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THE OLDEST MAMMALIAN PETROSALS FROM NORTH AMERICA

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ABSTRACT—Two fragmentary mammalian petrosals were collected in 1968 and 1969 from the Upper Jurassic Morrison Formation, Bone Cabin Draw, Wyoming, and from the Early Cretaceous Kelvin Formation near Coalville, Utah. The Morrison petrosal (AMNH 104830) came from a mammal with a petrosal as primitive as that of the morganucodonts. This specimen could belong to one of the Morrison triconodonts, a docodont, a very primitive therian, or the last of the morganucodonts. The Kelvin petrosal (AMNH 95184) is extremely fragmentary, and its affinities within the Mammalia are uncertain. No other mammals are known from this locality.

INTRODUCTION

CRANIAL REMAINS of Mesozoic mammals are extremely rare. The oldest mammalian petrosals previously described from North America are latest Cretaceous in age (Clemens, 1966; MacIntyre, 1972; Archibald, 1979), and clearly belong to either placentals or marsupials. Triconodont petrosals from the Late Triassic and Jurassic of England have been described (Kermack, 1963; Kermack et al., 1981). Several Early Cretaceous triconodontid skulls are known from the Cloverly Formation of Montana, but they have not yet been described (Jenkins and Crompton, 1979). The skull structure of the multituberculates has been described by Hahn (1969) and Kielan-Jaworowska (1971). No cranial material has yet been described that can be attributed to the Docodonta or to the non-tribosphenic Theria ("pantotheres"), although a dryolestid therian skull has been reported (Henkel and Krebs, 1977) from the Jurassic of Portugal.

In the summers of 1968 to 1970, a joint expedition of the American Museum of Natural History (AMNH) and Yale University collected Mesozoic mammalian remains in Wyoming. This expedition reopened the famous "mammal quarry," Quarry Nine, in the Upper Jurassic Morrison Formation at Como Bluff, Wyoming. This quarry, first worked by the crews of Othniel C. Marsh of Yale University in the 1880's (Ostrom and McIntosh, 1966), is the source of the vast majority of pre-Cretaceous mammalian remains described from North America. The 1968–1970 excavations produced a number of teeth and jaws (Prothero, 1981) and a battered mammalian petrosal. In the 1969 field season, prospecting by Dr. Thomas H. Rich (then of the American Museum) produced another petrosal fragment from the Lower Cretaceous Kelvin Formation near Coalville, Utah. These two specimens are the oldest mammalian cranial fragments so far reported from North America.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA *incertae sedis*
THE MORRISON PETROSAL
Figures 1A, B

Specimen.—AMNH 104830, a right petrosal fragment missing much of the pars mastoidea.

Occurrence.—"Chuck's Prospect," Bone Cabin Draw, Carbon County, Wyoming (Prothero, 1981).

Geologic horizon.—Morrison Formation, Upper Jurassic (Tithonian).

Description.—The cerebellar (dorsal) surface is shown in Figure 1A. It is slightly concave, with a large broken vestibular area shown in a hachured pattern. At the anterior end, the dorsal surface of the promontorium (cochlear housing) is smooth and slightly convex. In the center of this surface is a single fenestra that penetrates to the fenestrae on the tympanic side. This fenestra is very small and steep-walled, and from its position it would seem to correspond to the foramen for the cochlear branch of the acoustic (VIII) nerve. It does not have the typical morphology of the internal auditory meatus, which normally bears the acoustic nerve. In most mammals (MacIntyre, 1972; Cifelli, 1982), the internal auditory meatus is a broad shal-

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low pit with three foramina separated by a crista. Through these foramina pass the facial (VII) nerve, and two branches of acoustic (VIII) nerve. The lack of such a meatus with its three foramina is known only in some recently described petrosals of *Morganucodon* (Kermack et al., 1981). (The possibility that *Morganucodon* is a junior synonym of *Eozostrodon* is presently very controversial—see Clemens, 1979). The single foramen on the dorsal surface of the promontorium has been interpreted by Kermack et al. (1981) as bearing the acoustic nerve alone; the facial nerve in *Morganucodon* seems to pass laterally via a separate channel (Figure 2). On the lateral edge of the Morrison petrosal is a small, broken sulcus which may correspond to some portion of the canalis facialis (aquaeductus fallopii). A distinct cranial opening for the facial canal, which in *Morganucodon* is anterolateral to the opening for the acoustic nerve (Kermack et al., 1981), is not preserved in the Morrison petrosal. Apparently the anterior portion of the path of the facial nerve did not penetrate the petrosal very deeply in AMNH 104830. There was probably a completely roofed foramen for the acoustic nerve in the undamaged specimen, as is the case in most reptiles and primitive mammals (J. Hopson, pers. commun.).

Medial to the foramen for the acoustic nerve is a broad jugular notch, which curves around the tympanic side. In *Morganucodon* this notch is the petrosal portion of the jugular foramen; the medial portion is formed by the exoccipital (Kermack et al., 1981, p. 86). Through this foramen passed the internal jug-

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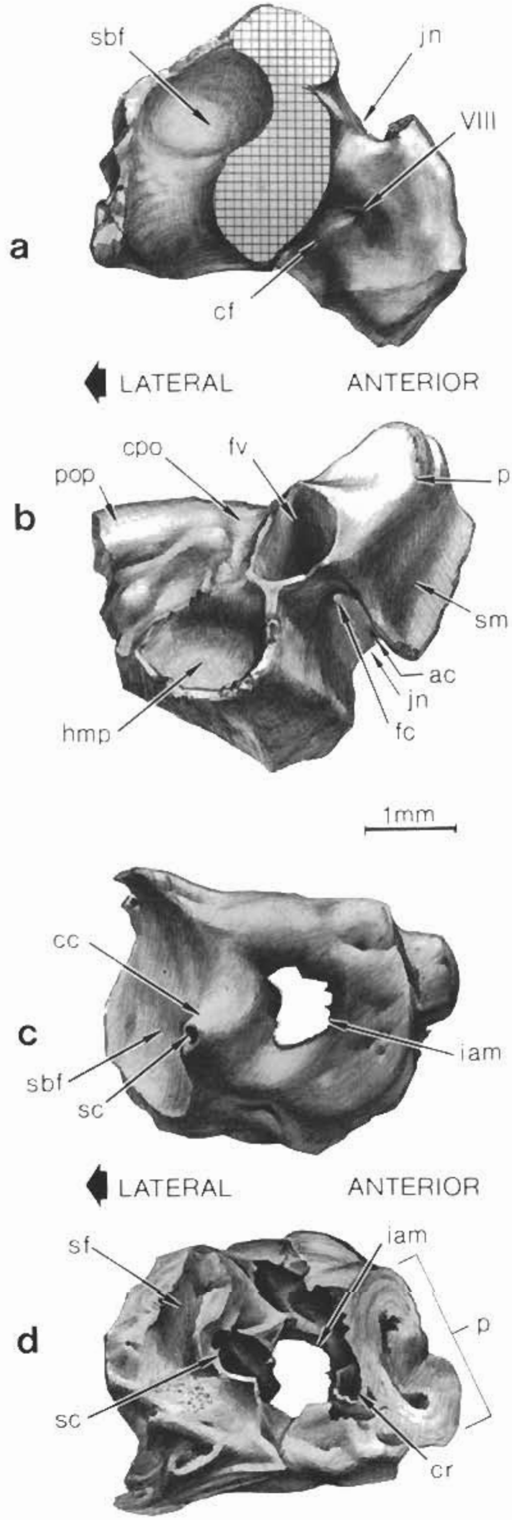

FIGURE 1—*A*, AMNH 104830, cerebellar (dorsal) view and *B*, tympanic (ventral) view. Hachured areas broken. *C*, AMNH 95184, cerebellar (dorsal) view and *D*, tympanic (ventral) view. Abbreviations: ac, aquaeductus cochleae; cc, crus commune; cf, canalis facialis; cpo, canalis prooticus (or possibly sulcus facialis); cr, base of cochlear recess; fc, fenestra cochleae; VIII, foramen for acoustic (VIII) nerve; fv, fenestra vestibuli (ovalis); hmp, pit for levator hyoidei muscle; iam, internal auditory meatus; jn, jugular notch; p, promontorium; pop, paroccipital process; sbf, subarcuate fossa; sc, ?broken vertical semicircular canal; sf, sulcus facialis; sm, sulcus medialis.

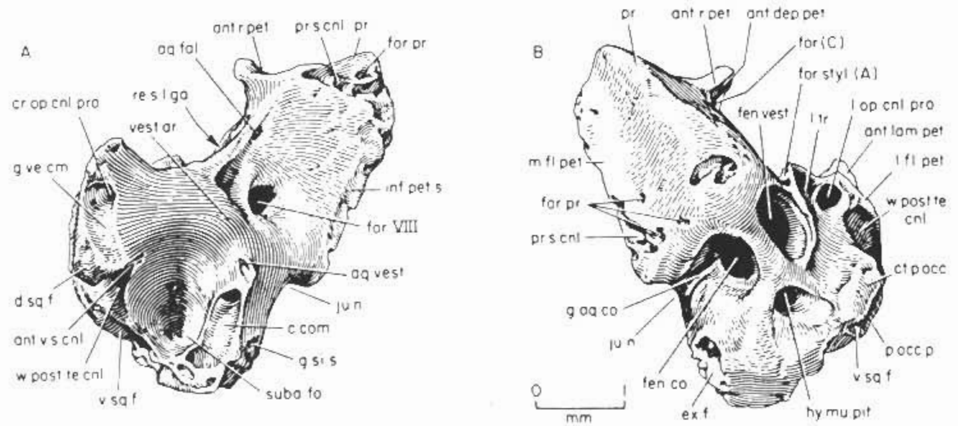

FIGURE 2—Petrosal of *Morganucodon*. British Museum (Natural History) M.21175. *A*, Cerebellar (dorsal) view and *B*, tympanic (ventral) view. From Kermack et al. (1981, Fig. 81). Abbreviations: ant. dep. pet., anterior depressor of petrosal; ant. lam. pet., anterior lamina of petrosal; ant. r. pet., anterior ridge of petrosal; ant. v.s. cnl., anterior vertical semicircular canal; aq. fal., aquaeductus fallopii; aq. vest., aquaeductus vestibuli; c. com., crus commune; cr. op. cnl. pro., cranial opening of canalis pro-oticus; ct. p. occ., crest on paroccipital process; d. sq. f., dorsal squamosal facet; ex. f., facet for exoccipital; fen. co., fenestra cochleae; fen. vest., fenestra vestibuli; for. VIII, foramen for eighth cranial nerve; for. pr., foramen for circum-promontorium plexus; for. styl. (A), foramen stylomastoideum primitivum; g. aq. co., groove for aquaeductus cochleae; g. si. s., groove for sigmoid sinus; g. ve.c.m., groove for vena cerebralis media; hy. mu. pit, pit for levator hyoidei muscle; inf. pet. s., inferior petrosal sinus; ju. n., jugular notch; l. fl. pet., lateral flange of petrosal; l. op. cnl. pro., lateral opening of canalis pro-oticus; l. tr., lateral trough; m. fl. pet., medial flange of petrosal; p. occ. p., paroccipital process; pr., promontorium; pr. s. cnl., circum-promontorium plexus of sinus canals; re. s. l. ga., recess for semilunar ganglion; suba. fo., subarcuate fossa; vest. ar., vestibular area; v. sq. f., ventral squamosal facet; w. post. te. cnl., wall of post-temporal canal.

ular vein and the glossopharyngeal (IX) and vagus (X) nerves. The jugular notch is particularly prominent on the tympanic side.

The vestibular area of the petrosal is badly damaged. None of the internal canals associated with the inner ear are visible. Posterior to this area is a broad elliptical subarcuate fossa which is slightly broken on its posterior rim. The floor of the subarcuate fossa is smooth and without any major foramina, as in *Morganucodon*. Most other mammals (except leptictids and rabbits) show this type of subarcuate fossa, or have lost it altogether. There is no indication in AMNH 104830 of a foramen leading from the floor of the fossa to the cranial opening of the canalis pro-oticus, as in *Ornithorhynchus* (Simpson, 1938), or a foramen leading to the exterior, as in *Oligokyphus* (Kühne, 1956). Lateral to the subarcuate fossa is a broad, smooth, slightly concave area which presumably housed portions of the crus commune. No external trace of the crus commune is visible, however. The posterior edge, where the petrosal contacted the squamosal, is broken.

The tympanic (ventral) surface is shown in Figure 1B. The promontorium is shaped like a flattened triangular prism. The anterior end of the promontorium has been broken, exposing the cochlear recess. The recess does not appear to spiral, although this is difficult to determine from the manner in which the specimen is broken. The promontorium of AMNH 104830 bulges slightly ventrally, as in *Morganucodon* and most other mammals. Although the promontorium of AMNH 104830 is slightly broken, it is clear from the small size of the ventral bulge and the anteriorly tapered shape that the unbroken promontorium would have been very small and could not have housed a spiral cochlea. The promontorium of AMNH 104830 is comparable in size to those reported for *Morganucodon* (Kermack et al., 1981). It is much smaller than the long bladelike promontoria occurring in the triconodonts *Triconodon* and *Trioracodon* (Kermack, 1963), in the multituberculates (Kielan-Jaworowska, 1971, Fig. 12), and in the monotremes (Simpson, 1938). Advanced therian promontoria are greatly inflated and much more rounded in form, due to the presence of a spiral cochlea (MacIntyre, 1972; Cifelli, 1982).

On the medial side of the promontorium is a broad flange running from the jugular notch to the broken anterior tip. On the medioventral surface of this flange is a broad trough-shaped sulcus medialis. According to MacIntyre (1972, p. 291), it may have contained the medial branch of the internal carotid artery and the inferior petrosal sinus vein. But Cifelli (1982, pers. commun.) finds that the inferior petrosal sinus vein lies intracranially to the sulcus medialis in many mammals, and may have done so in the petrosals described by MacIntyre (1972). But there is no groove on the promontorium to indicate that the medial branch of the internal carotid did not pass along the sulcus medialis.

Posterior to the promontorium are two major fenestrae which serve as landmarks on nearly all petrosals: the fenestra vestibuli and fenestra cochleae. On the lateral side of the Morrison petrosal, a large circular fenestra vestibuli (ovalis) faces ventrolaterally. The rim of the fenestra vestibuli is deeply socketed with a raised lip. The nearly circular shape indicates that the footplate of the stapes was also circular, the primitive condition for mammals (Archibald, 1979).

On the medial side of the fenestra vestibuli is a narrow groove which opens anteromedially. It is separated from the fenestra vestibuli by a narrow bony bar. Deep in the posterolateral end of this groove is a large foramen, the fenestra cochleae (rotunda). The interior structure of the cochlea has been broken in such a way that the internal interconnection of the fenestra vestibuli, fenestra cochleae, and the acoustic foramen has been accentuated. In the anterior wall of the groove is a small foramen which may represent the aquaeductus cochleae. The groove terminates anteromedially with a broad jugular notch. The morphology of this groove is strikingly similar to the condition shown in *Morganucodon* and the monotremes. In advanced therian mammals, the processus recessus separates this groove into the fenestra rotunda and the canaliculus cochleae (Goodrich, 1930; Kermack, 1963; Kermack et al., 1981, p. 86). The processus recessus appears to be a derived character distinguishing therians from other mammals, since it does not occur in multituberculates (Kielan-Jaworowska, 1971), monotremes, or *Morganucodon*. The presence of a fenestra rotunda bordered by the processus recessus is thus a synapomorphy for the Theria.

Curving around the posterolateral rim of the fenestra vestibuli is a narrow sulcus which is usually called the sulcus facialis (MacIntyre, 1972). If this interpretation is correct, it would have contained the facial (VII) nerve, the vena capitis lateralis, and possibly the stapedial artery. It would have been partially roofed by the tegmen tympani (Cifelli, 1982). At the posterior end of the groove, the facial nerve would have passed through the foramen stylomastoideum primitivum. However, in well-preserved petrosals of *Morganucodon*, Kermack et al. (1981, p. 99–101) have interpreted the course of the facial nerve very differently. In *Morganucodon*, the facial nerve does not enter via the internal auditory meatus, as discussed above. Instead it passes through the facial canal (aquaeductus fallopii) below the prefacial commissure. It then passes out of the petrosal via the foramen stylomastoideum primitivum, which Kermack et al. locate anterolateral to the fenestra vestibuli. The groove posterolateral to the fenestra vestibuli is interpreted by Kermack et al. (1981, p. 87) as the broken floor of the canalis pro-oticus, which bore the vena cerebralis media. This condition also obtains in *Ornithorhynchus* (Hochstetter, 1896).

Hopson (pers. commun.) agrees with the conventional interpretation that this groove in *Morganucodon* is the sulcus facialis (*contra* Kermack et al., 1981). It thus contained both the facial nerve and the vena capitis lateralis (from which the vena cerebralis media branches to enter the canalis pro-oticus). In his opinion, the foramen labeled "for VII" in *Morganucodon* by Kermack et al. (1981) is for the vena capitis lateralis.

The Morrison petrosal is too poorly preserved to decide with certainty between these two interpretations of the course of the facial nerve. I have labeled the controversial groove the "canalis pro-oticus" ("cpo," Figure 1B), but the possibility that it is actually the sulcus facialis should be kept in mind.

At the posterior end of the canalis pro-oticus (?= sulcus facialis) and posterior to the fenestra vestibuli is a large, deep spheroidal pit in the center of the mastoid region. This feature is seen in *Oligokyphus* (Kühne, 1956), *Trioracodon* (Kermack, 1963), and *Morganucodon* (Kermack et al., 1981). Kermack et al. (1981, p. 93) interpret this pit as the origin of the "levator hyoideus muscle, which is found in monotremes, and is the homologue of the stapedius muscle in therians (Edgeworth, 1935)." In therians, the stapedius muscle originates from the fossa muscularis minor, which is in approximately the same position as the pit on AMNH 104830.

Posterior to the fenestra vestibuli is a large paroccipital process, which is broken at the end. The ventral surface is ridged and irregular, presumably for attachment of the hyoid. The lateral edge of the paroccipital process is thin, so the squamous facets are not as well developed as in *Morganucodon* (Kermack et al., 1981, p. 93). The posteromedial portion of the mastoid (posterior to the hyoid muscle pit) is broken, so little can be said about the articulation with the exoccipital.

Discussion.—Although the Morrison petrosal bears a striking resemblance to the petrosal of *Morganucodon*, most of this resemblance is due to features which are primitive for the Mammalia. AMNH 104830 is clearly not from an advanced therian mammal, since it lacks the following characters which are derived for the advanced Theria: 1, spiral cochlea; 2, inflated promontorium; 3, fenestra rotunda formed by processus recessus. The Morrison petrosal also lack the bladelike promontorium seen in *Trioracodon* and *Triconodon*, the multituberculates, and the monotremes. AMNH 104830 differs in small details from the morganucodont petrosals, but none of these differences can be shown to unite it with anything else. Many of these differences may also be due to poor preservation or individual variation. Thus, the most that can be said about the affinities of the Morrison petrosal is that it is a completely primitive mammalian petrosal that did not come from a monotreme, a multituberculate, certain triconodonts, or an advanced therian.

That leaves a number of candidates from which the Morrison petrosal could have come. The Morrison mammalian fauna includes a number of primitive therians presently known only from teeth (Prothero, 1981), multituberculates, docodonts, two triconodonts (*Trioracodon, Priacodon*), two amphilestids (*Phascolodon, Aploconodon*), but no morganucodonts. Morganucodonts are presently known only from the Rhaetic and Liassic (Jenkins and Crompton, 1979; Clemens, 1979). Since AMNH 104830 does not belong to *Trioracodon* or to the multituberculates, there are four possibilities as to its affinities: 1, it belongs to one of the Morrison amphilestids or to *Priacodon*; 2, it is from a docodont, for which no petrosal is presently known; 3, it represents the last known morganucodont, and the teeth of this form are not yet known from the late Jurassic; 4, it is the petrosal of one of the many primitive therians presently known only from teeth, and lacks the features seen in the advanced tribosphenic Theria. Unfortunately, there is presently no way of deciding among these possibilities until more cranial material of Mesozoic mammals is found. Lacking any derived characters to assign it to a definite group, its relationships cannot be resolved beyond Mammalia *incertae sedis*.

THE KELVIN PETROSAL
Figures 1C, D

Specimen.—AMNH 95184, a right petrosal fragment.

Occurrence.—"Sloan's Dinosaur Eggshell locality" (Jensen, 1970), located east of Coalville, about 150 m north of Route 133 at about 6,000 ft (1,830 m) elevation, NW¼ SE¼ NE¼ sec. 7, T2N R6E, Turner Hollow 7½-minute quadrangle, Summit County, Utah.

Geologic horizon.—Kelvin Formation, middle lower Cretaceous (Aptian–Albian) (Crittenden, 1963; Hale and Van de Graaf, 1964; Ryer, 1976).

Description.—AMNH 95184 is a fragment of the dorsomedial portion of a mammalian petrosal. Most of the specimen consists of the rim of bone surrounding the internal auditory meatus. This rim is a broad, slightly concave shelf with a few shallow pits. The internal auditory meatus is broad and ovoid in shape, unlike the shape of the acoustic foramen seen in the Morrison petrosal. The meatus in the Kelvin petrosal was apparently shallow, judging from the condition of the broken floor of the meatus. None of the nerve foramina or cristae usually found on the floor of the meatus are preserved.

The posterodorsal part of the specimen consists of the anterior wall of the fossa subarcuata. It is broadly rounded and steeply sloping, but only about a third of this fossa is preserved. There is a small, posteriorly-facing perforation on the lip of the fossa subarcuata. This may represent an exposed part of the vertical semicircular canal near the crus commune.

In ventral view (Figure 1D), it appears that only the undersurface of the rim of the internal auditory meatus is preserved. The broken base of the promontorium can be seen, but not enough of the cochlear recess is present to determine whether the cochlea was coiled. The more ventral portions of the petrosal bone, containing the fenestrae cochleae and vestibuli, and the mastoid region are all missing. There is a deep groove which appears to be the sulcus facialis, curving around the posterolateral rim of the broken internal auditory meatus. Posterior to the sulcus facialis is a rim of bone that would contain the gyrus of the horizontal semicircular canal. Around the broken floor of the internal auditory meatus is a broad cavity that would contain the base of the cochlea. This cavity extends into the cancellous recess anterior to the internal auditory meatus. The recess is partially obscured by a ventrolaterally-directed shelf of bone that is part of the broken base of the promontorium.

Discussion.—Although the basal portion of the cochlear recess is present, not enough is preserved to determine whether the cochlea was coiled. AMNH 95184 is too poorly preserved to determine its affinities within the Mammalia.

CONCLUSION

AMNH 104830 and AMNH 95184 are presently the oldest mammalian cranial fragments described from North America. AMNH 104830 comes from the Upper Jurassic Morrison Formation at Bone Cabin Draw, Wyoming, and AMNH 95184 was found in the Lower Cretaceous Kelvin Formation, near Coalville, Utah. The Morrison petrosal is very similar to the petrosal of *Morganucodon*, but it shows no derived characters that would assign it to a specific mammalian group. It is definitely not the petrosal of an advanced therian, a multituberculate, a monotreme, or the triconodonts *Trioracodon* or *Triconodon*. It could be the petrosal of: 1, one of the Morrison triconodonts known only from teeth; 2, a docodont; 3, the last known morganucodont; or 4, a primitive non-tribosphenic therian.

The Kelvin petrosal is too poorly preserved to determine its affinities within the Mammalia. It is presently the only known mammal fossil from this locality, so it cannot be assigned to any of the taxa presently known from teeth. Indeed, it is the only Early Cretaceous petrosal presently described. It is approximately contemporaneous with Early Cretaceous mammals from Texas, England, and Mongolia. Further work on the Kelvin locality may prove very fruitful.

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