 'Anthracotherioids'. *Palaeontology* 44: 827-853.

Hooker, J.J. & Weidmann, M. 2000. The Eocene mammal faunas of Mormont, Switzerland. Systematic revision and resolution of dating problems. *Schweitzerische Paläontologische Abhandlungen* 120: 143 pp.

Kowalevsky, W. 1874. Monographie der Gattung *Anthracotherium* Cuv. und Versuch einer natürlichen Classification der fossilen Huftiere (2). *Palaeontographica, Neue Folge* 2: 211-290.

Lange-Badré, B. & Mathis, C. 1992. Données nouvelles sur les créodontes proviverrinés des zones MP16 et MP17 des Phosphorites du Quercy. *Bulletin du Muséum national d'Histoire naturelle de Paris* (4C)14: 161-184.

Leidy, J. 1869. The extinct mammalian fauna of Dakota and Nebraska including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. *Journal of the Academy of Natural Sciences of Philadelphia* (2)7:1-472.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, 1 (editio decima, reformata). Holmiae (Salvii): 1-824.

Mathis, C. 1985. Contribution à la connaissance des mammifères de Robiac (Éocène supérieur): Creodonta et Carnivora). *Bulletin du Muséum national d'Histoire naturelle de Paris* (4C)4: 305-326.

Mathis, C. 1987. Précisions sur le genre *Paramiacis* Mathis (Carnivora, Miacidae). *Bulletin du Muséum national d'Histoire naturelle de Paris* (4C)3: 313-326.

Matthes, H.W. 1952. 1. Abhandlung: Die Creodontier aus der mitteleozänen Braunkohle des Geiseltals. *Hallesches Jahrbuch für mitteldeutsche Erdgeschichte* 1: 201-240.

Matthew, W.D. 1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. *Memoirs of the American Museum of Natural History* 9: 289-567.

Michaux, J. 1964. Diagnoses de quelques paramyidés de l'Eocène inférieur de France. *Compte rendu sommaire des Séances de la Société Géologique de France* (1964)4: 153-154.

Miller, G.S. & Gidley, J.W. 1918. Synopsis of the supergeneric groups of rodents. *Journal of the Washington Academy of Sciences.* 8: 431-448.

Owen, R. 1845. *Odontography: or a treatise in the comparative anatomy of the teeth: their physiological relations, mode of development, and microscopical structure, in the vertebrate animals.* London (Hippolyte Baillière): xli-lxxiv, 289-655.

Owen, R. 1848. Descriptions of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London* 4: 103-141.

Pictet, F.-J. & Humbert, A. 1869. Mémoire sur les animaux vertébrés trouvés dans le terrain sidérolithiques du canton de Vaux et appartenant à la faune eocène. Supplément. Geneva. *Matériaux pour la paléontologie Suisse, ou, Recueil de* *monographies sur les fossiles du Jura et des Alpes* 5: 121-197.

Pilgrim, G.E. 1941. The dispersal of the Artiodactyla. *Biological Reviews* 16: 134-163.

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

Sigé, B. 1976. Insectivores primitifs de l'Eocene supérieure et Oligocène inférieure d'Europe occidentale. Nyctitheriides. *Memoires du Muséum National d'Histoire naturelle de Paris* (*C. Science de la Terre)* 34: 1-140.

Sigé, B., Crochet, J.-Y. & Insole, A. 1977. Les plus vieilles taupes. *Géobios Mémoire Spécial* 1: 141-157.

Simpson, G.G. 1928. A new mammalian fauna from the Fort Union of southern Montana. *American Museum Novitates* 59: 259-293.

Stehlin, H.G. 1906. Die Säugetiere des schweizerischen Eocaens. Critischer Catalogue der Materialen, 4. *Dichobune-Mouillacitherium-Meniscodon-Oxacron. Abhandlungen der Schweizerischen Paläontologische Gesellschaft* 33: 597-690.

Stehlin, H.G. 1912. Die Säugetiere des schweizerischen Eocaens. *Adapis*. *Abhandlungen der schweizerischen paläontologischen Gesellschaft* 38: 1165-1298.

Stehlin, H.G. 1940. Zur Stammersgeschichte der Soriciden. *Eclogae Geologicae Helvetiae* 33: 298-306.

Sudre, J. 1969. Les gisements de Robiac (Eocène supérieur) et leurs faune de mammifères. *Palaeovertebrata* 2: 95-156.

Sudre, J. 1972. Révision des artiodactyles de l'Eocène moyen de Lissieu (Rhône). *Palaeovertebrata* 5: 111-156.

Sudre, J. 1978. Les artiodactyles de l'Eocène moyen et supérieur d'Europe occidentale (systématique et évolution). *Mémoires et Travaux de l'Institut de Montpellier de l'Ecole Pratique des Hautes Etudes* 7: 1-229.

Szalay, F.S. & Delson, E. 1979. *Evolutionary history of the Primates*. London (Academic Press Inc.): 580 pp.

Teilhard de Chardin, P. 1915. Les carnassiers des Phosphorites du Quercy. *Annales de Paléontologie* 9: 101-191.

Trouessart, E.L. 1879. Catalogue des mammiféres vivants et fossiles. Insectivores. *Revue et Magazine de Zoologie pure et appliqué* (3)7: 219-285.

Valen, L. van 1965a. Paroxyclaenidae, an extinct family of eurasian mammals. *Journal of Mammalogy* 46: 388-397.

Valen, L. van 1965b. Some European Proviverini (Mammalia, Deltatheridia). *Palaeontology* 8: 638-665.

Viret, J. 1961. *In*: Piveteau, J. *Traité de Paléontologie* 6(1). Paris (Masson): 887-1084.

Weitzel, K.1933. *Kopidodon macrognathus,* Wittich, ein Raubtier aus dem Mitteleozän von Messel. *Notizblatt des Vereins für Erdkunde zu Darmstadt* (5)14: 81-88.

Wood, A.E. 1970. The European Eocene paramyid rodent, *Plesiarctomys. Verhandlungen der Naturforschenden Gesellschaft in Basel* 80: 237-278.

Zittel, K.A. von 1893. *Handbuch der Paläontologie*, 4. *Vertebrata (Mammalia)*. München, Leipzig (Oldenbourg): 799 pp.