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PALEONTOLOGY AND GEOLOGY OF THE BRIDGER FORMATION, SOUTHERN GREEN RIVER BASIN, SOUTHWESTERN WYOMING

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Abstract

Recently recovered Bridgerian material of *Entomolestes grangeri* verifies its allocation to the Erinaceidae. *E. grangeri* may have possessed five premolars as do *Litolestes ignotus* and an undescribed erinaceid from the Tepee Trail Formation. These taxa, along with *Leipsanolestes*, compose the early Tertiary record of the Erinaceidae.

Introduction

The Bridgerian insectivore *Entomolestes grangeri* (Matthew, 1909) has long been a subject of taxonomic confusion. The species was based on the holotype, AMNH 11485, partial left mandible with worn P_3-M_3 and five alveoli anterior to P_3. Although Matthew (1909:542) also tentatively referred to *E. grangeri* an unspecified number of fragmentary jaws, these apparently were never catalogued as such in the collections of the American Museum of Natural History: their ultimate catalogue numbers and identifications are not known. Thus AMNH 11485 remained the type and only known specimen of *E. grangeri*.

Matthew (1918) recognized a second species of *Entomolestes*, *E. nitens*, from the lower part of the Willwood Formation, Wyoming, which was subsequently recorded from a number of other North American Wasatchian localities (McKenna, 1960; Delson, 1971; Guthrie, 1967, 1971; Robinson, 1968b; Krishtalka, 1976a) and

European Sparnacian-Cuisian deposits (Russell, et al., 1975).

Until recently the distinctions and relationships between *Entomolestes* and other early Tertiary insectivores, notably *Litolestes*, *Leipsanolestes*, *Scenopagus*, *Talpavus*, *Leptacodon* and *Nyctitherium*, were unclear, as was pointed out by McGrew (1959), McKenna (1960) and Robinson (*in* McKenna et al., 1962; Robinson, 1968b). Many of these genera are now more strictly defined and their affinities better understood. Following Robinson's (1968b) and Butler's (1972) observation that the two species of *Entomolestes* were not congeneric, Krishtalka (1976a) referred *E. nitens* to *Macrocranion*, an adapisoricid previously described only from Europe (Weitzel, 1949; Tobien, 1962; Russell et al., 1975). Krishtalka (1976a) also reviewed and placed in the Adapisoricidae *McKennatherium*, *Scenopagus*, *Ankylodon* and *Talpavus*, which Robinson (*in* McKenna et al., 1962) had correctly separated from *Nyctitherium*. The latter, along with *Leptacodon sensu stricto* and *Pontifactor* compose the Nyctitheriidae (Robinson, 1968a; McKenna, 1968; West, 1974; Krishtalka, 1976b). *Leipsanolestes* and *Litolestes*, referred to the Erinaceidae (Krishtalka, 1976a), extend the record of that family to the mid-Paleocene.

Much of the above work stemmed from the recovery in recent years of abundant dental remains of these insectivores by bulk processing (underwater screening) of fossiliferous matrix from a number of Paleocene and Eocene localities. West (1974, 1976) has applied this collecting technique to the rich Bridgerian, early middle Eocene sediments of the Green River Basin, resulting in the recovery of many well preserved microvertebrate remains. Among these are numerous partial jaws of *Entomolestes grangeri* (see Table 1), which now allow a more detailed analysis of its dental morphology, systematics and relationships than was previously possible when only the holotype was known.

Homologies of the anterior dentition

Prior to the recovery of the new material of *E. grangeri*, teeth anterior to P_3 (fig. 1) were unknown. The five alveoli on the holotype anterior to P_3 (fig. 1) were considered to have contained single-rooted I_{2-3} C P_{1-2} (Robinson, 1968b), or single-rooted I_{2-3} C P_1 and a double-rooted P_2, since the alveolus for P_2 is hourglass-shaped and elongate (Krishtalka, 1976a). One of the recently recovered jaws of *E. grangeri*, AMNH 91832, preserves a double-rooted P_2 and P_4 and alveolus for P_3 (fig. 2). This specimen, along with the holotype, which has a two-rooted P_3, makes it clear that the last three premolars of *E. grangeri* have two roots, whereas the two alveoli anterior to P_2 were filled with two single-rooted teeth,

presumably C and P_1. Similarly, the last three premolars in the Paleocene erinaceid *Litolestes ignotus*, presumably $P_2P_3P_4$, have two roots, and the two teeth anterior to these are single-rooted and usually designated C and P_1. The two-rooted $P_2P_3P_4$ in *L. ignotus* may also be interpreted as being $P_3P_4P_5$, since the tooth behind I_3—the alleged canine—is fully premolariform and may instead represent P_1 (or dP_1), the first of five premolars in a dental complement of 3 incisors, 5 premolars and 3 molars (Krishtalka, 1976a; Schwartz and Krishtalka, 1976). A Uintan erinaceid from the Tepee Trail Formation has a similar dental array in both the upper and lower dentition, including five lower premolariform teeth of which the last three are double-rooted and the first two single-rooted. Its lower dental formula may likewise be interpreted as 3 incisors, single-rooted P_1 (or dP_1) P_2, double-rooted $P_3P_4P_5$ and 3 molars (personal observation and interpretation of material made available to L.K. by M.C. McKenna). If *E. grangeri* is closely related to *L. ignotus* and the Tepee Trail erinaceid, as proposed elsewhere (Krishtalka, 1976a), the alveolus in the holotype for the alleged canine may also have been filled with a single-rooted premolariform tooth—a P_1 (or dP_1) in a premolar set of five, of which the last three, double-rooted as in *L. ignotus* and the Tepee Trail erinaceid, also represent $P_3P_4P_5$.

Since teeth anterior to the two-rooted antepenultimate premolar in *E. grangeri* are still unknown, the evidence for considering the last three premolars as $P_3P_4P_5$ is indirect. The occurrence of five premolars is primitive for all, and seems to be retained in some, plesiadapiformtarsiiform primates (Schwartz, MS; Schwartz and Krishtalka, in press), adapisoricids (Krishtalka, 1976a), nyctitheriids (Krishtalka, 1976b), plagiomenids (Schwartz and Krishtalka, 1976), erinaceids (Krishtalka, 1976a; Schwartz and Krishtalka, 1976) and the Cretaceous forms *Kennalestes* (McKenna, 1975) and *Gypsonictops* (Lillegraven, 1969; Clemens, 1973). In accordance with these interpretations, and the close resemblances of the known antemolar and molar teeth of *E. grangeri* to those of *L. ignotus* and the Tepee Trail erinaceid, the three posterior double-rooted premolars of *E. grangeri* are here considered homologous to $P_3P_4P_5$.

Description

P_3 and P_4 (figs. 1,2) have a laterally compressed, somewhat procumbent crown that resembles in lateral view a rectangle tipped anteriorly on edge. The anterior slope of both crowns is short and gentle, whereas the posterior slope is comparatively longer and steeper. A small, raised cuspule forms the talonid.

P_5 (figs. 1-3), although premolariform, is broader and more nearly molariform than P_{3-4}. The trigonid consists of a large, dominant protoconid, a lower metaconid on the lingual face of tne protoconid, a small paraconid arising from the anterior part of the base of the protoconid and a well formed precingulid. The talonid is extremely short, with a single cuspule joined to the trigonid by a weak cristid obliqua.

The molars of *E. grangeri* (figs. 1,3) are, at first glance, easily confused with those of some adapisoricids, notably *Scenopagus* and *Talpavus*, and especially resemble those of other early Tertiary erinaceids, *Litolestes ignotus*, *Leipsanolestes* and the Tepee Trail erinaceid. On all of the specimens of *E. grangeri* that preserve the first two molars M_1 is longer and wider than M_2. On the holotype, M_1 appears to be equal in size to M_2 (Krishtalka, 1976a), but this is due to breakage and wear of the paraconid on M_1. As in *L. ignotus*, *Leipsanolestes* and the Tepee Trail erinaceid, the lower molars of *E. grangeri* show a progressive reduction in size from M_1 to M_3. The cusps on the molars lean markedly lingually.

The trigonid on M_1 is triangular, with a large protoconid and a somewhat lower and smaller metaconid. In end view, the size of the protoconid (from its external margin to the ventral point of the protocristid) is broader than the corresponding width of the metaconid (from its lingual margin to the ventral protocristid notch). The paraconid, fully cuspate, arises from the anterior part of the base of the trigonid and juts anterolingually, so that the trigonid is completely open. Significantly, the paraconid is low, and, in lingual view, the notch between it and the metaconid is lower than that between the entoconid and metaconid (the talonid notch). The talonid on M_1 is about as long as, but wider than, the trigonid. The entoconid is high, the hypoconid much lower. The posterior edges of both cusps are aligned along the straight posterior margin of the crown, so that the hypocristid runs directly lingually from the hypoconid. The hypocristid ends in a tiny hypoconulid at the posterior part of the base of the entoconid. The cristid obliqua originates labially on the trigonid wall, below the protoconid and labial to its apex. As a result, the cristid obliqua is nearly parallel to the entocristid and the hypoflexid area is extremely shallow. Characteristically, the entocristid is high and, in lingual view, slopes anteroventrally from the apex of the entocristid toward the base of the crown and then curves anterodorsally up the posterolingual corner of the metaconid. The resultant talonid notch is much higher than the point of contact between the cristid obliqua and the trigonid. The internal faces of the elongate hypoconid and entoconid slope ventromedially to form a V-shaped talonid basin.

M_2 is virtually identical to M_1, except for its smaller size and a less anteriorly oriented paraconid. On M_3, which is slightly shorter and about one-third as wide as M_2, the talonid is more elongate with respect to the trigonid than on M_{1-2}.

Discussion and conclusions

The new material of *E. grangeri* verifies the dental distinctions between it and *Talpavus nitidus* noted by Robinson (1968b) and the assignment of *E. grangeri* to the Erinaceidae (Krishtalka, 1976a). The ultimate premolar of *T. nitidus* has subequal protoconid and metaconid and a moderately sized talonid without a basin. On P_5 of *E. grangeri* the protoconid is dominant and the talonid is extremely short and unicuspid, with a very narrow basin between the cristid obliqua and the lingual margin of the crown. The molars of *Talpavus* and other adapisoricids do not decrease progressively in size from M_1 to M_3. They bear a compressed paraconid, a wider metaconid than protoconid, a rounded talonid basin and a medial hypoconulid (Krishtalka, 1976a). The notch between the metaconid and paraconid occurs somewhat higher than or at the same level as the talonid notch, and the latter is at the same height as the point of contact between the cristid obliqua and the trigonid. In contrast, the molars of *Entomolestes* and other erinaceids do progressively decrease in size from M_1 to M_3, the paraconid is lower, fully cuspate and oriented more anteriorly, the protoconid is wider than the metaconid, the talonid basin is V-shaped, the hypoconulid is tiny and lingual in position and the hypoflexid area is shallower. In *E. grangeri* the paraconid-metaconid notch is lower than the talonid notch, and the latter, formed by a high entocristid, occurs above the point of contact between the cristid and obliqua and the trigonid. Aside from *Talpavus*, the ultimate premolars of the other adapisoricids (*Scenopagus*, *McKennatherium*, *Ankylodon*, *Macrocranion*) are readily distinguished from those of *E. grangeri* and other early Tertiary erinaceids as described elsewhere (Krishtalka, 1976a). The same distinctions apply to the Tepee Trail erinaceid.

The North American early Tertiary record of the Erinaceidae consists of four taxa: *Litolestes ignotus* (Tiffanian), *Leipsanolestes seigfriedti* (Tiffanian-Wasatchian), *Entomolestes grangeri* (Bridgerian) and the Tepee Trail erinaceid (Uintan). As discussed above and elsewhere (Krishtalka, 1976a; Schwartz and Krishtalka, 1976), these may have had a dental complement of 3 incisors, 5 premolars and 3 molars. The evidence for such a dental formula is strong in *Litolestes* and the Tepee Trail erinaceid, but is less conclusive for *E. grangeri*. Teeth anterior to the ultimate premolar in *Leipsanolestes* are unknown.

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TABLE 1

Dimensions of type and referred specimens of *Entomolestes grangeri* from Bridgerian deposits in the Green River Basin, Wyoming. (L — length; AW — anterior width; PW — posterior width; W — width)

	P_5		M_1			M_2			M_3		
AMNH #	L	W	L	AW	PW	L	AW	PW	L	AW	PW
11485 (type)	1.2	0.9	1.5+	1.0	1.2	1.5	1.0	1.0	1.3	0.8	0.8
91815	1.2	0.9	1.7	1.0	1.1						
91816	1.2	1.0	1.7	1.2	1.3						
91823	1.2	1.0	1.8	—	1.3						
91828	1.3	1.0	1.8	1.2	1.3						
91832	1.3	1.0									
91834	1.2	0.9	1.7	1.1	1.2	1.6	1.1	1.2			
91812			1.8	1.0	1.2	1.6	1.0	1.0			
91817			1.5	1.0	—	1.3	0.9	1.0			
91825			1.7	1.1	1.2						
91826			1.7	1.0	1.1						
91829			—	—	1.3	1.5	1.3	1.3	—	—	0.8
91831			1.7	1.1	1.2	1.5	1.1	1.1			
91838			1.6	1.1	1.2						
91839			1.7	1.1	1.1						
91819						1.5	1.0	1.1	1.3	0.8	0.8
91821						1.6	1.3	1.3			
91827						1.4	0.9	1.0			
91830						1.5	1.0	1.1			
91833						1.5	1.2	—			
91837						1.6	—	—	1.3	—	—

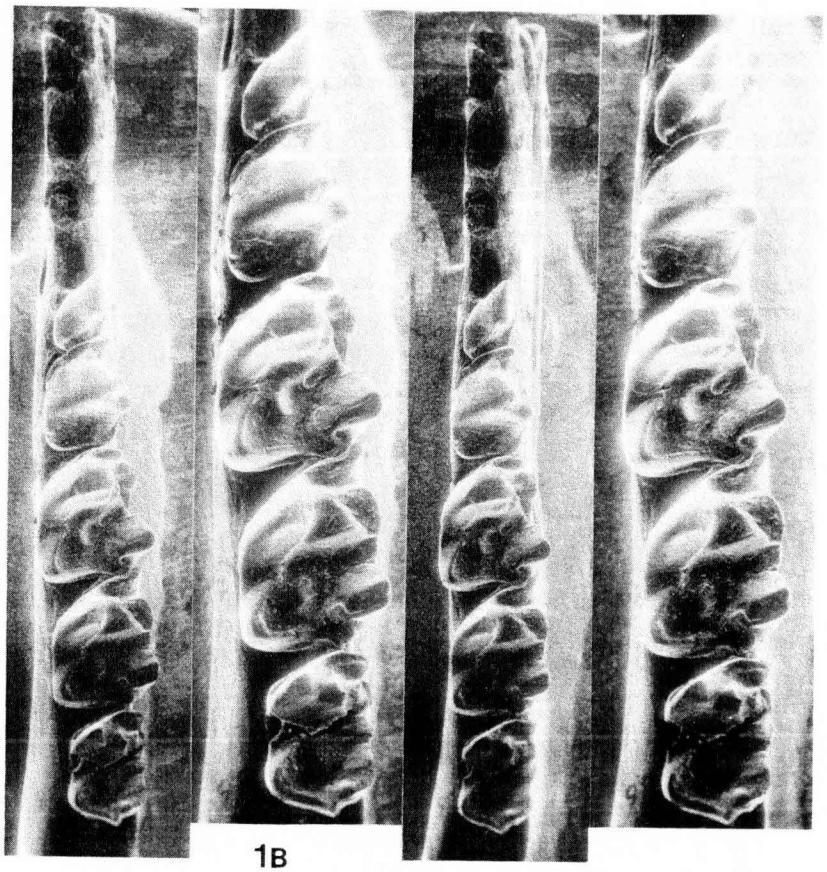
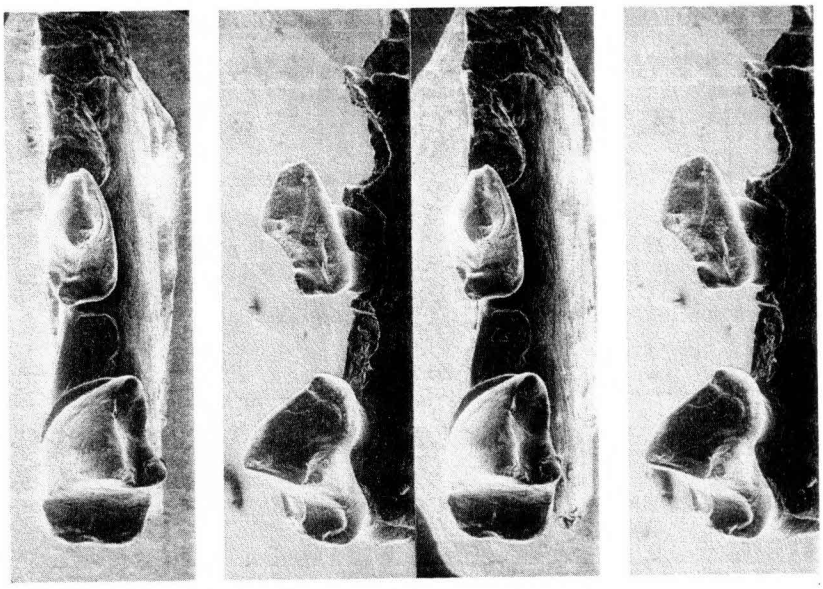


Figure 1. *Entomolestes grangeri*, AMNH 11485, holotype. (A) occlusal view, anterior alveoli and $P_{4\text{-}5}M_{1\text{-}3}$, approx. x 12.5; (B) occlusal view, $P_{4\text{-}5}M_{1\text{-}3}$, approx. x 17.



2A 2B

Figure 2. *Entomolestes grangeri*, AMNH 91832, P_3, P_5 and alveoli for P_2 and P_4; (A) occlusal view; (B) lingual view; both approx. x 17.

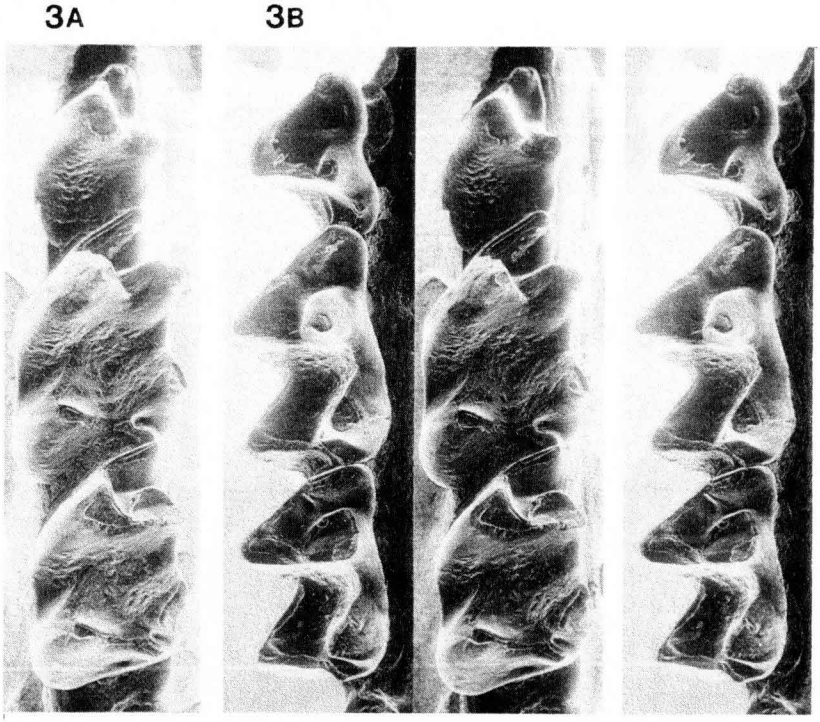


Figure 3. *Entomolestes grangeri*, AMNH 91834, P_5-M_2; (A) occlusal view; (B) lingual view; both approx. x 18.