

A possible omomyid (Primates: Omomyidae) periotic bone from the Eocene deposits at Hordle, Hampshire

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Abstract. An isolated primate periotic bone is reported from the Upper Eocene deposits at Hordle, Hampshire. The fragmentary nature of the specimen makes definitive identification problematic. However, similarities to specimens of the omomyid Genus *Necrolemur* suggest a possible omomyid identity. This is supported by the close association of the specimen with a number of well-preserved molars from *Microchoerus erinaceus*, a relatively abundant species in the Hordle deposits. However, the specimen exhibits a number of differences to the accepted omomyid morphology, most notably in the dimensions of the stapedial canal, which is wider than that of the promontorium canal.

Key words: fossil, mammal, *Necrolemur*, stapedial canal.

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I. INTRODUCTION

Mammal faunas from the late Middle Eocene to Early Oligocene are particularly well-represented in southern England (HOOKER, 1989). Amongst these faunas, primates are represented by the primitive Plesiadapidae and by two euprimate families, the Omomyidae and Adapidae. Until recently, British specimens of these taxa were confined to dental remains. However, excavations in the Upper Eocene Beds at Hordle (HARRISON *et al*, *in prep*) have led to the recovery of a number of periotic bones from small mammals, including marsupials and lipotyphlans (NORRIS & HARRISON, *in prep*) together with the single, fragmentary primate periotic described herein.

Because of its compact nature, the cochlear portion of the periotic bone, a complex endochondral ossification of the mammalian basicranium, is one of the few non-dental structures to survive in specimens of small fossil mammals (MACINTYRE, 1972). For this reason, the periotic has been widely scrutinised as a source of characters for studies on the higher-level relationships of mammals (for example, MACINTYRE, 1972; KIELAN-JAWOROWSKA, POPLIN & PRESLEY, 1986; GRAY-BEAL *et al*, 1989; WIBLE, 1990). HOOKER (1986: 370, text-fig. 53) describes a petrosal, possibly belonging to *Plagiolophus curtisi creechensis* from the Marinesian of Creechbarrow and lists some other Palaeothere specimens from continental Europe. However no petrosals of small mammals have been described from the British Eocene.

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II. LOCALITY, MATERIALS AND METHODS

The Upper Eocene beds of Hordle Cliff form part of the British Headonian. The three main strata containing mammals are known as the Mammal, Crocodile and Rodent Beds, and are described by CRAY (1973). They belong to the European Land Mammal Age Zone MP17, considered to be 36-39.5 m.y.b.p approximately. (HOOKER, 1989); the Rodent Bed is around 0.75 million years more recent than the Mammal and Crocodile Beds. The Beds are composed of sedimentary clays.

The specimen was extracted through screen-washing through a Nylon mesh of 0.5 mm aperture, with subsequent use of dilute acetic acid to break down resistant clay nodules. Details of the technique, using a Ward sieving machine (WARD, 1981) are given by HARRISON et al. (*in prep*).

Comparisons were made with specimens of *Erinaceus europaeus*, *Tupaia javanica*, *Loris tardigrada* and *Galago senegalensis* from the collections in the University Museum of Natural History at Oxford and *Galagoides demidovii* and *Galago crassicaudatus* from the collections of the Harrison Zoological Museum. In addition, detailed comparison was made with a specimen of *Necrolemur antiquus* in the collections of the Natural History Museum, London, from which the floor of the bulla had been dissected (NHM M4490).

The terminology used in the text and figures follows that of MACINTYRE (1972).

III. DESCRIPTION OF SPECIMEN

HZM 70.28094

Locality: "Rodent Bed", Hordle Cliff, nr Milford-on-Sea, Hants

Specimen is a fragmentary pars cochlearis from a right periotic. The tympanic face of the promontorium is crossed by the canal of the internal carotid artery, which splits mesial to the fenestra cochleae into promontorial and stapedial canals (Fig. 1a). The diameter of the stapedial canal is equal to, or slightly greater than that of the promontorial canal. The bony ventral portion of the canals is missing from the specimen, and the distal portions of both promontorial and stapedial canals are obscured by damage to the ventral surface of the pars cochlearis. This damage has also affected the area around the fenestra cochleae and fenestra vestibuli, leaving only the lateral and mesial margins of these openings respectively. The remnants of the fenestra vestibuli suggest a horizontally-orientated, elongate opening. Lateral to the fenestra vestibuli, further damage to the specimen has breached the wall of the facial nerve canal. This channel runs in a caudo-rostral orientation along the mesial face of a large, ventrally-directed process, which is tentatively identified as a remnant of a bony annular bridge.

The tympanic face is crossed by a number of remnants of periotic septa. A septum bordering the pars cochlearis on the caudal, mesial and rostral sides is interpreted as the remains of the roof of the

tympanic cavity; there is no evidence of any sutures separating this septum from the body of the petriotic. At the point where the canal of the internal carotid artery contacts the septum there is a slight depression, interpreted here as the dorsal margin of the post carotid foramen. The marginal septum is contacted mesially and rostrally by two further septa arising from the body of the pars cochlearis. In addition a third septum, arising from the ventral surface of the facial canal, runs rostrally, before diverting mesially to contact the latter of the two septa above.

Study of the cerebellar face (Fig. 1b) suggests that much of the rostral half of the specimen has been lost; in addition, the caudal portion of the petrosal has broken away along the rostral margin of the subarcuate fossa, leaving only the region around the large internal auditory meatus intact. The foramen acousticum inferius of the internal auditory meatus is both broader and deeper than the fo-

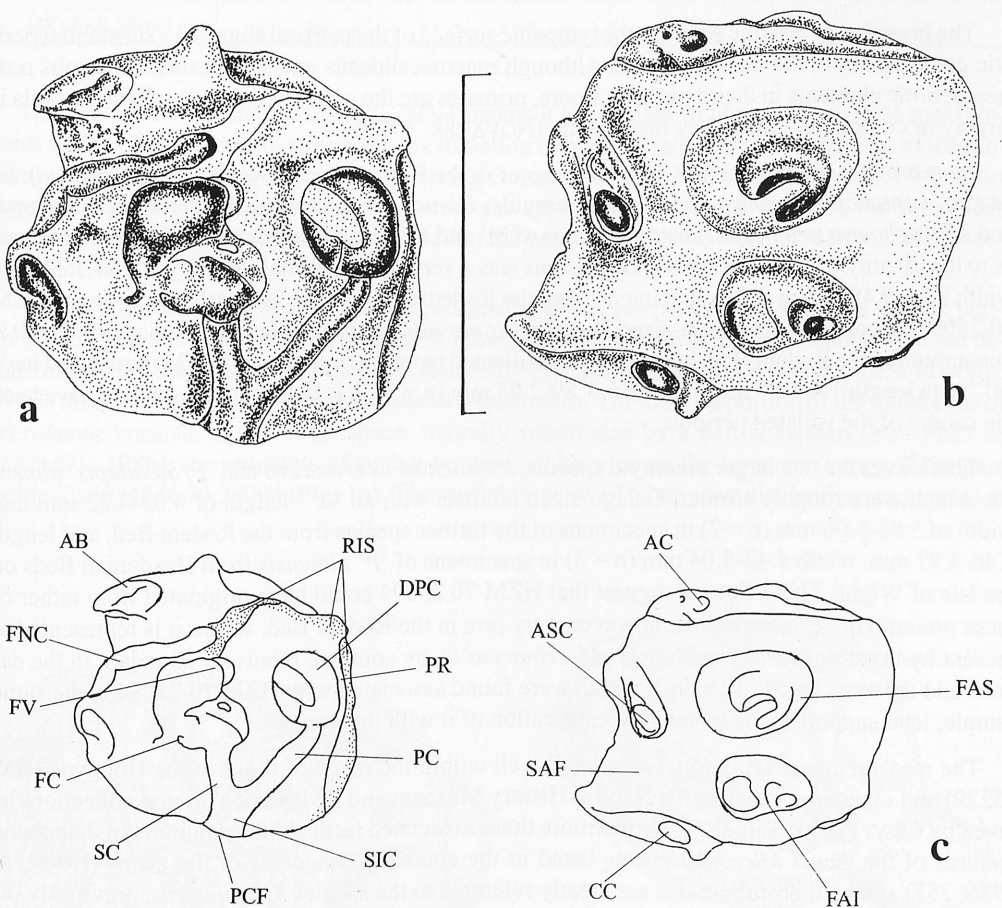


Fig. 1. HZM 70.28094. Partial right periotic. a) tympanic face, b) cerebellar face. Scale = 5 mm. c) outline diagrams of a) and b) above with identified structure listed and labelled as below: AB – Annular bridge, AC – Aqueductus cochleae, ASC – Anterior (superior) vertical semicircular canal, CC – Crus commune, FC – Fenestra cochleae, FAI – Foramen acousticum inferius of IAM, FAS – Foramen acousticum superius of IAM, FNC – Facial nerve canal, FV – Fenestra vestibuli, IAM – Internal auditory meatus, PCF – Postcarotid foramen, PC – Promontorial canal, PR – Promontorium, SAF – Subarcuate fossa, SC – Stapedial canal, SIC – Sulcus of internal carotid artery.

ramen acousticum superius. The interior of the crus commune has been exposed by the damage to the subarcuate fossa, as has the anterior (superior) vertical semicircular canal, which is exposed in cross-section.

IV. DISCUSSION

The prominent sulcus for the stapedial artery on the surface of the pars cochlearis, combined with the elliptical shape of the fenestra vestibuli, suggests that this specimen is from a placental mammal. As a caveat, however, it should be noted that of the four eutherian synapomorphies of the periotic identified by WIBLE (1990) only the shape of the fenestra vestibuli can be confirmed; the remaining features (absence of the prootic canal, absence of prootic sinus and presence of the capsuloparietal emissary vein) are obscured by damage to the specimen.

The presence of periotic septa on the tympanic surface of the petrosal suggests a substantial periotic contribution to the auditory bulla. Although macroscelideans and some erinaceomorphs possess periotic elements in their tympanic floors, primates are the only mammals in which the bulla is largely or completely formed by the periotic (NOVACEK, 1977).

Four primate species are now known to occur in the Rodent Bed (HARRISON et al, *in prep*): an adapid, *Leptadapis magnus*, and three omomyids; *Pseudoloris parvulus*, '*Protoadapis*' *ulmensis* and *Microchoerus erinaceus*. The dimensions of M^1 and M^2 in these species provide some guidance as to the identity of HZM 70.28094. *Leptadapis* was a very robust animal (M^2 length 7.56-7.74 mm, width 9.36-9.48 mm, $n = 2$ in specimens from the Rodent Bed), which is clearly too large for HZM 70.28094. In contrast, the mouse-sized *Pseudoloris parvulus* is the smallest Headonian primate. It is uncommon in the Rodent Bed, but specimens collected recently from the Hordle Mammal Bed have M^{1-2} with length 1.4-1.50 mm and width 1.89-2.05 mm ($n = 3$). It is therefore too small to have been the source of the isolated periotic.

This leaves the two larger omomyid species, *Microchoerus erinaceus* and '*Protoadapis*' *ulmensis*, which were roughly similar, Galago-sized animals with an M^{1-2} length of 4.03-4.22 mm and width of 5.02-5.06 mm ($n = 2$) in specimens of the former species from the Rodent Bed, and length 3.46-3.97 mm, width 4.42-5.04 mm ($n = 3$) in specimens of '*P*' *ulmensis* from Headonian Beds on the Isle of Wight. These figures suggest that HZM 70.28094 could have originated from either of these omomyids. '*P*' *ulmensis* is, however, very rare in the Rodent Bed, where it is represented at present by two fragmentary teeth only. *M. erinaceus* is, by contrast, relatively abundant in the deposit and the teeth listed in Table 1, which were found associated with HZM 70.28094 in the same sample, lend support to the tentative identification of it with this species.

The measurements set out in Table 1 fall well within the range of those of the Holotype (BM 25229) and other specimens in the Natural History Museum and Sedgwick Museum collections as given by CRAY (1973: Table 15). Furthermore these associated teeth exhibit a number of diagnostic features of the genus *Microchoerus* as listed in the emended Diagnosis of the genus (HOOKER, 1986: 257) and by their robust size are clearly referable to the species *M. erinaceus*, previously recorded from the Rodent Bed by CRAY (1973) and HOOKER (1987). The four maxillary molars found in association provide the most important diagnostic features of *Microchoerus*. These are the pronounced enamel wrinkling; the subquadrate outline of M^2 , its large paraconule and metaconule, the latter double; its mesostyle present and the hypocone almost as large as the protocone (Fig. 2a). The procumbent, spatulate I_1 (Fig. 3a) and C_1 with prominent mesio-lingual crest (Fig. 3b) provide further evidence of a robust omomyid in the sample. In contrast, the M^{1-2} of '*P*' *ulmensis* have minimal wrinkling of the enamel, less quadrate outline, a single metaconule and no mesostyle.

Table 1

Specimen no.	Nature of specimen	Crown length (mm)	Crown width (mm)	Figure no.
HZM 64.28088	M ² dex.	4.22	5.02	Fig. 2a
HZM 65.28089	M ² sin	4.03	5.06	—
HZM 66.28090	M ³ dex	3.07	4.10	Fig. 2b
HZM 67.28091	M ³ sin	3.07	4.10	—
HZM 68.28092	I ₁ dex	5.12	2.27	Fig. 3a
HZM 69.28093	C ¹	3.58	2.43	Fig. 3b

The incomplete nature of HZM 70.28094 makes it impossible to obtain any precise measurements which might enable an approximate estimation of body weight. Direct comparison of the molars and the periotic with specimens of the living *Galagoides demidovii* and *Galago crassicaudatus* suggests an animal much larger than the former and approximately similar in size to the latter. This admittedly circumstantial evidence suggests that the periotic may have originated from *Microchoerus erinaceus*.

The assignment of the specimen to *Microchoerus erinaceus* is tentative, since, as yet, the periotic of *Microchoerus* has not been described. However, comparison of HZM 70.28094 with the periotic of another member of the omomyid subfamily Microchoerinae, *Necrolemur* (NHM M4490), reveals the striking similarities between the two specimens. The anterior portion of the middle ear of *Necrolemur* consists of one large space, rostrally subdivided by a partial septum (MACPHEE & CARTMILL, 1986); the remnants of such a septum can be seen on the tympanic space of the pars cochlearis in HZM 70.28094 (Fig. 1a). The partial remains of a bony annular bridge are present in

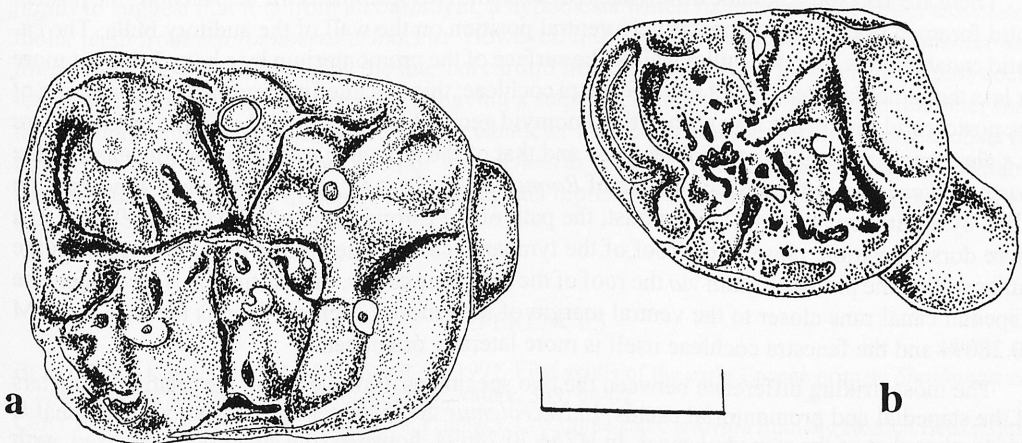


Fig. 2. Occlusal views of a) HZM 64.28068, M² dex., and b) HZM 66.28090, M³ dex. Scale = 2mm.

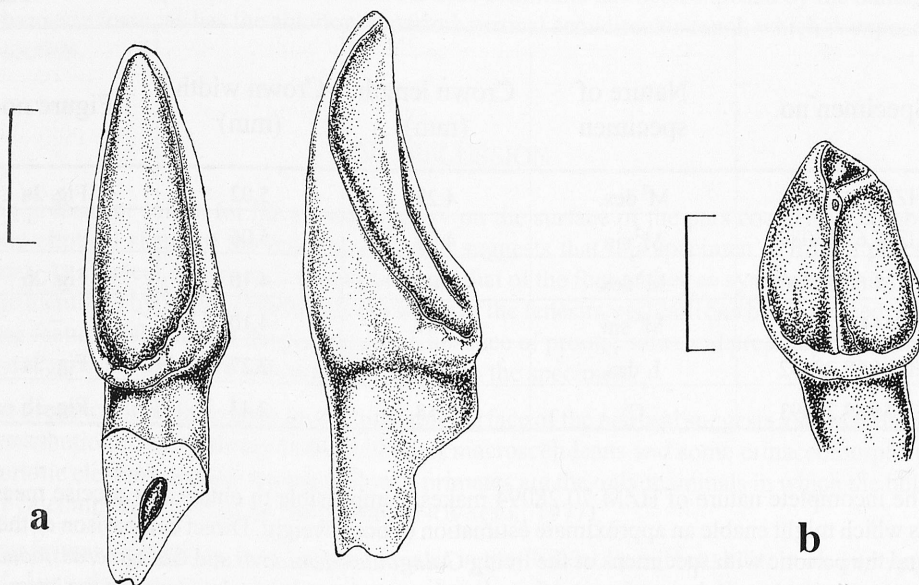


Fig. 3. Occlusal views of a) HZM 68.28092, I1 dex., and b) HZM 69.28093, C¹ dex HZM 69.28093, C¹ dex. Scale = 2 mm.

the Hordle specimen; this structure is a feature of *Necrolemur*. Finally, in both specimens, the internal carotid follows a transpromontorial path across the ventral surface of the promontorium. It should be stressed, however, that these features are not particularly distinctive or unique to the omomyids: for example, the transpromontorial path of the internal carotid is a condition seen in the majority of primates of modern aspect (MACPHEE et al, 1995). Indeed, MACPHEE & CARTMILL (1986) use the three characters discussed above as an example of similarities between *Necrolemur* and the adapid primate *Smilodectes*.

There are also some notable differences between the two specimens. In *Necrolemur*, the postcarotid foramen occupies a comparatively ventral position on the wall of the auditory bulla. The carotid canal crosses from the bullar wall to the surface of the promontorium by a bony bridge at more or less the same transverse level as the fenestra cochleae; this so-called posteromedial positioning of the postcarotid foramen is also seen in the omomyid genus *Rooneyia*, as well as in the lorises. There is a clear gap between the roof of the canal and that of the tympanic cavity in *Necrolemur* and the *Loris tardigradus*; in figured specimens of *Rooneyia* (eg. SZALAY, 1975) this space appears to be filled by a thin bony septum. In contrast, the path of the carotid canal of HZM 70.28094 lies in a more dorsal position, close to the roof of the tympanic cavity. The carotid canal crosses from the bullar wall to the promontorium *via* the roof of the tympanic cavity. In addition, in *Necrolemur*, the stapedial canal runs closer to the ventral margin of the fenestra cochleae than is the case in HZM 70.28094 and the fenestra cochleae itself is more laterally orientated.

The most striking difference between the two specimens, however, is in the relative diameters of the stapedial and promontorial canals. In *Necrolemur* the diameter of the promontorial canal is greater than that of the stapedial canal. In HZM 70.28094, however, the situation is reversed, with the stapedial canal being broader than the promontorial canal. Marked canal disproportion has long been the subject of debate regarding the relationships of the omomyids and adapids. It has been

argued by some authors, e.g. SZALAY (1975, 1977) and LUCKETT & SZALAY (1978) that in adapid primates the promontory canal is consistently smaller than the stapedia canal, whereas in omomyids, this size relationship is reversed. In the anthropoid haplorhines the promontory canal is larger than the stapedia canal, which leads LUCKETT & SZALAY (1978) to argue that enlargement of the promontory canal relative to the stapedia canal is a derived character uniting the omomyids and the anthropoids. This view has been contested by MACPHEE & CARTMILL (1986) who point out that enlargement of the promontorial canal is also seen in some adapid taxa, notably in *Notharctos* (GINGERICH, 1973), some specimens of *Adapis* (GINGERICH & MARTIN, 1981) and *Smilodectes* (MACPHEE & CARTMILL, 1986); in the adapine *Mahgarita*, the canals are of similar diameter (MACPHEE & CARTMILL, 1986).

The argument that a relatively small stapedia canal is a consistent feature of the Omomyidae is also undermined by the observation that the Early Eocene omomyid *Shoshonius cooperi* has stapedia and promontorium canals of more or less equal diameter (BEARD et al, 1991), combined with a ventrolateral postcarotid foramen. More puzzlingly, MACPHEE et al (1995) refer to *Microchoerus* as possessing a stapedia canal which is smaller than its promontorium canal, a statement based on observations of an as yet undescribed skull of *Microchoerus* from France (MACPHEE, pers comm.). If this is so, then there are two possible inferences which may be drawn from the Hordle periotic. Either it comes from a different primate species and its close association with the molars of *Microchoerus* is a taphonomic artefact, a hypothesis which is not supported by DLH's experience of the Hordle site; or, alternatively, the relative diameter of the two canals is not consistent between individuals of this species, mirroring the within-species variability in canal diameter observed in some adapids (GINGERICH, 1973). Given the comparatively small number of specimens of these species available, the possibility of as yet undescribed intraspecific variability in cranial morphology is a very real one.

V. CONCLUSIONS

The Hordle specimen HZM 70.28094 is probably too fragmentary to yield more than the most basic information about the taxonomic affinities of its owner. The specimen would appear to be an incomplete right periotic bone from a small primate, with a posteromedially positioned postcarotid foramen and a transpromontorially directed internal carotid artery. The remnants of a bony annular bridge are present. The specimen exhibits sufficient similarities to the periotic of *Necrolemur antiquus* to suggest that it is from an omomyid, a hypothesis which receives support from associated molar teeth from *Microchoerus erinaceus*. However, it differs from specimens of *Necrolemur* and *Rooneyia* in the path followed by the internal carotid from the postcarotid foramen to the pars cochlearis, and from all known omomyids in having a stapedia canal which is greater in diameter than the promontorium canal. Whilst the former character may be distinctive for this species, observations from the only known specimen of *Microchoerus* for which basicranial material is available suggests that the relative dimensions of the canals represents an example of a character which is variable within species.

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