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Mammalian periotic bones from the Eocene deposits at Hordle, Hampshire

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Abstract. Three specimens of isolated mammalian periotic (petrosal) bones are described from the Upper Eocene Beds of Hordle Cliff. One specimen is identified as a didelphid marsupial, possibly of the genus *Amphiperatherium*. The remaining specimens are identified as periotics of lipotyphlan insectivores. The larger specimen is identified as an erinaceomorph and exhibits similarities to both amphilemurids and dormaaliids. It is possible that it represents the first specimen of a periotic from the amphilemurid *Gesneropithex grisollensis*, although this cannot be confirmed on the basis of periotic morphology alone. The smaller of the two specimens may represent a nyctithere, possibly *Scraeva* or *Saturninia*, but the fragmentary and isolated nature of the specimen makes confirmation of its identity impossible. Although the identification of the three specimens remains tentative, they are notable as the first examples of basicranial remains from these groups in the Eocene of Britain.

Key words:Didelphidae, Amphilemuridae, Nyctitheriidae, Headonian.

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I. INTRODUCTION

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 (MACINTYRE 1972; KIELAN-JAWOROWSKA et al. 1986; GRAYBEAL et al. 1989; WIBLE 1990). We present details of three new periotics of small mammals from the Eocene beds at Hordle, Hampshire. 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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Museum, has provided much assistance in our research. We are grateful to Professor J. R. WIBLE of the University of Louisville, Kentucky, for his comments on the marsupial periotic described herein. The specimen of *Didelphis albiventris* was obtained for the Harrison Zoological Museum by Mrs N. PENDLETON.

II. LOCALITY

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, from which most specimens are 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.).

III. DESCRIPTION OF SPECIMENS

Four types of specimen were identified, of which one, a possible omomyid primate periotic from the Rodent Bed, is described separately (NORRIS & HARRISON, 1998). The remainder are fragmentary specimens, termed Petrosals A, B and C.

A. Petrosal Type A (Figs 1A-D)

HZM 171.27021

"Mammal Bed", Hordle, nr Milford-on-Sea

Specimen is a fragmentary pars cochlearis from a right petrosal. There is no evidence for the presence of promontorial or stapedial canals on the tympanic face of the promontorium (Fig. 1A). The rostral tympanic process is poorly developed and there is no evidence of peripheral septa, suggesting that the petrosal does not contribute to the walls or floor of the tympanic cavity. The fenestrae cochleae and vestibuli are rounded in shape. The facial nerve sulcus is partially preserved, but the position of the prootic canal cannot be determined because of damage to/absence of the pars canalicularis.

Study of the cerebellar face (Fig. 1B) suggests that the pars cochlearis is more or less complete but the pars canalicularis is absent caudally from margin of subarcuate fossa. The internal auditory meatus is very large, with a deeply-recessed foramen acousticum superius. The opening of the facial nerve canal into the foramen acousticum superius is relatively large. The sulcus of the inferior petrosal sinus is present, but poorly developed.

B. Petrosal Type B

HZM 245.28628 (Figs 2A-D)

"Crocodile Bed", Hordle, nr Milford-on-Sea

Specimen is a fragmentary pars cochlearis from a left petrosal. Sulci for prootic and stapedial arteries may be faintly discerned on the surface of the promontorium (Fig. 2A). There is a moderately substantial rostral tympanic process, extending medially to form a distinct shelf and rostrally to the apex of the petrosal (the anteromedial corner of the petrosal). The caudal tympanic process is not

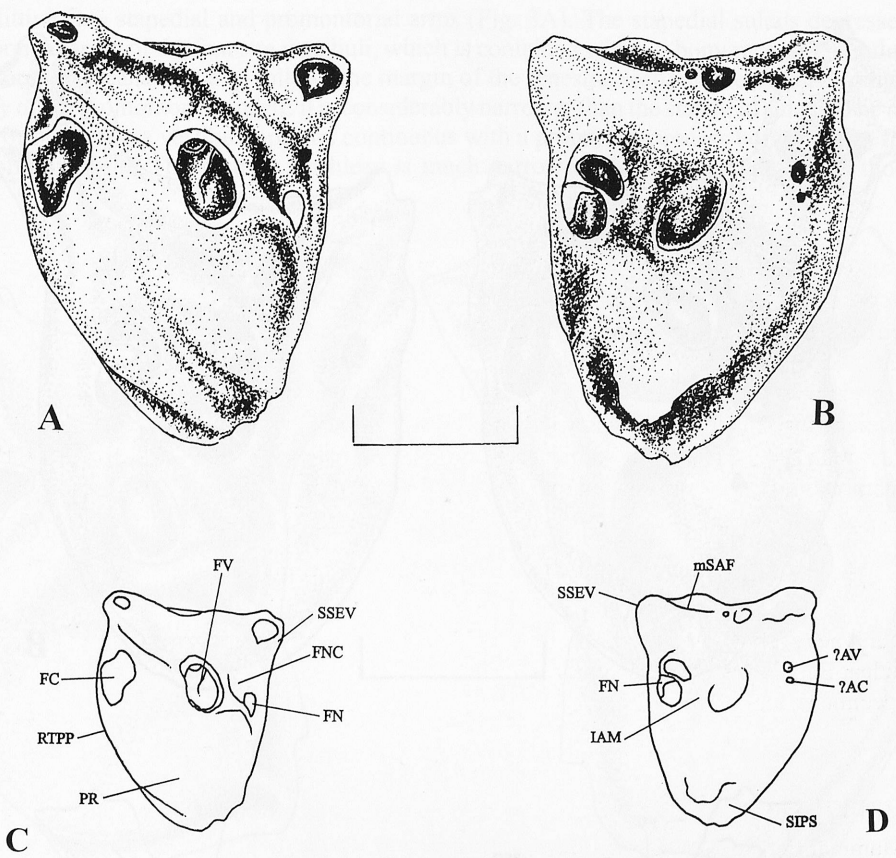

Fig 1. Petrosal A. HZM 171.27021. ?*Amphiperatherium sp.* Hordle Cliffs, nr. Milford-on-Sea, Hampshire. "Mammal Bed", Headonian, Upper Eocene. A. & C.: tympanic face. B. & D.: cerebellar face. AC – acqueductus cochleae; AV – acqueductus vestibuli; FC – fenestra cochleae; FN – facial nerve foramen; FNC – facial nerve canal; FV – fenestra vestibuli; IAM – internal auditory meatus; mSAF – margin of subarcuate fossa; PR – promontorium; RTPP – rostral tympanic process; SIPS – sulcus of inferior petrosal sinus; SSEV – sulcus of sphenoparietal emissary vein. Scale for A and B = 2 mm.

extensively developed and does not completely enclose the fenestra cochleae. The fenestra cochleae is moderately elongate and the diverticulum which leads into its fossula is comparatively broad and not closely constricted by the lateral portion of the caudal tympanic process. Antero-ventrally, the rostral tympanic process ends abruptly at the margin of a depressed and roughened area, which is interpreted as the remnants of the hiatus Falopii. This diagnosis is supported by an apparent sulcus running from the postulated hiatus Falopii to the facial nerve foramen. This is interpreted as the exposed floor of the canal of the greater petrosal nerve, the roof being absent. Lateral to this canal are the remnants of a bony plate, which is assumed to be part of the exposed surface of the petrosal in the middle cranial fossa.

On the cerebellar face, little remains of the subarcuate fossa, other than its ventral rim (Fig. 2B). The internal auditory meatus is relatively large, with a deep foramen acousticum inferius. The foramen acousticum superius is elongate and is largely obscured from lateral view by the crista petrosa. The opening of the aqueductus cochlea is visible caudal to the opening of the IAM. The specimen is bordered ventrally by the rostral tympanic process, which forms the mesial margin of a deep sulcus of the inferior petrosal sinus.

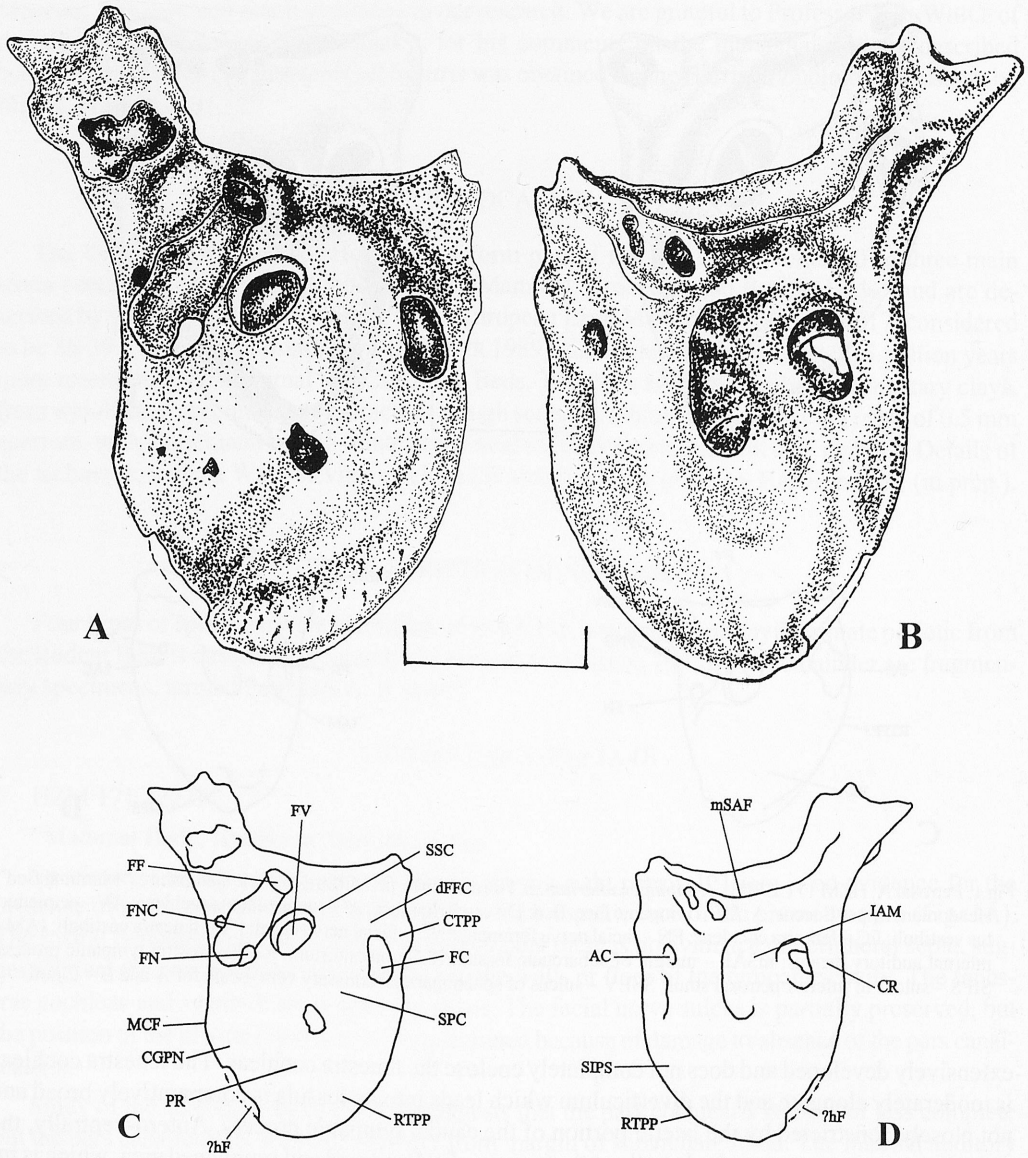

Fig. 2. Petrosal B. HZM 245.18628. *?Gesneropithex grisollensis*. Hordle Cliffs, nr. Milford-on-Sea, Hampshire. "Crocodile Bed", Headonian, Upper Eocene. A. & C.: tympanic face. B. & D.: cerebellar face. CGPN – canal of the greater petrosal nerve; CR – crista petrosa; CTPP – caudal tympanic process; dFFC – diverticulum of fossula fenestra cochleae; FF – secondary facial foramen; hF – hiatus Falopii; MCF – exposure of periotic in middle cranial fossa; SPC – sulcus of the prootic canal; SSC – sulcus of the stapedial canal. Other captions as for Fig. 1. Scale for A and B = 2 mm.

C. Petrosal Type C (Figs 3A-D)

HZM 204.27517

"Mammal Bed", Hordle Cliff, nr Milford-on-Sea

Specimen is a fragmentary pars cochlearis from a right petrosal. The shallow sulcus of the lateral carotid artery crosses the tympanic face of the promontorium ventral to the fenestra cochleae, be-

fore splitting into stapedial and promontorial arms (Fig. 3A). The stapedial sulcus depresses the raised bony margin of the fenestra vestibuli, which is contained within a bony recess. The sulcus of the promontorial canal initially follows the margin of the fenestra vestibuli, before diverging onto the body of the promontorium itself: it is considerably narrower than the stapedial sulcus. The raised margin of the fenestra vestibuli appears continuous with a prominent process bordering the lateral face of the petrosal. The fenestra cochleae is much narrower and more elongate than those of

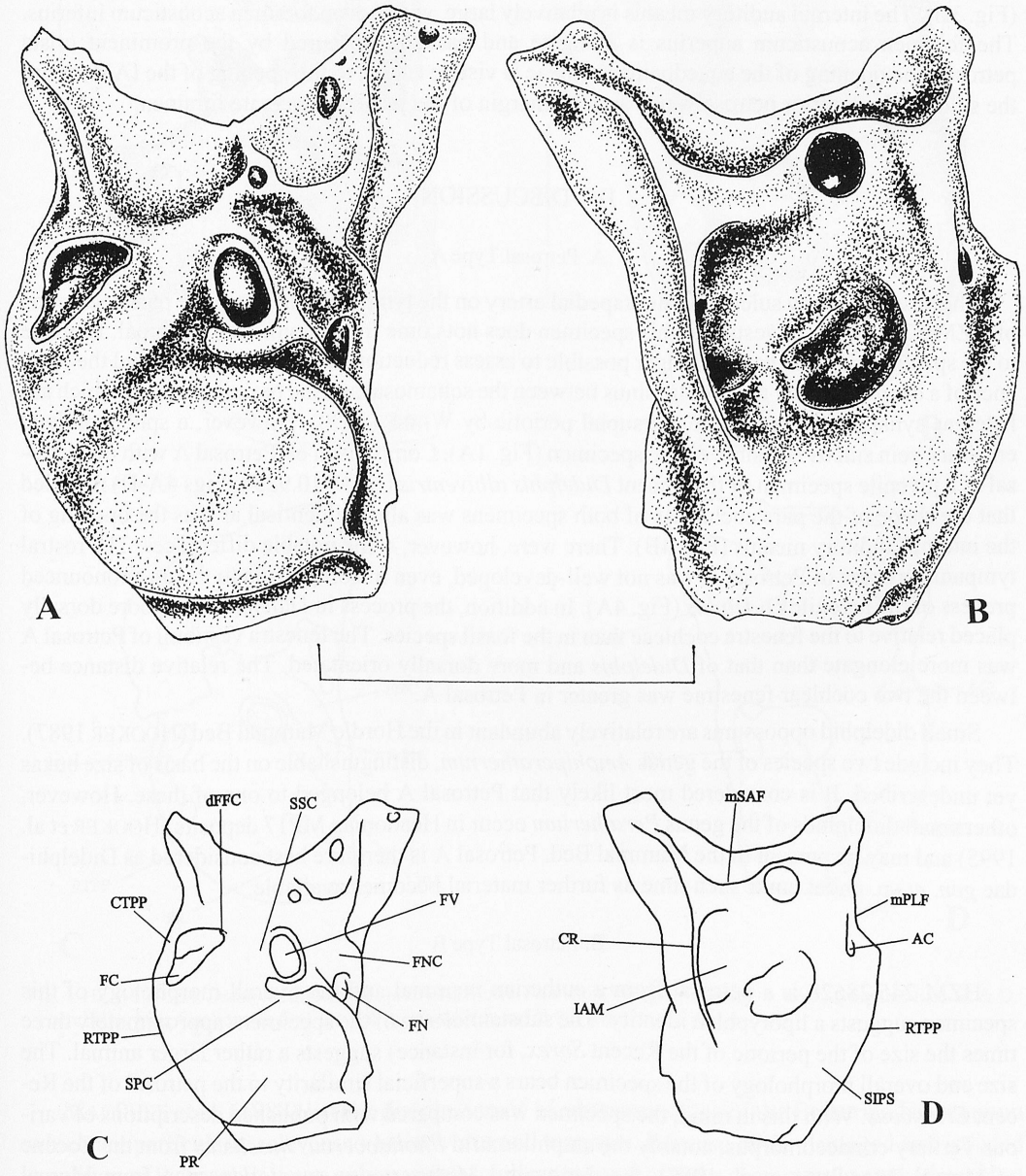

Fig. 3. Petrosal C. HZM 204.27517. ?Nyctitheriidae, gen. et sp. undet. Hordle Cliffs, nr. Milford-on-Sea, Hampshire. "Mammal Bed", Headonian, Upper Eocene. A. & C.: tympanic face. B. & D.: cerebellar face. mPLF – margin of the posterior lacerate foramen. All other captions as for Figs 1 & 2. Scale for A and B = 2 mm.

Petrosals A and B. It is deeply recessed, being bordered caudally by a bony wall, interpreted as the base of more substantial lateral caudal tympanic process than that of Petrosal B. Unlike the condition seen in the latter specimen, in Petrosal C this structure closely confines the diverticula leading into the fossula fenestrae cochleae. The rostral tympanic process is small, but marked. The roof of the facial nerve canal is absent.

The cerebellar face is demarcated by the broken margin of the subarcuate fossa and the rostral tympanic process; as with the other two specimens, much of the pars canalicularis is missing (Fig. 3B). The internal auditory meatus is relatively large, with a deep foramen acousticum inferius. The foramen acousticum superius is elongate and partially obscured by the prominent crista petrosa. The opening of the aqueductus cochleae is visible caudal to the opening of the IAM, as are the sulci of the inferior petrosal sinus and the margin of the posterior lacerate foramen.

IV. DISCUSSION

A. Petrosal Type A

The absence of any sulcus for the stapedial artery on the tympanic surface of the pars cochlearis of HZM 171.27021 suggests that this specimen does not come from a eutherian mammal. Damage to the specimen means that it is longer possible to assess reduction of the prootic canal and the presence of a deep sulcus for the prootic sinus between the squamosal and the periotic, both of which are listed as synapomorphies of the marsupial periotic by WIBLE (1990). However, a sphenoparietal emissary vein sulcus is visible on the specimen (Fig. 1A). Comparison of Petrosal A with the petrosal of a juvenile specimen of the Recent *Didelphis albiventris* (HZM 10.9254: Figs 4A-D) revealed that the shape of the pars cochlearis of both specimens was almost identical as was the opening of the internal auditory meatus (Fig. 4B). There were, however, some notable differences. The rostral tympanic process of Petrosal A was not well-developed, even in comparison to the un-pronounced process of the juvenile *Didelphis* (Fig. 4A). In addition, the process in *Didelphis* was more dorsally placed relative to the fenestra cochleae than in the fossil species. The fenestra vestibuli of Petrosal A was more elongate than that of *Didelphis* and more dorsally orientated. The relative distance between the two cochlear fenestrae was greater in Petrosal A.

Small didelphid oppossums are relatively abundant in the Hordle Mammal Bed (HOOKER 1987). They include two species of the genus *Amphiperatherium*, distinguishable on the basis of size but as yet undescribed. It is considered most likely that Petrosal A belonged to one of these. However, other small didelphids of the genus *Peratherium* occur in Headonian MP17 deposits (HOOKER et al. 1995) and may be present in the Mammal Bed. Petrosal A is therefore best considered as Didelphidae *gen. et* sp. undet. until such time as further material becomes available.

B. Petrosal Type B

HZM 245.28628 is a petrosal from a eutherian mammal and the overall morphology of this specimen suggests a lipotyphlan identity. The substantial size of the specimen (approximately three times the size of the periotic of the Recent *Sorex*, for instance) suggests a rather larger animal. The size and overall morphology of the specimen bears a superficial similarity to the petrosal of the Recent *Erinaceus*. With this in mind, the specimen was compared with published descriptions of various Tertiary erinaceomorphs, notably the amphilemurid *Pholidocercus hassiacus* from the Eocene of Messel (MACPHEE et al. 1988), the dormaaliid *Macrocranion tupaiodon*, also from Messel (MACPHEE et al. ibid.), the brachyericid *Brachyerix macrotis* from the Miocene of western North America (RICH T. H. & RICH P. V. 1971) and *Diacodon alticuspis* (MACPHEE et al. 1983), an erinaceomorph of uncertain affinities from the early Eocene of New Mexico.

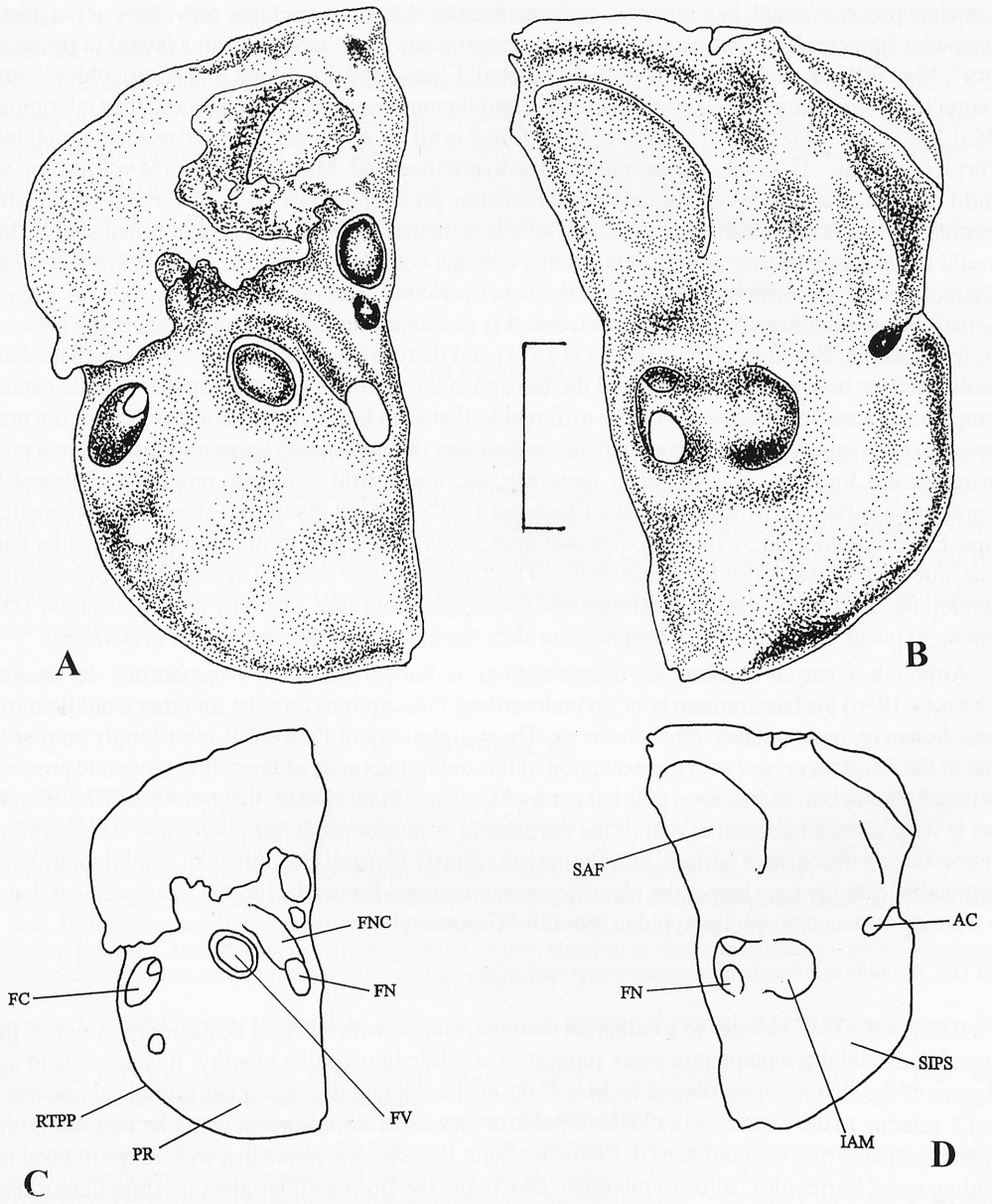

Fig. 4. HZM 10.9254. *Didelphis albiventris*, juv. Villa Morra, Asuncion, Paraguay. Recent. A. & C.: tympanic face. B. & D.: cerebellar face. Captions as for Figs 1 & 2. Scale for A and B = 2 mm.

MACPHEE et al. (1988) list the distribution of 15 character states of the Eutherian basicranium which are particularly relevent to insectivores and primates. Because of the damaged and isolated condition of Petrosal B, it was only possible to comment on 3 of these characters, namely the rostral tympanic process of the petrosal (Character 1: MACPHEE et al 1988), caudal tympanic process of the petrosal (Character 2: ibid.) and the participation of the petrosal in the tympanic roof (Character 8: ibid.). For the latter two characters, the character states seen in Petrosal B (Character 2.1 – caudal

tympanic process "small, incompletely encloses fossula of fenestra cochleae only; little or not pneumatised; Character 8.0 – petrosal participation in tympanic roof "limited to area lateral to promontory": MACPHEE et al. 1988) are widely distributed; Character 2.1 is found in the Soricoidea, some Tenrecidae, *Diacodon*, the Dormaalidae, the Amphilemuridae, the Erinaceinae and the Galericinae (MACPHEE et al. 1988) whilst Character 8.0 is found in all the above taxa, as well as the Leptictidae, Chrysochloridae, Talpinae, Desmaninae, Brachyericinae and Microsyopidae (MACPHEE et al. ibid.). The character state seen in the rostral tympanic process of Petrosal B, however, is more ambiguous. It is a fairly substantial structure, which is medially directed to form a broad shelf. This would appear to conform, to a limited extent, with the condition described by MACPHEE et al. as Character State 1.3, which is confined to the Brachyericinae. Having said so, however, the expansion of the rostral tympanic process in Petrosal B is nowhere near as extensive as that of the petrosal of, for example, *Brachyerix* (RICH & RICH 1971) and there is no clear evidence of a roughened articular surface between the petrosal and the basisphenoid. Furthermore, the condition of the caudal tympanic process in Petrosal B. is very different to that seen in the Brachyericinae, where the process is extensively developed, pneumatized, and closely delimits the stylomastoid foramen and posterior carotid foramen. It is possible, therefore, that the rostral tympanic process in Petrosal B represents a variant on MACPHEE et al's Character 1.2 ("small but distinct crest; restricted to medial aspect of promontorium; extends to petrosal apex; does not help to form meatus; no articular surface; does not form anterior tympanic wall"). This character state is found in some Soricoidea, some Leptictidae, *Diacodon*, the Dormaaliidae and the Amphilemuridae. The only one of the above taxa known to occur at Hordle is the Amphilemuridae, represented by *Gesneropithex grisollensis*.

Although a partial cranium of *Gesneropithex* is known from the Phosphorites du Quercy (HOOKER 1986) the basicranium is as yet undescribed. Descriptions do exist for other amphilemurid taxa, however, most notably *Pholidocercus*. The morphology of Petrosal B is strikingly similar to that of the *Pholidocercus* (with the exception of the ambiguous state of the rostral tympanic process, as noted above) but, as has been pointed out by MACPHEE et al. (1988), the periotic of *Pholidocercus* is itself almost identical to that of the dormaaliid erinaceomorph *Macrocranion*. It is therefore impossible on the basis of periotic morphology to identify Petrosal B as either an amphilemurid or a dormaaliid. For the time being, the identification of Petrosal B must be limited to a statement that it is from an erinaceomorph lipotyphlan, possibly *Geseneropithex*.

C. Petrosal Type C

HZM 204.27517 belongs to a eutherian mammal and, as with Petrosal B, the morphology of the rostral and caudal tympanic processes suggests a possible lipotyphlan identity. It is possible to apply two of the characters employed by MACPHEE et al. (1988) to this specimen, namely characters 1 and 2, relating to the rostral and caudal tympanic processes. It would appear that, like Petrosal B, the rostral tympanic process conforms to Character State 1.2, which is found in a wide range of taxa, including some Soricoidea, some Leptictidae, *Diacodon*, the Dormaaliidae and the Amphilemuridae. In Petrosal C, however, the status of the rostral tympanic process is not clear. It would appear to be a substantial structure, which closely confines the diverticulum leading into the fossula fenestrae cochleae, but there is no obvious evidence of pneumatisation. This is suggestive of MACPHEE et al.'s Character State 2.2 ("extensive, closely delimits or forms apertures for surrounding structures such as facial nerve and internal carotid, little or not pneumatised"), which is present in some tenrecids and in the desmans. Given the fragmentary nature of the specimen, however, it is not possible to confirm the full extent of the caudal tympanic process, beyond the fact that it is a more substantial structure than that of Petrosal B.

The Mammal Bed at Hordle is known to contain remains of a number of lipotyphlan species. Of the known members of the Hordle fauna, the early talpid *Eotalpa anglica* is probably too small for

Petrosal C, whilst the erinaceomorph amphilemurid *Gesneropithex grisollensis* is probably too large and would not, in any case, match the morphology of the specimen, not least in the morphology of the caudal tympanic process (see comments on Petrosal B above). Several small, shrew-like species of nyctithere, belonging to the genera *Scraeva* and *Saturninia* are also fairly abundant at Hordle and it is possible that Petrosal C originated from one of these. Unfortunately, there are no published descriptions of basicranial material from nyctitheres, which makes it impossible to confirm the identity of this isolated periotic. For the present, therefore, the specimen is best considered as Lipotyphla undet.

V. CONCLUSION

The identity of the three specimens described above remains tentative, and full consideration of their implications for the systematics of the groups concerned must await the discovery of specimens which are, for example, more closely associated with dental or other cranial remains. Nonetheless, these three specimens, together with the omomyid periotic described separately by the authors (NORRIS & HARRISON in press) are notable as the first examples of basicranial remains from these groups in the British Eocene.

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