# SKULL AND ENDOCRANIAL CAST OF *EORYCTES MELANUS,* A NEW PALAEORYCTID (MAMMALIA: INSECTIVORA) FROM THE EARLY EOCENE OF WESTERN NORTH AMERICA

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ABSTRACT—Early Eocene (Wasatchian) *Eoryctes melanus,* gen. et sp. nov., is a relatively large palaeoryctid insectivore (skull length ca. 32 mm, body weight ca. 51 gm) found in the Clarks Fork Basin of northwestern Wyoming. The skull has a short rostrum and prominent lambdoid plates. It appears to have lacked zygomatic arches. The middle ear cavity is large, with an enlarged epitympanic recess. Arteries of the middle ear include an internal carotid artery and a stapedial artery. Both are enclosed in bony tubes for their whole intrabullar course. The neopallium of the brain exhibits a rhinal fissure, a marginal sulcus, and a pseudosylvian sulcus. Venous blood from the cranial cavity drained mainly through the petro–occipital fissure. Endocranial volume is about 1.0 cm³, which is equivalent to a brain weight of 1.0 gm. The Jerison encephalization quotient (EQ) of *E. melanus* is estimated at 0.60 and the Martin EQ is estimated at 0.85. Proportional development of the brain indicates that olfaction was the dominant sense, although *Eoryctes* probably had acute hearing and a sensitive rostrum also. Palaeoryctidae appear to be most closely related to extinct Leptictidae and extant Lipotyphla, and are probably best included in the order or superorder Insectivora.

## INTRODUCTION

The family Palaeoryctidae is a poorly understood group of early placental mammals. The simple zalambdodont pattern of palaeoryctid molar teeth, the long stratigraphic range (Campanian through Eocene) of the group, and the fragmentary nature of most specimens have led to persistent taxonomic confusion that is still largely unresolvable. Van Valen (1966) included four subfamilies within Palaeoryctidae: Didelphodontinae, Deltatheridiinae, Palaeoryctinae, and Micropternodontinae. Butler and Kielan-Jaworowska (1973) placed deltatheridiines outside Palaeoryctidae near the base of the dichotomy between marsupials and placentals. Butler (1975) considered micropternodontines to be lipotyphlans. Kielan-Jaworowska (1981) added Campanian *Asioryctes* Kielan-Jaworowska, 1975, to Palaeoryctidae, but assigned it to the monotypic subfamily Asioryctinae. Fragmentary remains of Eocene palaeoryctids were described by Bown and Schankler (1982). Most recently, Wilson (1985) suggested that didelphodontines are not palaeoryctids. In this paper we are concerned only with Palaeoryctinae. We include three previously described genera in this subfamily: Paleocene *Palaeoryctes* Matthew, 1913, Paleocene *Pararyctes* Van Valen, 1966, and Eocene *Aaptorcytes* Gingerich, 1982. *Thelysia* Gingerich, 1982, may or may not be a palaeoryctine.

A new genus and species is described here, based on several partial skulls. This contributes greatly to our understanding of the cranial morphology of Palaeoryctinae, and provides a basis for future comparisons when the skulls of Didelphodontinae, Deltatheridiinae, and Micropternodontinae are better known. The

Oligocene leptictid *Leptictis dakotensis* (Leidy, 1868) formed the main basis for comparison in this study because skulls of this species are widely available for comparison, and they have been well described (Butler, 1956; Novacek, 1982, 1986). The original holotypes of *Palaeoryctes puercensis* Matthew, 1913 (AMNH 15923), and *Aaptorcytes ivyi* Gingerich, 1982 (UM 77923), and casts of the holotype of *Palaeoryctes punctatus* Van Valen, 1966, and type sample of *Pararyctes pattersoni* Van Valen, 1966, were also studied. Additional comparisons were made using published descriptions of *Palaeoryctes puercensis* Matthew, 1913 (see also McDowell, 1958, and Van Valen, 1966), and *Asioryctes nemegetensis* Kielan-Jaworowska, 1975 (see also Kielan-Jaworowska, 1981, 1984).

Anatomical terminology was drawn from the English version of Nomina Anatomica Veterinaria (Vienna, 1973) whenever possible.

**Abbreviations—AMNH,** American Museum of Natural History, New York; **UM,** Museum of Paleontology, University of Michigan, Ann Arbor.

## SYSTEMATIC PALEONTOLOGY

### Superorder INSECTIVORA (sensu Novacek, 1986)

### Order LIPOTYPHLA?

### Family PALAEORYCTIDAE Winge, 1917

The ordinal position of Palaeoryctidae is not well understood. Van Valen (1966) included this family in Deltatheridia, McKenna (1975) in Kennalestida, Szalay (1977) in Leptictimorpha, Kielan-Jaworowska (1981) and Bown and Schankler (1982) in Proteutheria,

Gingerich (1982) in Insectivora, and McKenna et al. (1984) in Soricomorpha. Most recently, Butler (1988) considered palaeoryctids unrelated to Lipotyphla. We think there is evidence for distant lipotyphlan and leptictid affinities, but refrain from discussing the affinities of "proteutherian" families until more and better material is described.

### *EORYCTES,* gen. nov.

**Type and Only Species**—*Eoryctes melanus,* sp. nov.

**Age and Distribution**—Early Wasatchian Land-Mammal Age of western North America.

**Diagnosis**—Differs from *Palaeoryctes* in having a more strongly inflected labial cingulum on upper molars (best seen as a lingual notch in occlusal view), a transversely elongated $P^4$, and a relatively smaller parastyle on $P^4$. Differs from *Palaeoryctes* cranially in having ossified tubes rather than grooves marking the course of arteries traversing the middle ear. Further differs from *Palaeoryctes* in having a hypoconid on lower molars that is positioned more labially. *Eoryctes* differs from *Pararyctes* in having a more strongly inflected labial cingulum on upper molars, and a transversely elongated $P^4$ with a relatively small parastyle. Lacks the strong lingual cingula on upper molars seen in *Pararyctes.* Further differs from *Pararyctes* in having a higher trigonid on lower molars. *Eoryctes* differs from *Asioryctes* in lacking $P_1$ and lacking a paraconid on $P_4$. Cranial differences from *Asioryctes* include the absence of a separate round foramen, the presence of an osseous bulla, the presence of osseous tubes for the middle ear arteries, and the small size of the retroarticular foramen. *Eoryctes* differs from *Aaptoryctes* in having a more strongly inflected labial cingulum on upper molars, in having uninflated $P^4$ and $P_4$, in lacking a paraconid on $P_4$, and in having a more labially positioned hypoconid on lower molars.

**Etymology**—*Eo,* Greek, morning, referring to the Eocene, and *oryctes,* Greek (masc.), digger, the common suffix for palaeoryctids.

**Discussion**—Romer (1966: 381) published the name *Eoryctes* in a list of genera in his classification of mammals, but did not include a species name, description, indication, or figure of the animal in question. *Eoryctes* Romer is a nomen nudum, unavailable for purposes of zoological nomenclature. *Eoryctes,* published here in combination with the name of a new species and valid indication, is now available as the name of an animal genus.

### *EORYCTES MELANUS,* sp. nov.
### Figures. 1–7

**Holotype**—UM 68074, cranium and fragment of dentary, collected by K. D. Rose and B. H. Smith.

**Type Locality**—University of Michigan locality SC-133 (NW ¼, Sec. 1, T55N, R102W, Park County) in the Clarks Fork Basin, Wyoming.

**Referred Material**—UM 72623, well preserved neurocranium with crushed basicranium (locality SC-2); UM 74113, orbital region of a skull with fragments of right $P^3$–$M^3$ and left $P^4$–$M^2$ (SC-47); UM 79657, isolated right $M_x$ (SC-213); UM 79703, neurocranium (SC-133); UM 80777, isolated left $M^2$ (SC-26); UM 82162, left and right dentaries with left crowns of $P_{3-4}$, roots of $M_1$, and anterior alveolus of $M_2$, and right alveolus for $I_1$, roots of $C_1$ and $P_{3-4}$, and anterior root of $M_1$ (SC-213); UM 87472, isolated right $M_x$ (SC-210).

**Age and Distribution**—Early Wasatchian Land-Mammal Age (early Eocene), of the Clarks Fork Basin, Wyoming. UM 80777 and UM 87472 are from zone Wa-1; the other specimens are from zone Wa-2 or Wa-3 in the system of range zones described by Gingerich (1983).

**Diagnosis**—As for genus.

**Etymology**—*melanus,* Greek, black, alluding to the color of available specimens. Undescribed palaeoryctid specimens representing a different genus and species occur in the middle and late Wasatchian of the Bighorn Basin. These are light in color, which may indicate that the two genera lived in different environments and were buried on different parts of a floodplain.

## DESCRIPTION

### Cranial Morphology

The holotype skull (UM 68074, Figs. 1–3) was preserved in a calcium carbonate soil nodule and prepared using a combination of mechanical and chemical methods. It is possible to determine the extent of most bones because sutures remain unfused. The orbital and temporal fossae, and the basicranium are especially well preserved. The nasal cavity is somewhat deformed but the braincase is undistorted. The part of the rostrum anterior to $P^3$ is missing, and the left maxilla is displaced slightly posterodorsally. Areas of minor damage include the lacrimals, zygomatic arches, pterygoids, ventral walls of the osseous auditory bulla, right promontorium, and supraoccipitals.

The most complete cranium, UM 68074 (holotype), augmented by UM 82162 (anterior dentary), indicates that skull length in *Eoryctes melanus* was about 32 mm. UM 68074 measures 15 mm in maximum breadth across the lambdoid plates. UM 72623 measures 16 mm in maximum breadth across the lambdoid plates. These skulls are larger that those of either *Palaeoryctes puercensis* or *Asioryctes nemegetensis. Eoryctes melanus* is smaller than *Leptictis,* but resembles it in overall proportions of the skull. The dorsal surface of the cranium of *Eoryctes* differs from that of *Leptictis* in having a single sagittal crest on the midline. It also appears to have lacked zygomatic arches. *Asioryctes* had a relatively longer rostrum. The bullae in *Eoryctes* are inflated, and left and right bullae touch each other in the median plane, extending as far rostrally as the anterior side of the oval foramen. A large epitympanic recess is present posterior to the mandibular fossa. The bullae are broken in all specimens, but fragments indicate that the middle ear cavity had mainly osseous walls.

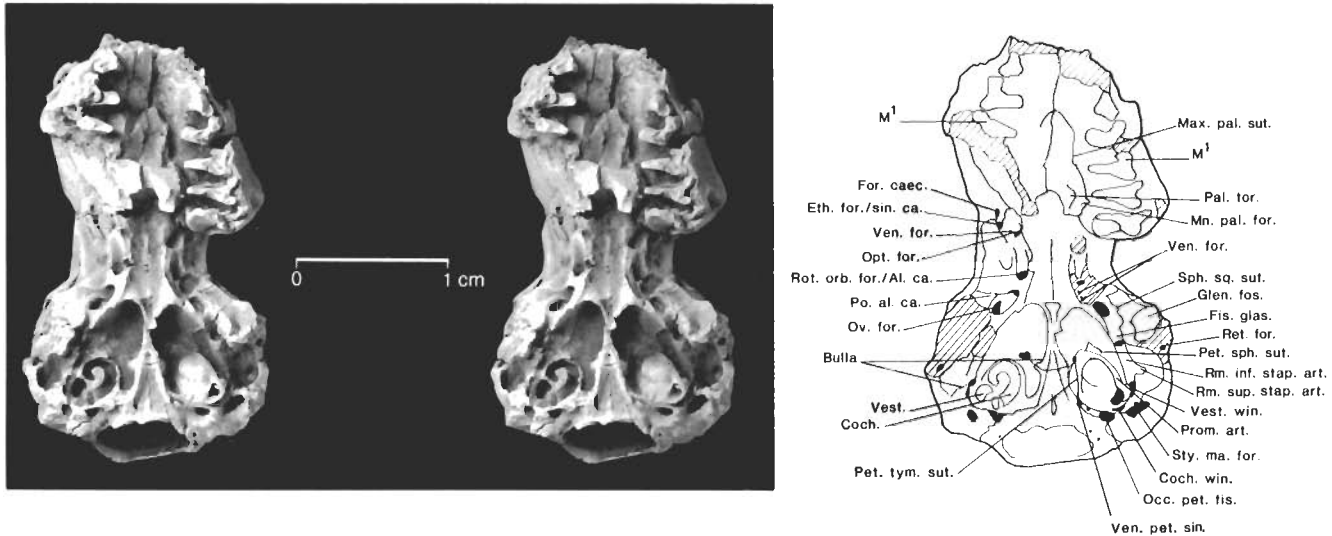**Nasal**—The posterior sides of both nasal bones are

FIGURE 1. Skull of holotype of *Eoryctes melanus,* gen. et sp. nov. (UM 68074). Stereophotographs and labelled line drawing of skull in ventral view.

Abbreviations—Foramina: **Alar. ca.**, alar canal; **An. inf. orb. ca.**, anterior opening of the infraorbital canal; **Coch. Win.**, cochlear window; **Eth. for./sin. ca.**, ethmoid foramen and sinus canal foramen; **For. caec.**, Foramen caecum for frontal diploic vein; **Lac. for.**, lacrimal foramen; **Mn. pal. for.**, minor palatine foramen; **Occ. pet. fis.**, fissure between occipital and petrosal; **Opt. for.**, optic foramen; **Ov. for.**, oval foramen; **Par. em. for.**, parietal emissary foramina; **Po. al. ca.**, posterior opening of alar canal; **Po. inf. orb. ca.**, posterior opening of infraorbital canal; **Py. fen.**, piriform fenestra; **Ret. for.**, retroarticular foramen; **Rot.-orb. for./Al. ca.**, rotundo-orbital foramen and anterior opening for alar canal; **Sty. ma. for.** Stylomastoid foramen; **Ven. pet. sin.**, foramen for ventral petrosal sinus.

Sutures: **Fr. lac. sut.**, suture between frontal and lacrimal; **Fr. max. sut.**, suture between frontal and maxilla; **Fr. nas. sut.**, suture between frontal and nasal; **Fr. pal. sut.**, suture between frontal and palatine; **Fr. par. sut.**, suture between frontal and parietal; **Mas. occ. sut.**, suture between mastoid and exoccipital; **Mas. sq. sut.**, suture between mastoid and squamosal; **Max. pal. sut.**, suture between maxilla and palatine; **Occ. pet. sut.**, suture between basioccipital and petrosal; **Par. sq. sut.**, suture between parietal and squamosal; **Par. mas. sut.**, suture between parietal and mastoid; **Pet. sph. sut.**, suture between petrosal and sphenoid; **Pet. sq. sut.**, suture between petrosal and squamosal; **Pet. tym. sut.**, possible suture between petrosal and tympanic (see text); **Sph. sq. sut.**, suture between sphenoid and squamosal.

Other structures: **Bulla**, wall of auditory bulla; **Coch.**, Cochlea; **Crib. pl.**, cribriform plate; **Epit. rec.**, epitympanic recess; **Ectotym.**, ectotympanic; **Fis. glas.**, Fissura glaseri; **Glen. fos.**, glenoid fossa; **Lamb. pl.**, lambdoid plate; **Pal. tor.**, postpalatine torus; **Pet. or Entotym.**, petrosal or entotympanic; **Prom.**, promontorium; **Prom. art.**, canal for promontorial part of internal carotid artery; **Rm. inf. stap. art.**, canal for inferior ramus of stapedial artery; **Rm. sp. stap.**, canal for superior ramus of stapedial artery; **Sag. cr.**, sagittal crest; **Tym. hy.**, tympanohyoid; **Vest.**, Vestibule.

preserved. They taper posteriorly and have a broad contact with the frontal, as in *Leptictis.* There is no contact with the lacrimal bone (in contrast to the configuration in *Asioryctes.*)

**Frontal**—The nasals are interposed between the frontals as they are in *Leptictis.* The nasofacial muscles originated from a rugose area adjacent to the nasofrontal suture. The sagittal crest starts approximately at mid-orbit, increasing in height posteriorly. The suture between the frontals and parietals runs laterally and ventrally approximately in the middle of the temporal fossa. After a short undulation posteriorly, it runs rostroventrally until it reaches the orbitosphenoid. At this point the frontal projects ventrally and houses the joint opening for the ethmoid foramen and sinus canal, and just anterior to it, a foramen for the frontal diploic vein. From the latter foramen a canal extends dorsally within the diploe of the frontal bone. This canal is visible because a mid-orbital break occurred partly

along this canal. At approximately 3 mm lateral to the midline of the skull the break changed direction and extended mediocaudally, whereas the canal continues its medial course and becomes invisible. From here the canal probably extends about 1–2 mm to the large canals projecting rostrolaterally from the olfactory bulbs. A similar condition is present in *Talpa europaea,* where the canal carries the frontal diploic vein (Thewissen, 1989).

The foramen for the sinus canal of *Eoryctes* is much smaller than that of *Asioryctes.* The suture between frontal and palatine extends obliquely dorsorostrally from this point in *Eoryctes.* There is no postorbital process.

**Parietal**—The parietals cover the dorsal and lateral surface of the braincase, reaching ventrally as far as the oval foramen. From the oval foramen, the suture with the sphenoid extends anterodorsally where it reaches the frontal and bends posterodorsally. The pos-
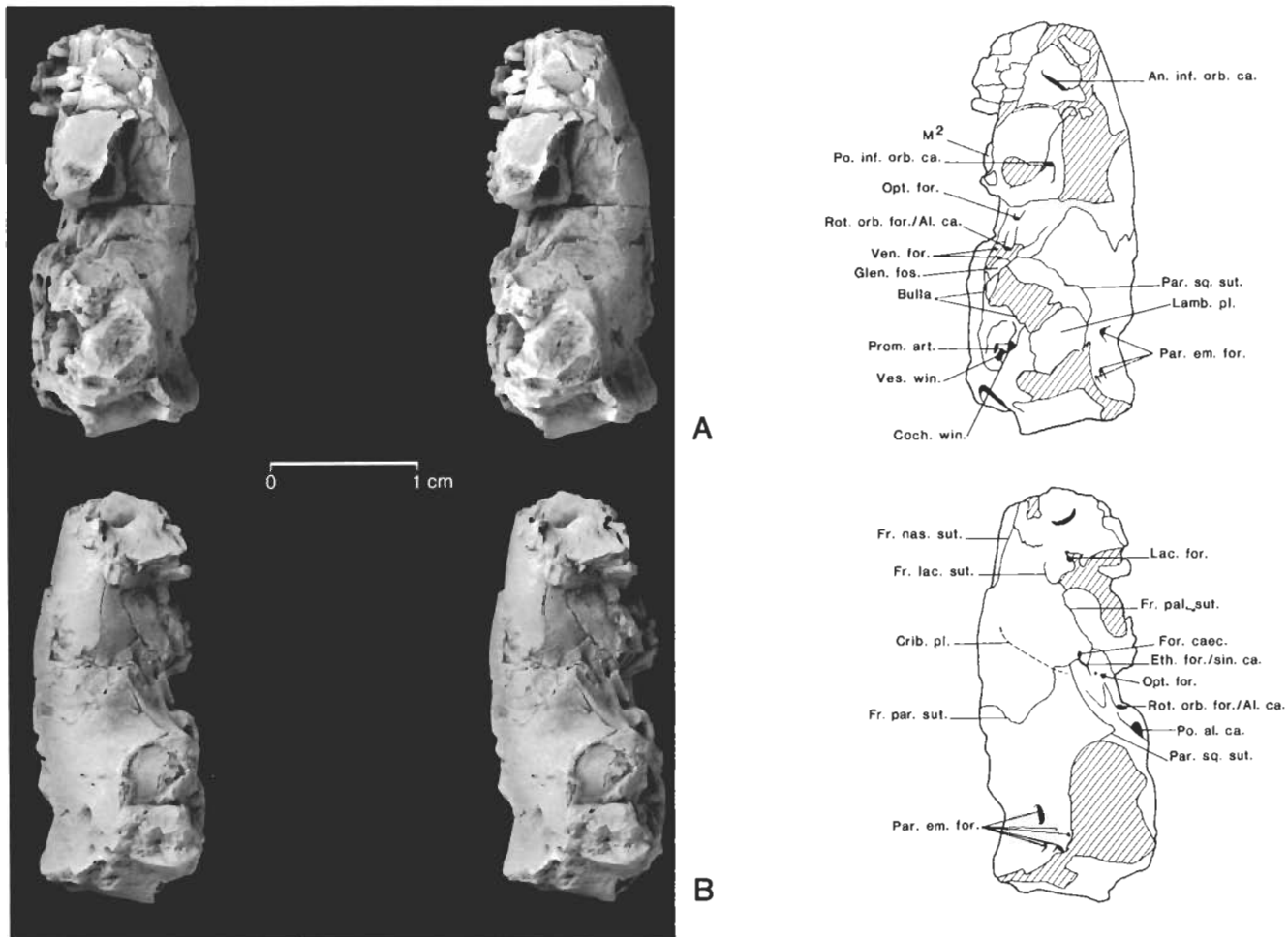
FIGURE 2.   Skull of holotype of *Eoryctes melanus,* gen. et sp. nov. (UM 68074). Stereophotographs and labelled line drawings of skull in left (**A**) and right (**B**) lateral view. The intersection of the cribriform plate with the frontal is indicated as a dashed line in Figure 2B. Abbreviations as in Figure 1.

terior suture of the parietal follows the outline of the lambdoid plate, bends dorsally at the nuchal crest, and undulates to the medial plain of the skull. The parietal touches the squamosal, petrosal, and occipital posteriorly. The sagittal crest is weaker than the nuchal crests.

One large and several small foramina pierce the parietal dorsal to the squamosal. Their position and size differs between the two sides of the holotype skull. On the right side a shallow groove extends from both foramina caudodorsally, indicating the course of a vessel. The largest foramen in the holotype matches the oval foramen in size. It is anterior to the smaller foramina and well dorsal to the suture between parietal and squamosal. A large groove extends dorsally and posteriorly from it. Four small foramina and one large foramen are present in this region in UM 72623, whereas UM 79703 has one small and one large foramen.

Cartmill and MacPhee (1980) described an artery piercing the skull in this position in *Tupaia,* and Wible (1987) stated that perforating branches of the stapedial artery pierce the parietal in this area in many placen-

tals. In *Eoryctes* these canals emerge endocranially in the large depression that houses venous sinuses and the parietal and superior rami of the stapedial artery. These foramina are probably partly venous (parietal emissary foramina) and partly arterial. Two smaller foramina trace the root of the nuchal crest dorsally on either side.

**Maxilla**—The anterior parts of the maxillae are not preserved in the available specimens of *Eoryctes.* On the dorsum of the skull the maxilla touches both the nasal and lacrimal. The anterior orbital rim appears to have been directly above $M^1$. The rostrum is broken at the suture between the frontal and maxilla. This suture extends from the lacrimal mediorostrally to the nasal, lying in approximately the same position as it does in *Leptictis.*

The posterior opening of the infraorbital canal is above $M^2$, and its anterior opening is over $P^4$. The canal is thus longer than in *Leptictis.* The anterior opening of the infraorbital canal measures about 1.6 mm in height and 0.8 mm in breadth. This is larger
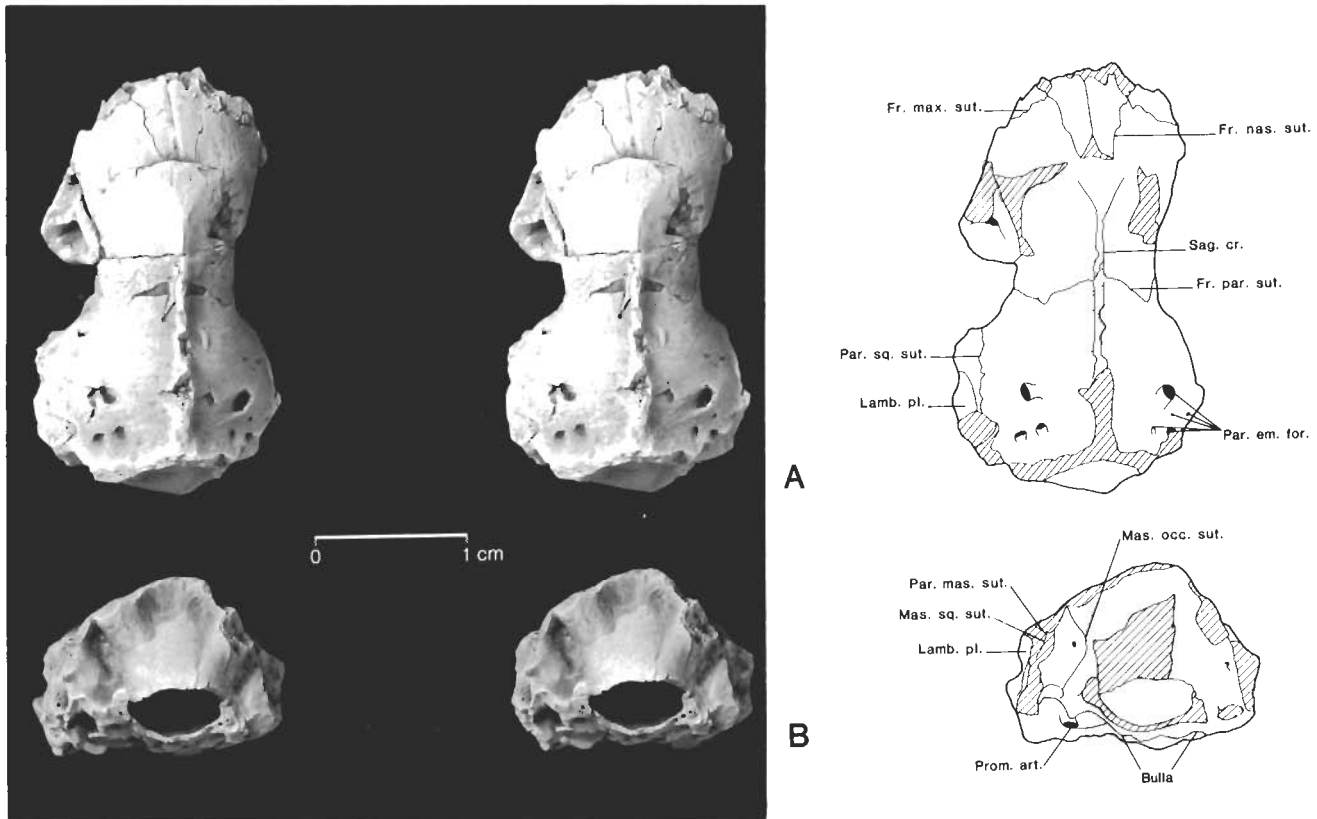
FIGURE 3. Skull of holotype of *Eoryctes melanus,* gen. et sp. nov. (UM 68074). Stereophotographs and labelled line drawings of skull in dorsal (**A**) and posterior (**B**) view. Abbreviations as in Figure 1.

than the infraorbital canal of either *Asioryctes* or *Palaeoryctes,* and it probably indicates that *Eoryctes* had a sensitive rostrum. There is no antorbital fossa.

The part of the maxilla ventral to the orbit is deep in *Eoryctes.* In contrast, the suborbital part of the maxilla is shallow in *Asioryctes.* A small area of the suborbital part of the maxilla is damaged in the holotype of *Eoryctes,* but this is preserved in UM 74113. The zygomatic process originating from it is very small and, while the tip of this process is damaged, it appears unlikely that *Eoryctes* had a complete ossified zygomatic arch. Again in contrast, the zygomatic arch of *Asioryctes* is complete.

The palate is distorted in the holotype of *Eoryctes,* but the main crack appears to have developed along the suture between the palatines and maxillae. This suture shows that each palatine indented the palatal portion of the maxilla as far anterior as $P^3$, and that the maxilla does not contribute to the postpalatine torus.

**Lacrimal**—Only a small part of the lacrimal is preserved on the right side of the skull, pierced by the lacrimal foramen. The facial process is damaged, but is was probably small, as in *Leptictis.* The lacrimal has a suture with the maxilla, the frontal, and the palatine.

**Ethmoid**—Parts of the ethmoid are visible in the anterior part of the cavity for the olfactory bulbs. The cribriform plate is partly exposed on the right side of the skull. Most of it is covered by matrix, but it appears to be flat. The position of its intersection with the frontal is indicated in Figure 2B. The cribriform plate is missing on the left side of the skull, and parts of the perpendicular lamina, the external lamina, and the ethmoidal labyrinth are visible.

**Palatine**—The perpendicular lamina of the palatine is large. Its suture with the frontal extends obliquely dorsorostrally from the posterior edge of the postpalatine torus to the dorsal side of the lacrimal bone, as it does in *Leptictis.* The sphenopalatine and caudal palatine foramina are not preserved. The postpalatine torus is broad anteroposteriorly but low dorsoventrally, and its height increases laterally. The postpalatine torus extends posteriorly on the sphenoidal process. A bony process emerging from the lateral side of the postpalatine torus from the boundary of the postpalatine notch. The postpalatine torus of *Asioryctes* and *Palaeoryctes* is weaker than that of *Eoryctes.*

**Sphenoid**—Sutures between bones of the sphenoid complex are obliterated, and these will not be discussed individually. The optic foramen is adjacent to the root of the pterygoid process of the palatine bone. On the right side of the holotype the foramen is damaged, and the optic canal in the sphenoid is exposed. The canal is approximately 2.8 mm long. Dorsal to it is a small

foramen, probably for a vein. The optic foramen is smaller than in *Leptictis* and *Asioryctes*. The round foramen and the sphenorbital fissure are confluent, forming the rotundo–orbital foramen. The rotundo–orbital foramen opens with the anterior opening of the alar canal and is about 3.2 mm posterior to the optic foramen. A groove extends anteriorly from the rotundo–orbital foramen.

The alar canal in *Eoryctes* is shorter than that of *Leptictis*. Its lateral wall is broken on the left side of the holotype skull, exposing two small foramina in its medial wall. The posterior of these corresponds to the suboval foramen of Novacek (1986). Study of the endocast confirms that these foramina are not for the transmission of parts of the fifth cranial nerve; there is no separate round foramen in *Eoryctes melanus*. Instead these small foramina probably carried vessels to the diploic space of the basisphenoid.

The oval foramen is about 0.8 mm posterior to the posterior opening of the alar canal and just medial to the most anterior part of the middle ear cavity. The sphenoid complex forms part of the dorsal wall of the middle ear cavity. The anterior edge of the middle ear cavity of UM 72623 is undamaged and rounded. The alisphenoid does not contribute to the anterior or ventral walls of the middle ear cavity. The suture between basisphenoid and petrosal extends mediolaterally. The piriform fenestra and the foramen for the entrance of the internal carotid artery into the braincase are on this suture. A small foramen in the sphenoid occurs anteriorly in the middle ear cavity. There is a posterior opening for the pterygoid canal in this position in *Erinaceus* (Butler, 1948). Van Valen (1966) interpreted a similar foramen in *Palaeoryctes* as transmitting the internal carotid artery. Because the internal carotid artery enters the braincase lateral to this foramen, the foramen probably transmits the pterygoid canal. Posterior to this, the bullae actually touch in the midline of the skull. The alisphenoid bears a process between the bulla and the glaserian fissure in UM 72623.

**Squamosal**—The lateral aspect of the squamosal is dominated by a large lambdoid plate: a shallow oval depression with a rugose texture, bounded by irregular ridges (Gawne, 1968). It is dorsal to the external auditory meatus, and its posterior ridge is continuous with the nuchal crest. The ridge that bounds the lambdoid plate on the anterior side is well posterior to the suture between parietal and squamosal. *Asioryctes* lacks a lambdoid plate.

A small fissure is present on the suture between squamosal and mastoid in *Eoryctes*. From the endocast it is not clear if this fissure opens into the braincase. The ventrolateral part of the squamosal is damaged, and the lateral sides of the mandibular fossa and zygomatic arch are not preserved. The medial part of the mandibular fossa is flat and bordered medially by a weak process. In UM 72623, the retroarticular process is large and the mandibular fossa cylindrical. The retroarticular foramen is anterolateral to the epitympanic recess. This foramen is much larger in *Asioryctes* than
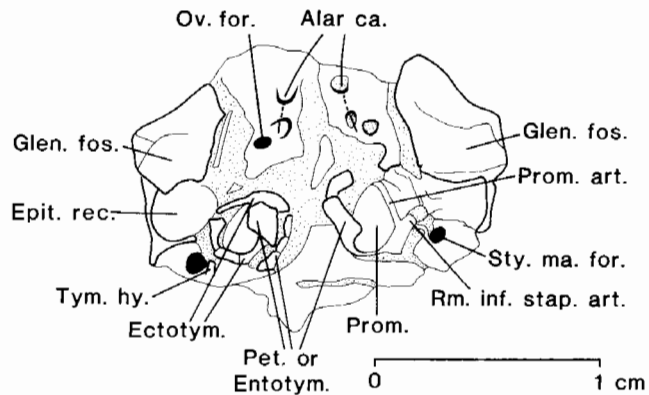


FIGURE 4.   Basicranium of referred specimen of *Eoryctes melanus*, gen. et sp. nov. (UM 72623), in ventral view. Abbreviations as in Figure 1.

in *Eoryctes*. A single small suprameatal foramen is present in the holotype, whereas two are present in UM 72623.

**Petrosal**—The mastoid portion of the petrosal is extensively exposed on the caudal aspect of the skull; it reaches dorsally as far as the suture between the squamosal and the parietal, and its medial edge is directly adjacent to the occipital condyle. There is no mastoid foramen on the suture between the occipital and mastoid, but a small mastoid emissary foramen pierces the dorsal portion of the mastoid. The mastoid emissary foramen is absent in UM 72623. The ventral side of the mastoid is broken in the holotype but present in UM 72623. It is rugose and there is no mastoid process. The stylomastoid foramen is large. The course of the facial nerve is not exposed in the middle ear cavity because it is covered by the tube for the inferior ramus of the stapedial artery.

A large epitympanic recess is present between the stylomastoid foramen and the glenoid fossa, dorsal to the external auditory meatus. The lateral part of the epitympanic recess is formed by the squamosal. *Asioryctes* and *Palaeoryctes* lack an epitympanic recess.

A flange of bone extends ventrally from the medial side of the middle ear to form a bony bulla. In the holotype all edges of the middle ear cavity are broken, but most are preserved in UM 72623. Posteriorly the bony bulla originated from the petrosal medial to and continuous with the canal for the internal carotid artery. The whole medial side of the petrosal also formed an origin for the bulla.

A large part of the medial wall of the bony bulla is preserved, in fragments, in UM 72623 (Fig. 4). No sutures are visible between the medial wall of the bulla and the promontorium, suggesting that the medial wall was formed by the petrosal. However, in UM 68074 a longitudinal fissure occurs on both sides of the skull between the promontorium and the medial wall: if this fissure is a suture and not a crack, then it is possible that the medial wall of the bulla is formed by a different bone, the entotympanic.

The ventral surface of the auditory bulla is fragmented in UM 72623, but visual refitting of the pieces suggests that there was no gap between the petrosal (or entotympanic) medially and the ectotympanic laterally. The lateral edge of the bony ventral surface of the bulla has a somewhat dorsally reflected flange, which in life probably articulated with the ectotympanic. Thus the ventral surface of the bulla was almost certainly ossified.

A large process, representing the fused tympanohyoid, occurs medial to the stylomastoid foramen. Medial to the stylomastoid foramen is the petro-occipital fissure, and medial to it, on the suture between petrosal and basioccipital, is the small foramen for the ventral petrosal sinus. The latter foramen is only preserved on the left side of the holotype.

The promontorium is large and rounded. A bony tube for the internal carotid artery, with a diameter of approximately 1.0 mm, is present on its posterolateral side. The artery is thus in a transpromontorial position (terminology of Wible, 1986). The arterial system of the middle ear was shielded ventrally by bone for all of its course inside the bony bulla. The internal carotid artery gives off a stapedial branch medial to the vestibular window. The bony tube for the promontory branch of the internal carotid artery is narrower (0.6 mm in the holotype) than the tube for the stapedial branch (0.8 mm), and the promontory branch extends anteriorly on the promontorium, disappearing at the suture between the petrosal and sphenoid. The tube for the stapedial artery extends laterally and is interrupted at the vestibular window. Lateral to the vestibular window this tube divides. The larger division, the inferior ramus of the stapedial artery, is not shielded dorsally (opening into the braincase). It runs anteriorly and leaves its bony sheath at the glaserian fissure. The inferior ramus is marked by a groove on the sphenoid, and it extends towards the oval foramen and alar canal. The sheath for the inferior ramus probably covers the facial canal in the middle ear cavity.

The smaller superior ramus of the stapedial artery runs laterally into the epitympanic recess and disappears into the braincase. The facial canal of *Palaeoryctes* and *Asioryctes* is exposed, and the arteries of the middle ear are in grooves. *Asioryctes* lacks a groove for the internal carotid artery on the promontorium. On the right side of the holotype skull the promontorium is broken and the vestibule, osseous labyrinth, and part of the semicircular canals are exposed.

**Ectotympanic**—The ectotympanic is present on the right side of UM 72623. It is displaced, cracked, and partly covered by bulla fragments. Its posterior crus consists of a short rounded process that widens ventrally to become a flat bony plate. It is 1.8 mm wide at its widest point. Only small fragments of the anterior crus of the ectotympanic are preserved.

**Occipital**—The suture between the occipital and the mastoid extends from the nuchal crest straight medially and bends ventrally near the foramen magnum. The latter part of the suture is in a depressed area, and

the part of the occipital over the foramen magnum is domed. The occipital condyles are broken in the holotype but partly preserved in UM 72623. The posterior opening for the condyloid canal is exposed in the holotype, opening into the foramen magnum. Ventrally, most of each basioccipital is covered by a large bony auditory bulla. The hypoglossal canal is obscured in the holotype but preserved in UM 72623. Contact of the basioccipital and basisphenoid is medial to the piriform fenestra.

**Dentary**—The dentary of UM 68074 (holotype, Fig. 5) is fragmentary; alveoli for the lower canine, $P_2$, and $P_3$ are preserved, and the crown of $P_4$ is present. In UM 82162, the anterior part of the mandibular ramus is preserved from $P_2$ to the anterior alveolus for $M_1$. The mandibular symphysis reaches as far posteriorly as $P_3$ in both, and mental foramina in the holotype are below the anterior root of $P_3$ and between the roots of $P_4$ on the labial side of the jaw. A small additional foramen occurs below $P_2$ in UM 82162.

## Dentition

The dental formula of *Eoryctes melanus* is $I^{3?}/_{3?}C^{1?}/_1$-$P^{3?}/_3M^3/_3$. Tooth crowns are known in the holotype (Figs. 1, 5) and in five of the referred specimens (Fig. 6).

**Upper Dentition**—$P^3$, $P^4$, and part of $M^1$ are preserved on the right side of the holotype, and $P^3$—$M^3$ are preserved on the left side. The labial sides of all upper teeth are damaged to varying degrees. The outline of $P^3$ is preserved on the right side of the holotype, whereas on the left side its crown is worn. $P^3$ has three roots of approximately equal size. There is no protocone, but the base of the crown bulges lingually where it covers the lingual root. The lingual side of the tooth is stronger in *Asioryctes nemegetensis*, but weaker in *Palaeoryctes puercensis*. The paracone is rounded anteriorly and has a sharp edge posteriorly. There is a small parastyle, and a cingulum is only present on the posterolabial side. The parastyle is absent in *Aaptoryctes ivyi*, weak in *Palaeoryctes puercensis*, and stronger than *Eoryctes* in *Asioryctes*. $P^3$ measures 2.0 mm in length and 1.3 mm in width in the holotype of *Eoryctes melanus*.

The left $P^4$ of the holotype lacks the posterior half of the crown, and the right $P^4$ is damaged labially. It is uninflated, unlike *Aaptoryctes*. The protocone is high crowned and narrow anteroposteriorly. The protocone is closer to the labial cusps in *Palaeoryctes puercensis* and *Pararyctes pattersoni* Van Valen, 1966. $P^4$ of *Eoryctes* widens labially. The parastyle is stronger than in *Palaeoryctes puercensis* and *Pararyctes pattersoni*, and there are no conules. The metacone of $P^4$ of UM 74113 is high and pointed, and the tooth has a broad posterolabial cingulum, unlike *Palaeoryctes puercensis*, *Pararyctes*, or *Aaptoryctes*. The protocone is on a medial shelf of the tooth and not rostrally displaced as in *Pararyctes*. The holotype $P^4$ measures 2.3 mm in length and 2.4 mm in width.
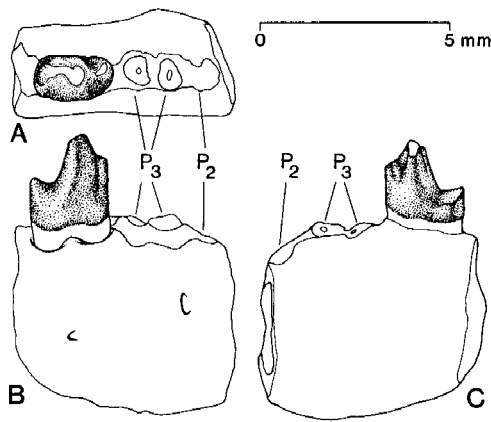
FIGURE 5. Left dentary of holotype of *Eoryctes melanus*, gen. et sp. nov. (UM 68074). Alveoli for $C_1$, single-rooted $P_2$, and double-rooted $P_3$, and crown of $P_4$ are shown in (A) occlusal, (B) labial, and (C) lingual view.

The upper molars are narrow lingually, and the protocone is high crowned (the lingual root of $M^3$ is visible in Fig. 2). Cingula are absent, unlike in *Pararyctes*. $M^1$ can be distinguished from $M^2$ by its more labially directed parastyle. $M^2$ has a preprotocrista, but no postprotocrista. No $M^2$ is known for *Palaeoryctes punctatus*, but $M^1$ has a postprotocrista. The parastyle and metastyle are on strong labial flanges that are separated by a deep notch in *Eoryctes*. This notch is stronger than in *Palaeoryctes puercensis, Palaeoryctes pattersoni*, and *Pararyctes*. There are no conules, unlike *Palaeoryctes punctatus*. UM 80777 is unworn, and its metacone is small and close to the paracone, making the tooth zalambdodont. There is no metastyle, but a crest runs from the metacone posteriorly to the cin-

gulum. In the holotype, $M^2$ measures 1.8 mm in length and 3.6 mm in width. $M^3$ measures 2.1 mm in length and 1.2 mm in width. $M^2$ in UM 80777 measures 1.8 mm in length.

**Lower Dentition** — Alveoli for two lower incisors are preserved in UM 82162. There is a small depression near the midline that may be either the base of the alveolus of $I_1$ or a nutrient foramen. The alveolus for $I_2$ is relatively large, measuring 1.0 MM labiolingually and 0.7 mm mediolaterally. The alveolus for $I_3$ is very small, indicating a tooth with a root only about 0.3 mm in diameter. A large $I_2$ flanked by much smaller $I_1$ and $I_3$ is a configuration typical of other palaeoryctids where anterior teeth are known. The canine of *Eoryctes melanus* measures 2.1 × 1.7 mm at the base of the crown.

$P_1$ is absent; $P_2$ has one root; and $P_3$ has two roots. $P_3$ of UM 82162 has a weak parastyle. A crest connects the protoconid to the only cusp on the talonid. $P_3$ measures 1.7 mm in length and 0.8 mm in width. $P_4$ is present in the holotype and UM 82162. It is uninflated, unlike *Aaptoryctes*, and has a large protoconid and a small paraconid. The paraconid is absent in both *Aaptoryctes* and *Asioryctes*. $P_4$ of *Eoryctes* lacks both a paracristid and a metaconid. A heavily worn crest connects the protoconid with the talonid. There is only one central cusp on the posterior extremity of the talonid. $P_4$ in the holotype measures 2.1 mm in length and 1.2 mm in width. $P_4$ in UM 82162 measures 2.2 mm in length and 1.1 mm in width.

Two lower molars are referred to *Eoryctes*: UM 79657 and UM 87472. Neither can be identified to tooth position. The protoconid is high and connected to the metaconid by a notched metacristid. The paracristid is present in both specimens, but weaker in UM 79657 than in UM 87472. The talonid is narrow, and the
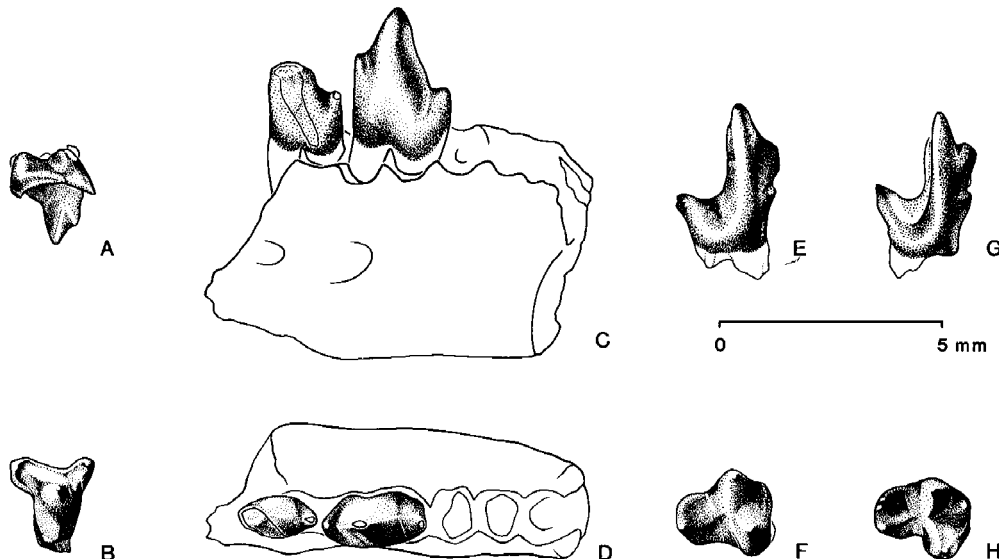


FIGURE 6. Referred specimens of *Eoryctes melanus*, gen. et sp. nov. A and B, Left $M^2$ (UM 80777); C and D, left dentary with $P_{3-4}$ (UM 82162); E and F, right $M_x$ (UM 79657); G and H, right $M_x$ (UM 87472); each in labial and occlusal view, respectively.
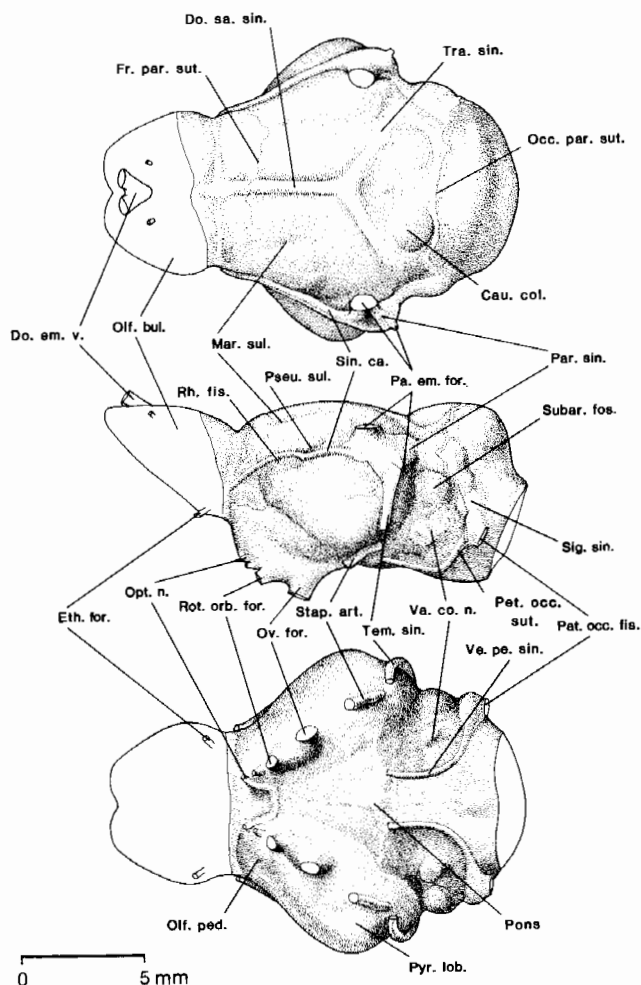
FIGURE 7. Endocast of holotype of *Eoryctes melanus*, gen. et sp. nov. (UM 68074) in **A**, dorsal; **B**, left lateral; and **C**, ventral view. Lateral view is a composite: some structures shown on the left side here are only visible on the right side of the endocast. Unstippled area was not cast and it is reconstructed on the basis of direct observation and measurement of the specimen.

Abbreviations—**Cau. col.**, caudal colliculus of mesencephalon; **Do. em. v.**, canal for dorsal emissary vein; **Do. sa. sin.**, canal for dorsal sagittal sinus; **Eth. for.**, ethmoid foramen; **Fr. par. sut.**, suture between frontal and parietal; **Mar. sul.**, marginal sulcus; **Occ. par. sut.**, suture between occipital and parietal; **Olf. bul.**, olfactory bulb; **Olf. ped.**, olfactory peduncle; **Opt. n.**, canal for optic nerve; **Ov. for.**, oval foramen; **Pa. em. for.**, parietal emissary foramen; **Par. sin.**, canal for parietal sinus; **Pet. occ. fis.**, petro-occipital fissure; **Pet. occ. sut.**, suture between petrosal and occipital; **Pons**, Pons; **Pseu. sul.**, pseudosylvian sulcus; **Pyr. lob.**, piriform lobe; **Rh. fis.**, rhinal fissure; **Rot. orb. for.**, rotundo–orbital foramen; **Sig. sin.**, sigmoid sinus; **Sin. ca.**, sinus canal; **Stap. art.**, canal for inferior ramus of stapedial artery; **Subar. fos.**, subarcuate fossa;**Tem. sin.**, canal for temporal sinus; **Tra. sin.**, canal for transverse sinus; **Ve. co. n.**, canal for vestibulo–cochlear nerve; **Ve. pe. sin.**, canal for ventral petrosal sinus.

crista obliqua is weak. A strong crest with three small cusps on its summit is present on the posterior side of the talonid. The cusps are higher than in *Pararyctes* and *Aaptoryctes,* and the talonid is weaker than in *Aaptoryctes.* The hypoconid is more labial than in *Palaeoryctes puercensis.* The paraconid and metaconid are closer to each other than they are in *Asioryctes.* UM 79657 measures 2.3 mm in length, 1.8 mm in trigonid width, and 1.1 mm in talonid width. UM 87472 measures 2.2. mm in length, 1.8 mm in trigonid width, and 1.1 mm in talonid width.

## BRAIN MORPHOLOGY

Information on the brain of *Eoryctes melanus* is preserved within the cranium. A latex endocast was made of most of the cranial cavity of the holotype, but the anterior parts of the olfactory bulbs were considered too delicate for casting because fragile parts of the ethmoid are exposed there. The endocast, partially reconstructed, is illustrated in Figure 7. The brain as a whole appears to have been relatively large for an early Eocene insectivore. As expected, the olfactory bulb is large and the olfactory tubercle and piriform lobe make up most of the cerebrum. There is very little neocortex. The midbrain is partially exposed, with large caudal colliculi or posterior corpora quadrigemina. The cerebellum is moderately large. Taken together, these proportions indicate that olfaction was the dominant sense in *Eoryctes.*

### Description of Endocast

Details are summarized under three headings: the size of the brain and its size relative to body size, organization of the neural system, and organization of the vascular system of the cranial cavity.

**Endocranial Volume**—The volume of the cranial cavity can be estimated in the holotype, UM 68074, by adding the volume of water displaced by the endocast (0.08 cm$^3$) to the volume of water needed to fill the anterior part of the olfactory bulbs (0.16 cm$^3$). Together these measures indicate that the brain of *Eoryctes melanus* was very close to 1.0 cm$^3$ in volume. Brain tissue has a density close to that of water, and the mass of the brain of *Eoryctes* was thus about 1 g.

Absolute brain size means little by itself; the more interesting quantity is the relationship of brain size to body size. Relative brain size is usually quantified as an encephalization quotient (EQ) or ratio of observed brain mass to expected brain mass for a given body mass. Teeth can be used to estimate body weight in many extant insectivores (Gingerich and Smith, 1984), but tooth size and body weight are poorly correlated in zalambdodont species. Skull length is correlated with body weight ($r = 0.97$) in a wide range of extant insectivores including zalambdodont species, and skull length yields a predicted body weight of 51 g for *Eoryctes melanus* (Fig. 8).

According to Jerison (1973), brain weight (E) scales

at the two-thirds power of body weight (P), the relationship being $E = 0.12 \ P^{0.67}$. Given a body weight of 51 g, the expected brain weight of *Eoryctes* is 1.67 g. The Jerison EQ of observed brain weight/expected brain weight is thus $1.00/1.67 = 0.60$.

According to Martin (1981), brain weight scales at the 0.76 power of body weight, the relationship being $E = 0.059 \ P^{0.76}$. This yields an expected brain weight for *Eoryctes* of 1.17, and a Martin EQ of observed/ expected is thus $1.00/1.17 = 0.85$. Martin (1981) noted that Jerison's formula overestimates expected brain sizes for small mammals, thus yielding anomalously small EQ values. Our result using Martin's formula indicates that the brain of *Eoryctes*, with an EQ of 0.85, was 85% as large as the brain of an average extant mammal of the same body weight. The brain of early Eocene *Eoryctes* is larger than one would expect for an extant "basal insectivore," falling rather in the group Bauchot and Stephan (1966) characterized as extant "evolved insectivores."

**Nervous System of the Cranial Cavity**—The cribriform plate was partly damaged during preparation, and it remains partly covered by sediment. Parts that are visible appear to indicate that it was flat. In the rhinencephalon, the olfactory peduncle is somewhat inflated and shows impressions for the optic nerves and optic chiasm. A small canal posterior to the optic nerve appears to enter the diploic space of the sphenoid. Posterior to this canal is the impression for the rotundo–orbital foramen and, more caudally, that for the oval foramen. The roots of the latter two branches merge, indicating the position of the semilunar ganglion. The piriform lobe is large and shows a longitudinal sulcus anteriorly on the right side. This sulcus is much shorter on the left side.

The rhinal fissure delimiting neocortex from underlying forebrain appears to follow the sinus canal in *Eoryctes,* as it does in *Leptictis* (Novacek, 1982). The rhinal fissure forms a depression in the endocast dorsal to the olfactory peduncles, and it terminates rostral to the parietal emissary foramina. A faint pseudosylvian fissure crosses the rhinal fissure on the left side, and a marginal sulcus is weakly developed on the suture between the frontal and parietal on both sides. The marginal sulcus forms a more or less circular depression of the left side of the endocast, and it is elongated on the right side. In contrast, the only other palaeoryctid for which an endocast is known, *Asioryctes,* lacks cerebral sulci (Kielan-Jaworowska, 1984).

The mesencephalon or midbrain is exposed at the dorsal surface of the endocast between the transverse sinus and the suture of the occipital and the parietal. Low swellings indicate the positions of left and right caudal colliculi, auditory centers, as in *Asioryctes* and *Leptictis*. Little detail is preserved on the cerebellum, and the vermis is not even set off. Laterally, a cast of the subarcuate fossa of the petrosal is visible, and ventral to it is the root for the vestibulocochlear nerve. The pons is visible as a small swollen area on the caudal part of the brain stem.
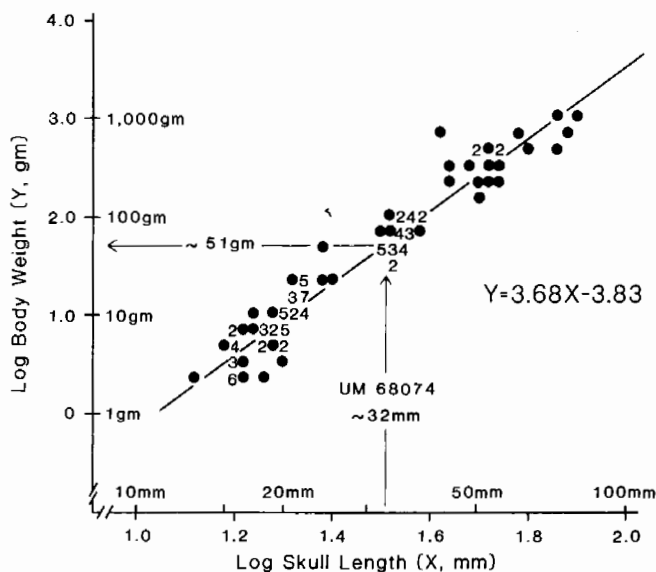
INSECTIVORES



FIGURE 8. Prediction of body weight from skull length in *Eoryctes melanus,* gen. et sp. nov. Scatter plot and regression showing relationship between body weight (ordinate, dependent variable) and skull length (abscissa, independent variable) for 64 species of extant insectivorous mammals [Chrysochloridae (1 species), Erinaceidae (5), Macroscelididae (2), Potomagalidae (1), Solenodontidae (1), Soricidae (33), Talpidae (14), Tenrecidae (3), and Tupaiidae (4); means for males and females plotted separately when both are available; data from Gingerich and Smith, unpublished]. Skull length of 32 mm in *Eoryctes melanus* (UM 68074) yields an estimated body weight of 51 g for this species.

**Vascular Structures of the Cranial Cavity**—Structures piercing the ethmoid foramen are visible on the lateral part of the ventral surface of the olfactory bulbs, and the larger impression of the frontal diploic vein originates dorsally in the median plane. A smaller diploic vessel lies posterolateral to the frontal diploic vein.

A large venous sinus, here called the parietal sinus, is present on the posterior part of the cerebrum and the anterior part of the cerebellum. Several vessels leave the braincase from the anterior part of this sinus, exiting though the parietal emissary foramina. The temporal sinus wraps around the piriform lobe of the brain, coursing ventrally from the parietal sinus and leaving the braincase through the retroarticular foramen. The sinus canal extends anteriorly from the parietal sinus. *Asioryctes* lacks a large parietal sinus and its sinus canal is situated more ventrally on the cerebrum.

The sigmoid sinus is larger than the temporal sinus, extending to the cerebellar part of the parietal sinus. The sigmoid sinus is irregularly shaped and ends at the petro-occipital fissure. The ventral petrosal sinus is medial to the petrosal and drains through a small foramen on the suture between occipital and petrosal. Small emissary foramina are also present on the suture

between the parietal and supraoccipital. The cerebellar portion of the parietal sinus receives the transverse sinus, which extends anteromedially, and is connected to the dorsal sagittal sinus in the midline of the skull.

The ventral side of the endocast has an impression for the inferior ramus of the stapedial artery. As described before, the stapedial artery and its branches are shielded by bone from the middle ear cavity, but the impression for the inferior ramus of the endocast indicates that this branch is within the braincase at the rostral aspect of the middle ear cavity. It disappears from the cranial cavity posteromedial to the glenoid fossa at the point where squamosal, petrosal, and sphenoid meet.

## DISCUSSION

Palaeoryctidae is a family of Cretaceous and Paleogene zalambdodont placentals. Palaeoryctids were undoubtedly insectivorous, and Van Valen (1966) suggested that *Palaeoryctes punctatus* was fossorial on the basis of a humerus associated with the holotype. *Eoryctes* also shows adaptations for a hidden life in the dark: it probably had poor vision (small optic foramen) but acute hearing (large bullae and epitympanic recess) and a sensitive snout (large infraorbital canal). Its lingually hypsodont upper molars may indicate habitual ingestion of sediment with food items.

Palaeoryctidae lack some characteristics of the order Lipotyphla but have others: palaeoryctids do not have a reduced orbital process of the palatine, nor a reduced retroarticular process, but *Eoryctes* has zalambdodont molars, no jugal, reduced zygomatic arch, and the posterior opening of the cochlear window found in some lipotyphlans (derived characters cited by Butler, 1956; McDowell, 1958; Novacek, 1986). Palaeoryctidae are also not Leptictida: they lack a molarized $P_4$ and $P^4$, an antorbital fossa, and a large exposure of the parietal on the occiput, and the anterior opening of the alar canal and the rotundo–orbital foramen are closer in Palaeoryctidae than in Leptictida (derived characters cited by Novacek, 1986). However, Paleogene Palaeoryctidae agree well with Novacek's (1986) definition of the superorder Insectivora, a group consisting of both Lipotyphla and Leptictida. These share with Palaeoryctidae extensive contact between the maxillary and frontal on the face, small facial expansion of the lacrimal, the presence of a glaserian fissure, and the presence of an elongate medial promontorium crest. The shape of the tympanohyoid of *Eoryctes* is different from that in the two orders recognized within Insectivora, but its fusion with the mastoid is shared. We include Palaeoryctidae in the order or superorder Insectivora sensu Novacek, 1986, and within this, Palaeoryctidae may be most closely related to Lipotyphla.

## ACKNOWLEDGMENTS

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