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PALEONTOLOGY AND GEOLOGY OF THE
BADWATER CREEK AREA, CENTRAL WYOMING

Part 13. The late Eocene Insectivora and Dermoptera

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ABSTRACT

Insectivores recovered from the Badwater Uintan and Duchesnean deposits include members of the families Adapisoricidae, Erinaceidae, Nyctitheriidae, Apternodontidae and Soricidae. These deposits provide the earliest known record of *Ankylodon*, *Domnina*, two other soricids, *Apternodus*, *Oligoryctes* and the dermopteran *Thylacaelurus*, as well as the latest occurrence of *Nyctitherium*, *Macrocranium* and *Talpavus*. The insectivore and dermopteran record support previous conclusions that currently sampled Bridgerian deposits do not preserve the real diversity of middle Eocene mammals.

INTRODUCTION

This study is an elaboration and revision of a part of a Master's thesis (Setoguchi, 1973) that dealt with the systematics of the insectivores and dermopterans from the late Eocene deposits of the Badwater Creek area. Recovery of additional material during the past three years from the Badwater localities (5, 5A, 5 Front, 5 Back, 6, Wood, 20) has considerably improved the insectivore record. Also, recent studies involving early Tertiary insectivores (Krishtalka, 1975, 1976a, 1976b) and Badwater faunas (Black, 1974; Krishtalka and Black, 1975) have clarified the

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systematics and relationships of some of the insectivore taxa and the stratigraphic positions of the Badwater localities. Among the latter, 5, 5A, 5 Front, 5 Back, 6 and Wood are probably Uintan, whereas 20, dated at 41 m.y., is now considered Duchesnean, or latest Eocene. The localities do not occur in the Tepee Trail Formation, as previously thought (Krishtalka and Black, 1975). A current geological review of the area should determine the formational status of the late Eocene Badwater deposits.

The Insectivora, as here understood, means essentially the Lipotyphla (see Butler, 1972; McKenna, 1975; Krishtalka, 1976a), and in this paper involves the erinaceomorph families Adapisoricidae and Erinaceidae, and the soricomorph families Nyctitheriidae, Geolabididae, Soricidae and Apternodontidae.

The material described is housed in the collections of the Carnegie Museum of Natural History (CM). All measurements are given in millimeters. All figures are stereophotographs and present occlusal views. Caps and lower case I, P, and M refer to upper and lower incisors, premolars and molars, respectively. Abbreviations in the tables are: L, length; W, width; AW, width of trigonid; PW, width of talonid.

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Order Insectivora

Family Adapisoricidae (Schlosser, 1887)

Macrocranium Weitzel, 1949

Two North American species of the Eocene insectivore *Entomolestes*, *E. nitens* (Matthew, 1918) and *Entomolestes* cf. *E. nitens* (McKenna, 1960a), were recently redescribed and referred to *Macrocranium*, (Krishtalka, 1976a), an adapisoricid also known from the middle Eocene of Europe (Weitzel, 1949; Tobien, 1962; Russell, et al., 1975). The recognition of *Macrocranium* in North American Wasatchian deposits increases the already considerable evidence of a Euramerican biota during the early Eocene (Savage, 1971; Szalay and McKenna, 1971; McKenna, 1971; Dawson, et al., 1976)—a conclusion recently verified by the recovery of a diverse early Eocene mammalian assemblage from Ellesmere Island (West and Dawson, in press).

Macrocranion robinsoni, new species
(Fig. 1; Table 1)

ETYMOLOGY: named after Dr. Peter Robinson for his extensive work with early Tertiary insectivores.

TYPE: CM 18645, Rm1-3, locality 6, Badwater Creek area, Wyoming, only known specimen.

DIAGNOSIS: size of *M. nitens*; differs from the latter in the reduction of m3 relative to m1-2.

DESCRIPTION: *Macrocranion* is distinguished from all other adapisoricids by the wide, elongate talonids on m1-2 and exodaenodont lower molars, especially, m1. CM 18645, the type and only known specimen of *M. robinsoni*, preserves m2-3 and a broken m1. As in other species of *Macrocranion*, the talonid of m2 is much longer and wider than the trigonid, the talonid basin is broadly excavated, the metaconid and protoconid are conical, bulbous cusps, and the paraconid is anteroposteriorly compressed into a low, broad crest that terminates anterior to the metaconid. The labial part of the hypoconid base is expanded labially and exhibits the exodaenodonty characteristic of m1-2 in *Macrocranion* (Krishtalka, 1976a; Russell, et al., 1975). Although much of m1 is broken away, the preserved margin of the crown indicates that the talonid was wider and much longer than the trigonid, as is the case on m2 of *M. robinsoni* and on m1-2 of other species of *Macrocranion*. Also characteristic of *M. robinsoni* and other adapisoricids are the high entoconid on the lower molars, the low hypoconid that becomes flat with wear, and the small median hypoconulid. In contrast with other known species of *Macrocranion*, m3 in *M. robinsoni* is reduced, in comparison with m1-2.

REMARKS: The Badwater material provides the latest occurrence of the genus *Macrocranion*, an adapisoricid also recovered from a number of Wasatchian localities but absent from Bridgerian assemblages. This disjunct distribution and its possible paleoecological interpretations are discussed at the end of this paper.

Talpavus Marsh, 1872

Species of this genus are now well known from Wasatchian (*Talpavus* cf. *T. nitidus*), Bridgerian (*T. nitidus*) and Uintan (*T. duplus*) localities (Robinson, 1968c; Krishtalka, 1976a). Material described as cf. *Talpavus* has also been recovered from the late Paleocene deposits of the Badwater Creek area (Krishtalka, et al., 1975). Among described adapisoricids, *Talpavus* most closely resembles *Scenopagus* in known parts of the dentition, but can be distinguished from the latter mainly by the structure of p4: p4 of *Talpavus* possesses an unbasined talonid and subequal protoconid and metaconid. The paraconid on m1-3 is a low, anteroposteriorly compressed crest, and the talonid on m2 is as wide as

the trigonid. The hypoconulid on m1-2 is low and weak and occurs posterolabial to the entoconid at the lingual end of a distinct hypocristid. In contrast, on p4 of *Scenopagus* the talonid is basined and the protoconid is larger than the metaconid. Lower molars of *Scenopagus* are proportionately wider, the paraconid is higher than in *Talpavus*, the m2 talonid is narrower than the trigonid, the hypoconulid is stronger and more distinct, and the hypocristid is much weaker.

Talpavus duplus Krishtalka, 1976a
(Fig. 2; Tables 1,2)

REFERRED SPECIMENS: p4: 15131, 15139, 15743; m1: 15096; m2: 15622; m3: 15649; P4: 15112; M1: 15011, 15055, 15127, 15641, 15644, 15725, 21630, 23857; M2: 15002, 15109, 15623, 15723; M1 or M2: 15009, 15012, 15013, 15024, 15643, 15722, 18194, 21628, 23951, 23952.

LOCALITIES: 5A, 5 Front, 5 Back.

KNOWN DISTRIBUTION: Uintan, Wyoming and Utah.

DESCRIPTION: The lower teeth described here do not differ significantly from those of *T. duplus* from the Uinta Basin (Krishtalka, 1976a). As is characteristic of *Talpavus*, p4 has an unbasined talonid and subequal protoconid and metaconid.

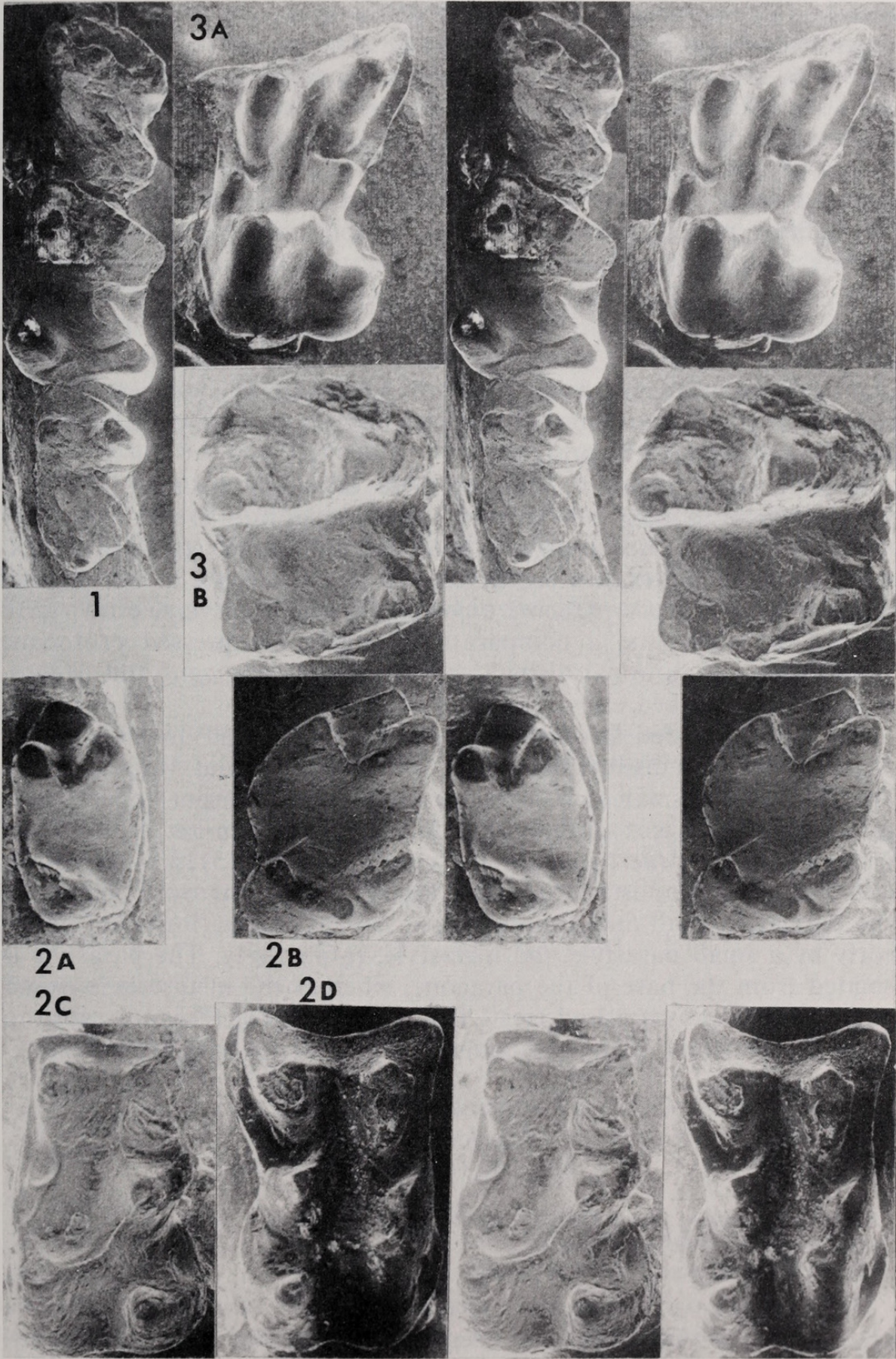
Since upper and lower molars of *Talpavus* have not been found in association, identification of the former is difficult. Guthrie (1967; 1971) ascribed a number of isolated upper molars from Lysite and Lost Cabin to *Talpavus*—an inference here considered tentative and in need of review, since part of the hypodigm was subsequently referred to *Scenopagus* (Krishtalka, 1976a). Similarly, the allocation here of isolated adapisoricid upper molars to *T. duplus* is tentative, with corroboration subject to the recovery of associated remains. However, the other insectivore taxa from Badwater are represented by both upper and lower molars that are distinct from those assigned here to *Talpavus*. Additionally, the association here of upper and lower molars of *T. duplus* is based on proper size, frequency distribution, and recovery from the geographically adjacent and temporally equivalent group of localities 5A, 5 Front, and 5 Back.

All but seven of the referred upper molars are lingual fragments. The crowns of the more nearly complete specimens are quadrate in occlusal view, with a shallow posterior emargination near the metaconule. As in other adapisoricids, the styler shelf is narrow, the conules are prominent, the paracone and metacone are subequal and conical, the proto-

Fig. 1. *Macrocranium robinsoni*, CM 18645, Rm1-3, holotype; approx. x 17.

Fig. 2. *Talpavus duplus*. (A) CM 15743, Rp4; (B) CM 15622, Lm2; (C) CM 15725, LM1; (D) CM 15002, RM2; all approx. x 21. ►

Fig. 3. *Ankylodon* sp. (A) CM 29495, LM1; (B) CM 31300, Rm2; both approx. x 19.



cone and hypocone are well developed, low and conical, and the paracingulum and metacingulum are strong. The upper molars are most similar to those of *Macrocranium nitens*, among known North American adapisoricids. As in *M. nitens*, the base of the hypocone on M1-2 of *T. duplus* is as broad as the protocone, and directly posterior to the latter; the posterior margin of the hypocone swings labially and anteriorly and meets the trigon below the metaconule; a weak ridge runs from the anterior face of the hypocone to the posterior face of the trigon below the postprotocrista.

In contrast to *T. duplus*, M1-2 of *Scenopagus* are much more transverse, and have much larger parastylar and metastylar areas, with deeper ectoflexi. Similarly, M1-2 of *Macrocranium nitens* are slightly more transverse than those of *T. duplus*; their parastylar and metastylar areas are somewhat more elaborate; and the protocones are more compressed anteroposteriorly.

In sum, comparison of M1-2 of these three adapisoricids reveals a morphological progression from a nearly quadrate crown with tiny stylar areas and an uncompressed protocone (*T. duplus*) to a semi-transverse crown with moderately developed stylar salients and a slightly compressed protocone (*Macrocranium*), to a very transverse crown with large stylar areas and a comparatively highly compressed protocone (*Scenopagus*). Additional distinctions between *Scenopagus* and *Macrocranium* are described elsewhere (Krishtalka, 1976a).

The single referred P4, CM 15112, is very worn and does not reveal structural features distinct from those of *Scenopagus* and *Macrocranium*. CM 15112 is too small to be referred to *M. robinsoni*, but appears suitable in size to be part of the upper dentition of *T. duplus*. As on P4 of *Scenopagus* and *Macrocranium*, the crown on CM 15112 is T-shaped, with a long (anteroposteriorly) labial segment and a narrow lingual area. The paracone is tall and dominant and is flanked anteriorly and posteriorly by a small parastyle and metastyle, respectively. The parastyle is isolated from the base of the paracone, whereas the metastyle is linked to the paracone by a raised crest. The lingual area of P4 is too worn to reveal the structure of the protocone or the presence of a hypocone.

Ankylodon Patterson and McGrew, 1937

Ankylodon sp.

(Fig. 3; Tables 1,2)

REFERRED SPECIMENS: m2: 31300; M1 or M2: 15018, 15702; M1: 29495; M2:15704.

LOCALITIES: 5A, 5 Front, 5 Back.

KNOWN DISTRIBUTION: Uintan, Wyoming.

DESCRIPTION AND REMARKS: The dentition of *Ankylodon* and the relationships of the genus have been briefly discussed elsewhere (Krishtalka, 1976a), and a full description of excellent Chadronian material is

forthcoming (Lillegraven and McKenna, MS). Although the material from Badwater—an m2, one complete and three fragmentary upper molars—is too sparse for specific identification, the teeth closely resemble comparable parts of the dentition of *Ankylodon*. On m2 (CM 31300) the talonid is narrower than the trigonid, the cusps are high and conical, the paraconid is compressed into a flat, wide, labiolingual shelf, and the hypoconulid is large and medial. However, compared to m2 of Chadronian *Ankylodon*, the trigonid on CM 31300 is less compressed antero-posteriorly, the talonid is proportionately shorter and narrower, and the hypocristid is weaker.

The single complete upper molar (CM 29495) closely resembles M1 of the Chadronian species of *Ankylodon*, which is represented in part by a nearly complete palate, a cast of which was kindly furnished by M. C. McKenna. Like M1 of the Chadronian *Ankylodon*, CM 29495 is transverse and has a strong hypocone on a wide postcingulum, a deep lingual valley between the hypocone and protocone, a tall paracone and metacone, a high postmetacrista, a labially expanded metastylar shelf, and a deep ectoflexus. M1 of the Chadronian *Ankylodon* is, however, more derived, in that the parastylar and metastylar (especially the latter) areas are more expanded, the valley between the hypocone and protocone is

Table 1. Dimensions of lower teeth of *Macrocranium robinsoni* n. sp., *Talpavus duplus*, *Ankylodon* sp. and erinaceid sp.

	p4		m1			m2			m3		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
<i>Macrocranium robinsoni</i>											
18645			1.7	—	—	1.8	1.4	1.5	1.7	1.1	0.9
<i>Talpavus duplus</i>											
15131	1.3	1.0									
15139	1.4	1.1									
15743	1.4	1.0									
15096			1.4	1.2	1.3						
15622						1.5	1.3	1.2			
15649									1.6	1.2	1.1
<i>Ankylodon</i> sp.											
31300						1.9	1.6	1.4			
erinaceid sp.											
15095			2.2	1.5	1.7						
14440						—	1.3	1.5			
15714						1.8	1.3	1.4			

Table 2. Dimensions of upper teeth of *Talpavus duplus*, *Ankylodon* sp. and erinaceid sp.

	M1		M2		M1 or M2	
	L	W	L	W	L*	W
<i>Talpavus duplus</i>						
15011	1.2*	2.0**				
15055	1.2*	1.9**				
15127	1.2*	—				
15641	1.3*	1.8**				
15644	1.1*	1.9**				
15725	1.3*	2.0**				
21630	1.2*	2.0**				
23857	1.4*	2.0**				
15002			1.4	2.1		
15109			1.4	2.0		
15623			1.2	2.0		
15723			1.3*	2.1		
15009					1.3	—
15012					1.2	—
15013					1.2	—
15024					1.2	—
15722					1.2	—
18194					1.4	—
15643					1.2	—
23951					1.3	—
23952					1.2	—
<i>Ankylodon</i> sp.						
29495	1.7	2.4				
15704			1.5*	2.2		
15702					1.5	—
erinaceid sp.						
15001	1.7*	2.8**				

*lingual length

**anterior width

wider, and the hypocone is higher. These features and the morphology of the Badwater *Ankylodon* M1 confirm an earlier diagnosis of that genus (Krishtalka, 1976a) and the described dental trends in the evolution of *McKennatherium*, *Scenopagus* and *Ankylodon*: in the upper molars, increase in size of the hypocone, postcingulum, the hypocone-protocone valley, and expansion of the styler salients.

The Badwater and Chadronian material represent two species of *Ankylodon*. The Badwater species is significantly smaller and, at least on M1 and m2, is more primitive than the Chadronian species. The

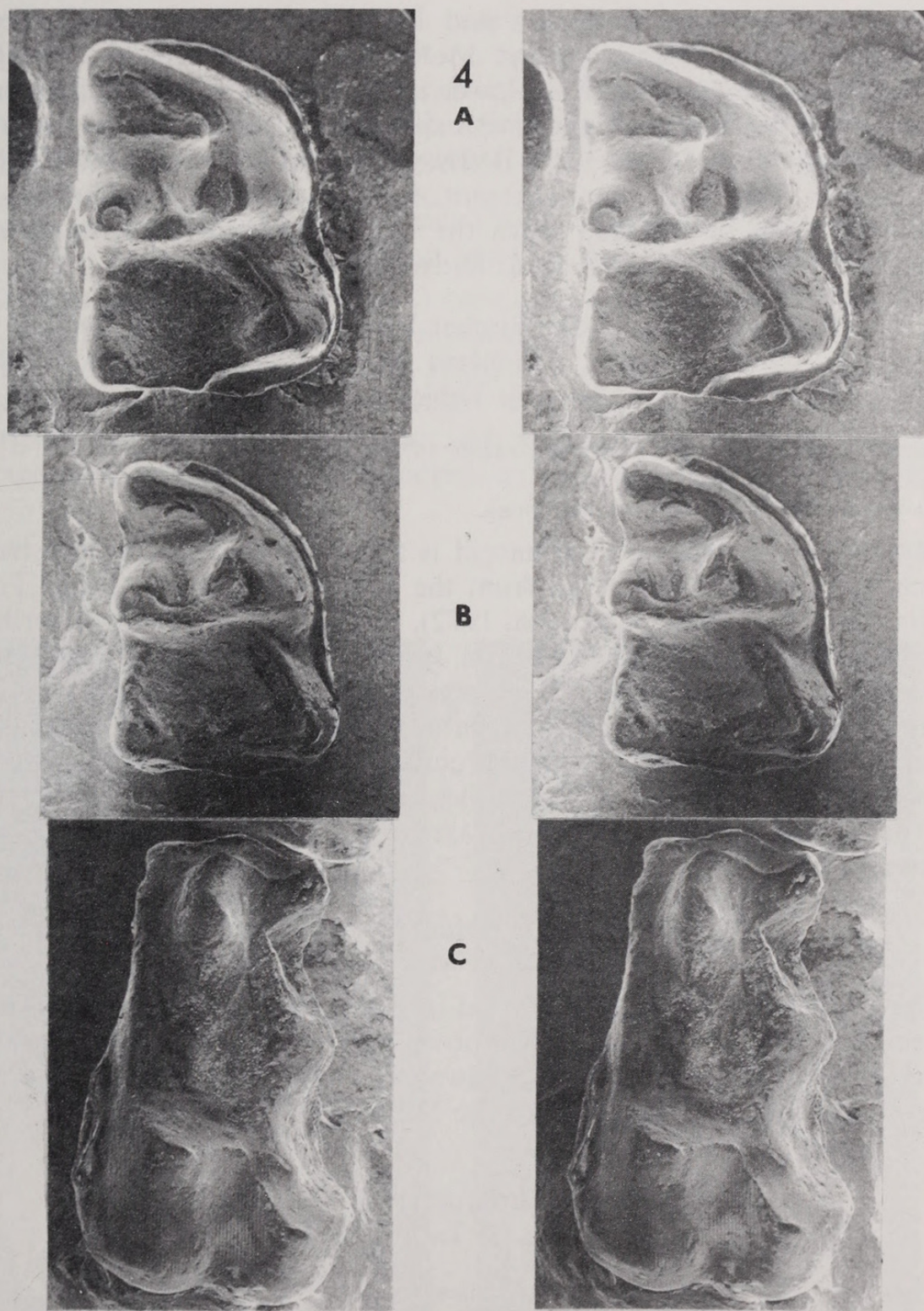


Fig. 4. Erinaceid sp. (A) CM 15095, Rm1; (B) CM 15714, Rm2; (C) CM 15001, LM1; all approx. x 18.5.

Orellan *A. annectens* Patterson and McGrew, 1937 [= *A. progressus* Galbreath, 1953 (Lillegraven and McKenna, MS; Setoguchi, 1973)] is unfortunately known only from lower teeth. These are also smaller than the lower molars of the Chadronian species but are similar in size and crown morphology to m2 of the Badwater species. The question whether the remains from Badwater represent *A. annectens* or a third species of *Ankylodon* can be resolved when the upper dentition of *A. annectens* and more complete material from Badwater are recovered.

Family Erinaceidae Fischer Von Waldheim, 1817

Erinaceid sp.

(Fig. 4; Tables 1,2)

REFERRED SPECIMENS: m1: 15095; m2: 14440, 15714; M1: 15001.

LOCALITIES: 5A, 5 Back, 6, Wood.

KNOWN DISTRIBUTION: Uintan, Wyoming.

REMARKS: The Badwater erinaceid is a new species also known from much more complete material from the East Fork locality, Tepee Trail Formation, Wyoming (McKenna, 1972), that is currently being described elsewhere (Krishtalka and McKenna, in prep.). The erinaceid characters of the lower molars include an m2 smaller than m1, an open trigonid, a compressed, yet cusped, anterior paraconid, a V-shaped talonid basin, a small hypoconulid, and a high entocristid that is nearly parallel to the cristid obliqua. This species resembles and appears to be closely related to the Tiffanian erinaceid *Litolestes ignotus* (Krishtalka, 1976a; Schwartz and Krishtalka, 1976).

Family Nyctitheriidae Simpson, 1928

Nyctitherium Marsh, 1872

The genus *Nyctitherium*, discussed in detail by Robinson (1968b) and Krishtalka (1976b), includes two known species, *N. velox* and *N. serotinum*, both Bridgerian. The Badwater occurrence of *Nyctitherium* extends the range of the genus to the Duchesnean.

***Nyctitherium christopheri*, new species**

(Fig. 5; Table 3)

ETYMOLOGY: named for Christopher A. Black.

HOLOTYPE: CM 27866, RP4-M3, locality 20.

REFERRED SPECIMENS: P4: 15023; M1 or M2: 15088, 31299; M2: 16009, 23799.

LOCALITIES: 5A, 5 Front, 5 Back, Wood, 20.

DIAGNOSIS: P4-M3 approximately 30% wider labiolingually than *N. velox* and *N. serotinum*; hypoconal shelf larger, flaring more posterolingually.

KNOWN DISTRIBUTION: Uintan, Duchesnean, Wyoming.

REMARKS: Only upper teeth of this new species have been recovered. Compared to *N. velox* and *N. serotinum*, P4 and the upper molars of *N.*

christopheri are larger and much more transverse buccolingually, the hypoconal shelf on P4-M2 is more expanded, the precingulum is reduced, and the ectoflexus on M2 is deeper. McKenna (pers. comm.) has also recovered remains of this species from the Uintan East Fork locality, Tepee Trail Formation, Wyoming (McKenna, 1972).

Family Geolabididae (McKenna, 1960b)

Centetodon Marsh, 1872

Lillegraven and McKenna (MS) have shown that the following genera are wholly or in part junior synonyms of *Centetodon*: *Domnina* (in part); *Geolabis*; *Metacodon*; and *Hypacodon*. This is a consequence of previous work by McKenna (1960b) who synonymized *Domnina* (in part), *Herpetotherium*, *Embassis*, and *Metacodon* with *Geolabis*, and erected a new Subfamily Geolabidinae to include *Geolabis*, *Hypacodon*,

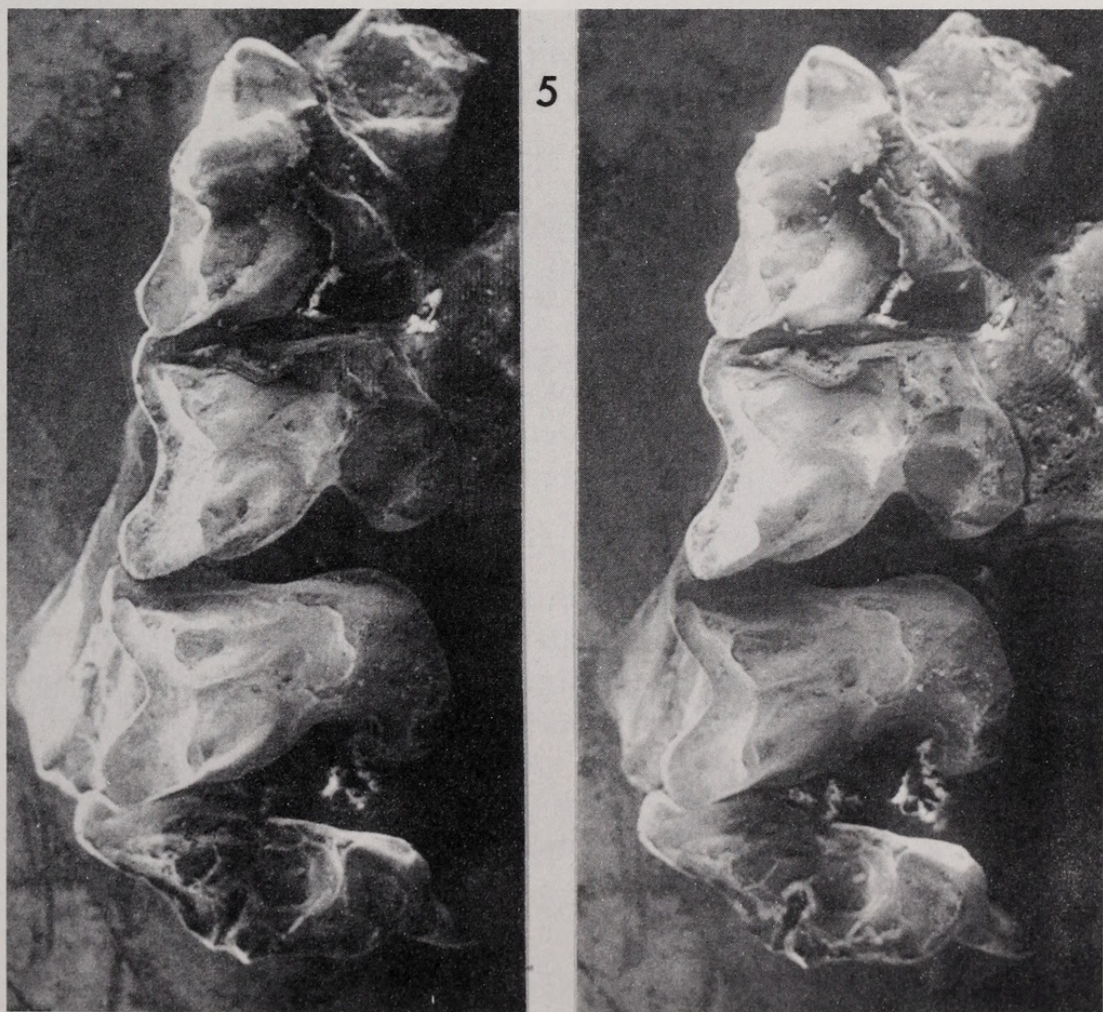


Fig. 5. *Nyctitherium christopheri*, CM 27866, RP4-M3, holotype; approx. x 18.

and *Myolestes*. Shortly thereafter, *Centetodon* was shown to be congeneric with *Hypacodon*, and referred to the Geolabidinae (McKenna, et al., 1962). Lillegraven and McKenna (MS) define eight species of *Centetodon* from Bridgerian through Arikareean deposits of North America. New species named in their manuscript are here termed *Centetodon* sp. B (from the Bridgerian of Wyoming), *Centetodon* sp. U (from the early Uintan of California), and *Centetodon* sp. C (from the Chadronian of Wyoming, Montana and Texas). The two known Bridgerian species of *Centetodon*, *C. pulcher* and *Centetodon* sp. B (Lillegraven and McKenna, MS), were also described from the Powder Wash deposits, Utah, by Krishtalka (1975).

These species, as well as the early Uintan *Centetodon* sp. U from California are distinct from Oligocene species in that the upper molars have one lingual root and subequal pre- and postcingula. Oligocene species of *Centetodon* described by Lillegraven and McKenna (MS) have upper molars with two lingual roots and a postcingulum larger than the precingulum. In these respects, the two species of *Centetodon* from the late Uintan deposits of Badwater are of Oligocene aspect.

Centetodon magnus (Clark, 1936)
(Fig. 6; Tables 3,4)

REFERRED SPECIMENS: m1: 29197; M1-3: 31292; M1: 31298; M2: 15019; M1 or M2: 23854, 31297.

LOCALITIES: 5 Front, 20.

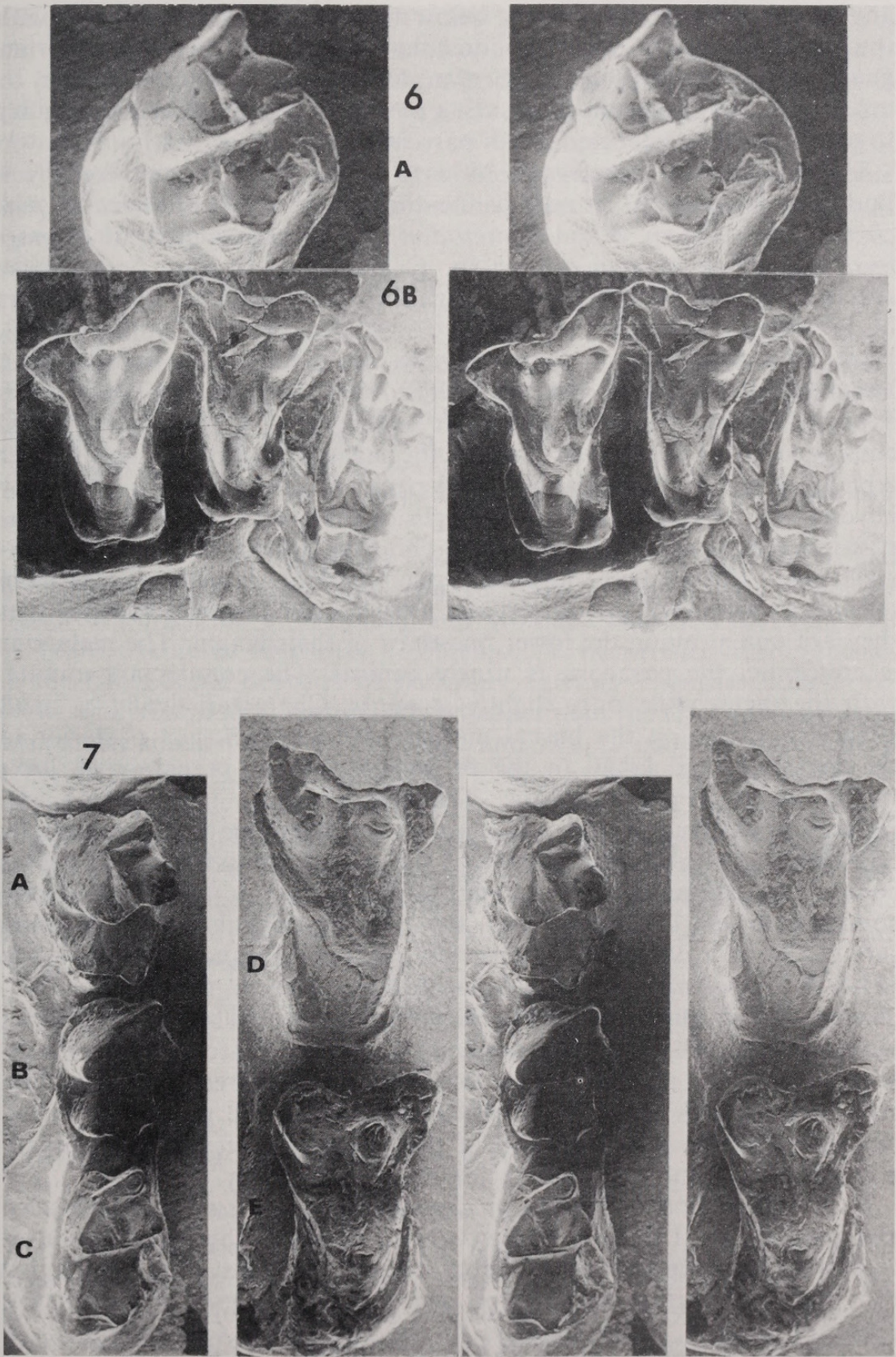
KNOWN DISTRIBUTION: Uintan, Duchesnean, Wyoming; Chadronian, Montana, South Dakota, Colorado; Orellan, Colorado.

DESCRIPTION AND REMARKS: The Badwater occurrence of *C. magnus* is the earliest known record of that species. *C. magnus* is much larger in comparative parts of the dentition than *Centetodon* sp. C, the other species of *Centetodon* recovered from the Badwater deposits, and described below.

As in other species of *Centetodon*, m1 of *C. magnus* has a very high trigonid and a much lower, narrower talonid. The protoconid and metaconid are tall and subequal, the paraconid is lingual and somewhat compressed anteroposteriorly, and the trigonid is open lingually between the metaconid and paraconid. The talonid is longer in comparison with the trigonid than in other Eocene species of *Centetodon*. The talonid cusps are low and equal in size, with the hypoconulid closer to the entoconid than the hypoconid. The cristid obliqua is straight in *C. magnus*

Fig. 6. *Centetodon magnus*. (A) CM 29197, Lm1; (B) CM 31292, LM1-3; both approx. x 13.

Fig. 7. *Centetodon* sp. C. (A) CM 16008, (B) CM 15137, (C) CM 15115, composite Lm1-3, approx. x 13; (D) CM 15619, RM1; (E) CM 16801, RM2; both approx. x 15.



and meets the trigonid directly below the protoconid, in contrast with the labially concave cristid obliqua that strikes the trigonid more lingually in *Centetodon pulcher*, *Centetodon* sp. B, and *Centetodon* sp. U. m2 repeats the morphology of m1, except for a more nearly triangular trigonid. m3 is shorter and much narrower than m1 or m2.

Upper molars of *C. magnus*, hitherto unknown, were recovered from Badwater locality 20. In contrast to the stratigraphically older *C. pulcher*, *Centetodon* sp. B and *Centetodon* sp. U, upper molars of *C. magnus*, like those of *Centetodon* sp. C and other known post-Eocene species of *Centetodon*, have two lingual roots. Otherwise, upper molars of *C. magnus* and other species of *Centetodon* are very similar. M1-2, essentially rectangular in occlusal view, are much longer labially than lingually, and are very transverse. The styler shelves are broad, with expanded metastylar and parastylar salients and a prominent buccal emargination of the crown. On M1 the metastylar area projects farther labially than the parastylar area, whereas the latter extends anteriorly beyond the remaining anterior margin of the crown. On M2 the parastylar salient is larger than on M1, and juts labially beyond the metastylar one. The paracone and metacone on M1-2 are quite distant from the buccal border of the crown, and arise from a common base, so that they are united along the lower one-third of their height. The metacone is crescentic; the paracone is nearly conical. The conules are minute, with the metaconule only slightly stronger. Characteristically, a small stylocone occurs on the buccal margin of the crown, just posterior to the parastyle, and labial to the paracone. A weak preparacrista links the paracone to the stylocone. The postmetacrista is very high and slopes posterolabially from the apex of the metacone to the metastyle, and defines the posterior margin of the metastylar salient. The protocone, which forms the lingual apex of the crown, is anteroposteriorly compressed, and leans anteriorly. Pre- and postcingula occur on either side of the base of the protocone, but are not continuous lingually. On M1-2 of *C. magnus* these cingula are broader than on those of *Centetodon* sp. C and other Eocene species of *Centetodon*. There is no distinct hypocone on M1-2 of *C. magnus*, although the postcingulum terminates lingually in a raised crest that may be interpreted as a definite cusp. Strong pre- and postprotocristae run from the protocone to the parastyle and the posterior wall of the metastylar area and demarcate a broad paracingulum and metacingulum, respectively.

Of the three Eocene species of *Centetodon* recognized by Lillegraven and McKenna (MS), only *Centetodon* sp. U, from the early Uintan of California, was represented by upper molars. These have a single lingual root that shows incipient division into a wider anterior and narrower posterior column. Upper molars of the Bridgerian *Centetodon* sp. B recovered from Powder Wash (Krishtalka, 1975) reveal a lingual root of

similar structure, except that on a few of the upper molars the root is partially bifurcate. The presence of two lingual roots on upper molars of both species of *Centetodon* from Badwater reveals a morphocline in the division of the upper molar lingual root in the evolution of *Centetodon* during the Eocene. *Centetodon* sp. B seems close to the ancestry of *Centetodon* sp. U. Their molar morphology implies that either of these species may have been involved in the ancestry of the two species of *Centetodon* from Badwater.

Centetodon sp. C, Lillegraven and McKenna (MS)
(Fig. 7; Tables 3,4)

REFERRED SPECIMENS: p4: 15695; m1: 15092, 15605, 16008, 16897, 18226, 23856, 23939, 29111, 29396, 29397; m2: 14547, 15004, 15060, 15064, 15120, 15137, 21631, 23863, 29398, 29399; m3: 15065, 15067, 15115, 18215, 23861; M1: 15125, 15619, 31293, 31294; M2: 15010, 16801, 31295, 31296; M3: 15128.

LOCALITIES: 5, 5A, 5 Front, 5 Back, Wood, 20.

KNOWN DISTRIBUTION: Uintan, Duchesnean, Wyoming; Chadronian, Wyoming, Montana, Texas.

DESCRIPTION: This species of *Centetodon*, named by Lillegraven and McKenna (MS), is based on material recovered from the early Oligocene Chadron Formation of Wyoming and Montana and the Chambers Tuff of Texas. As noted above for *C. magnus*, the occurrence of this species in the late Eocene deposits of Badwater extends its earliest known record. *Centetodon* sp. C is somewhat smaller than the Orellan *C. marginalis*, much smaller than *C. magnus*, and like *C. magnus*, differs from other Eocene species in having upper molars with two lingual roots.

The morphology of the lower and upper molars of *Centetodon* sp. C, except for their smaller size, is virtually identical to that described above for *C. magnus*. The pre- and postcingula are weaker on M1-2 of *Centetodon* sp. C and do not extend as far lingually around the base of the protocone. The styler shelf is narrower in *Centetodon* sp. C, and the styler salients are less expansive.

Family Apternodontidae (Matthew, 1910)
Apternodus Matthew, 1903
Apternodus sp. cf. *A. illifensis*
(Fig. 9; Tables 3,4)

REFERRED SPECIMENS: m2-3: 27437; m3: 23868; M1-2: 29012.

LOCALITY: 20.

KNOWN DISTRIBUTION: Duchesnean, Wyoming.

DESCRIPTION AND REMARKS: The material referred here is much larger than that of *Oligoryctes* sp. described below, but is similar in size and morphology to *Apternodus*, especially the Chadronian *A. illifensis* (Galbreath, 1953). Like *A. illifensis*, the dental remains from locality 20 are smaller than those of *A. brevirostris* (Schlaikjer, 1934) and *A. gre-*

goryi (Schlaikjer, 1933), and m3 has a longer talonid than in the latter two species and *A. mediaevus* (Matthew, 1903). As in *A. illifensis*, M1-2 have complete cingula from the parastyle to the metastyle, but lack a definite protocone or hypocone. In contrast, the cingula on M1-2 of *A. brevirostris* are not complete and, as in *A. gregoryi*, bear a distinguishable protocone and hypocone lingually. Upper teeth of *A. mediaevus* are unknown. This record of *Apternodus* is the earliest known occurrence of the genus.

Table 3. Dimensions of upper teeth of *Nyctitherium christophi* n. sp., *Centetodon magnus*, *Centetodon* sp. C, *Apternodus* sp. cf. *A. illifensis* and *Oligoryctes* sp.

	P4		M1		M2		M3	
	L	W	L	W	L	W	L	W
<i>Nyctitherium christophi</i> n. sp.								
27866	2.1	—	1.7	2.4	1.6	2.6	1.3	2.6
15023	—	2.4						
15088*			1.6**	—				
16009					1.6	2.6		
23799					1.6	2.7		
<i>Centetodon magnus</i>								
31292			2.0	2.9	1.7	2.9	1.4	2.5
31298			2.1	—				
<i>Centetodon</i> sp. C								
15125			1.6	2.4				
15619			1.7	2.4				
16801					1.5	2.3		
15128							0.7	1.5
<i>Apternodus</i> sp. cf. <i>A. illifensis</i>								
29012			2.5	4.0	1.9	3.9		
<i>Oligoryctes</i> sp.								
23866			1.0	1.6				
23942			1.0	—				

*M1 or M2

**Lingual length

Table 4. Dimensions of lower teeth of *Centetodon magnus*, *Centetodon* sp. C, *Apternodus* sp. cf. *A. illifensis* and *Oligoryctes* sp.

	p4			m1			m2			m3		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW	
<i>Centetodon magnus</i>												
29197			2.2	1.5	1.3							
<i>Centetodon</i> sp. C												
15695	1.6	1.1										
15092			1.7	1.2	1.0							
15605			1.7	1.2	—							
16008			1.8	1.3	1.1							
16897			1.7	1.2	1.1							
18226			1.6	1.2	1.0							
29111			1.6	1.2	1.0							
29397			1.7	1.2	1.1							
14547						1.8	1.3	1.0				
15060						1.7	1.2	1.0				
15120						1.6	1.1	0.9				
15137						1.6	1.2	1.0				
21631						1.7	1.2	1.0				
29398						1.8	1.3	1.1				
29399						1.7	1.2	1.0				
15065									1.7	1.0	0.8	
15067									1.5	1.0	0.8	
15115									1.6	1.0	0.8	
18215									1.5	1.0	0.8	
<i>Apternodus</i> sp. cf. <i>A. illifensis</i>												
27437						2.2	1.8	—	2.0+	1.4	—	
23868									2.1	1.3	—	
<i>Oligoryctes</i> sp.												
23867**			0.7*	0.9	—							
23869**			0.7*	1.0	—							
23940**			0.9	1.0	—							
23941**			0.8*	1.1	—							

*trigonid length only

**m1 or m2

Oligoryctes Hough, 1956*Oligoryctes* sp.

(Fig. 8; Tables 3,4)

REFERRED SPECIMENS: m1 or m2: 23867, 23869, 23940, 23941; m3: TTM 2454; M1: 23866, 23942.

LOCALITIES: 5 Front, Wood, 6.

KNOWN DISTRIBUTION: Uintan, Wyoming.

REMARKS: These isolated teeth are much smaller than similar parts of the dentition of *Apternodus*, but are equal in size to the Chadronian *Oligoryctes cameronensis*. A characteristic feature of the species—a single cusp on the posterior margin of the talonid on m3 as high as the protoconid (Hough, 1956)—is absent on the isolated m3 from Badwater. This material may be referable to a new Uintan species of *Oligoryctes* presently being described by McKenna (MS).

Family Soricidae (Fischer Von Waldheim, 1817)

The soricid remains from the late Eocene of Badwater are the earliest known record of that family. On the basis of size and crown morphology, the material—isolated premolars and molars and two partial dentaries—is separable into three groups. One is identified as a species of *Domnina*; the other two are non-heterosoricine soricids.

Subfamily Heterosoricinae Viret and Zapfe, 1951

Domnina Cope, 1873*Domnina* sp. cf. *D. gradata*

(Fig. 10; Tables 5, 6)

REFERRED SPECIMENS: m1-3: 23797; m1-2: 15005; m1: 19776, 23865; m2: 15117, 16062, 23864; m3: 16997, 18198; P4: 15014; M1: 16996.

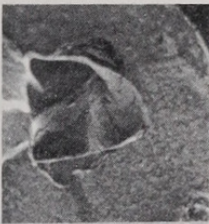
LOCALITIES: 5A, 5 Front, Wood, 20.

KNOWN DISTRIBUTION: Uintan, Duchesnean, Wyoming.

DESCRIPTION: Patterson and McGrew (1937) and Repenning (1967) have thoroughly described *Domnina gradata* from the Orellan of Colorado, South Dakota, and Nebraska. In the absence of preserved mandibular condyles or the antemolar dentition, *Domnina*, as well as all other heterosoricines, are best defined by P4 and M1 that lack both an emargination of the posterior border of the crown and the resultant posterior expansion of the hypoconal shelf. Instead, the posterior margin of P4 and M1 of *Domnina* is nearly straight, and the crown is quadrate in occlusal view. Such is the case on CM 15014 and CM 16996, isolated P4 and M1. The labial half of P4 is formed as a high wall that tapers

Fig. 8. *Oligoryctes* sp. (A) CM 23940, Rm1 or m2; (B) CM 23866, LM1; both approx. x 15.

Fig. 9. *Apternodus* sp. cf. *A. illifensis*. (A) CM 27437, Rm1-2; (B) CM 29012, RM1-2; both approx. x 17.



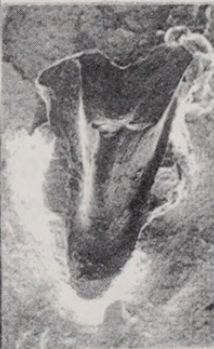
8A



8B



9A



9B



posterolabially from the paracone to the metastylar tip of the crown. A low parastyle juts anteriorly from the base of the paracone. Although the lingual part of the crown is worn on CM 15014, the protocone appears to have been very weak or absent, as is also the case on P4 of *D. gradata*. On M1 the paracone, metacone, and mesostyle are united to form a W-shaped ectoloph, with the paracone situated more buccally than the metacone.

The lower molars referred here are similar to those of *Domnina* but differ from those of *Trimylus* in that a high entocristid joins the entoconid to the posterior face of the metaconid and closes the talonid basin lingually. In *Trimylus* a deep notch isolates the entoconid from the metaconid (Repenning, 1967). The lower molars, larger than those of the Chadronian *D. thompsoni* (Simpson, 1941), are closer in size and crown morphology to those of *D. gradata*. In both the Badwater species and *D. gradata*, the mental foramen occurs below m1; the labial cingulid on m1 is not continuous around the base of the protoconid; the hypoflexid notch is deep; and the cristid obliqua meets the trigonid lingually, below the ventral apex of the protocristid. The m1 of the Badwater form is only slightly smaller than the observed size-range of m1 of *D. gradata*.

Soricid sp. A.
(Fig. 11; Tables 5, 6)

REFERRED SPECIMENS: m1-2: 15098; m1: 15025, 15642, 15677, 18196; m1 or m2: 15705; M1: 15712, 16800; M2: 15107, 15113.

LOCALITIES: 5A, 5 Front, 5 Back, Wood.

KNOWN DISTRIBUTION: Uintan, Wyoming.

DESCRIPTION: The material referred here is significantly smaller than that of *Domnina* sp. cf. *D. gradata*. The upper molars differ from those of *Domnina* and other heterosoricines in possessing a flaring hypoconal flange that is accentuated by an emargination of the posterior margin of the crown. On the lower molars the external cingulid is much weaker than in *Domnina* sp. cf. *D. gradata*, and the cristid obliqua meets the trigonid labially, below the protoconid, so that the hypoflexid notch is much shallower than in *Domnina*. The lower molars, however, resemble heterosoricines and soricines but differ from crocidurines and most limnoecines in that the hypoflexid notch emerges labially at the level of the external cingulid (Repenning, 1967). In the absence of preserved p4, m3, and a mandibular condyle it is difficult to establish the subfamilial or generic affinities of this material. The upper and lower molars are here tentatively assigned to the same species of soricid on the basis of size association and parsimony, although recovery of additional material may imply the occurrence of more than one taxon.

Table 5. Dimensions of lower teeth of *Domnina* sp. cf. *D. gradata* and soricid sp. A.

	m1			m2			m3		
	L	AW	PW	L	AW	PW	L	AW	PW
<i>Domnina</i> sp. cf. <i>D. gradata</i>									
23797	2.0	1.3	1.5	1.8	1.4	1.5	1.6	1.2	0.8
15005	—	—	1.3+	1.7	1.5	1.5			
19776	2.0	1.4	1.6						
23865	2.1	1.3	1.5						
15117				—	1.3	—			
16062				1.8	—	—			
23864				1.8	1.3	1.4			
16997							1.5	1.1	0.7
18198							1.5	1.2	0.8
soricid sp. A									
15098	1.7	1.3	1.4	1.7	1.4	1.4			
15025	1.7	—	1.3						
15642	1.7	—	—						
15677	1.6	1.3	1.3						
18196	1.7	1.4	1.4						

Table 6. Dimensions of upper teeth of *Domnina* sp. cf. *D. gradata*, soricid sp. A and soricid sp. B

	P4			M1			M2		
	L*	L**	W	L*	L**	W	L*	L**	W
<i>Domnina</i> sp. cf. <i>D. gradata</i>									
15014	1.7	1.1	1.7						
16996				2.1	2.0	2.3			
soricid sp. A.									
15712				1.7	1.7	2.0			
16800				1.7	1.6	2.1			
15107							1.6	1.5	2.1
15113							1.5	1.5	2.0
soricid sp. B									
29198	2.1	1.3	2.4						

*labial length

**lingual length

Soricid sp. B
(Fig. 12; Table 6)

REFERRED SPECIMEN: P4: 29198.

LOCALITY: 20.

KNOWN DISTRIBUTION: Duchesnean, Wyoming.

DESCRIPTION: CM 29198, a right P4, is essentially T-shaped in occlusal view, with an elongate buccal margin and a narrow lingual area. The posterior margin is deeply excavated between the metastylar and lingual regions of the crown, so that the hypoconal shelf is accentuated. The paracone, a tall, conical cusp, forms the broader anterior end of a high crest that tapers toward the posterobuccal corner of the crown. A wide internal cingulum runs along the base of the crest. A low parastyle extends anteriorly from the base of the paracone, which occupies most of the labial half of the crown. The protocone, lower than, and anterolingual to, the paracone, is highly compressed anteroposteriorly, and forms the anterolingual corner of the tooth. Protocristae are faint and conules are absent. The hypoconal flange runs posteriorly and dorsally from the base of the protocone and ends labially midway along the transverse width of the crown. The lingual margin of the flange is eroded, but a hypocone does not seem to have been present.

REMARKS: CM 29198, with a posteriorly emarginate crown, is a P4 of a non-heterosoricine shrew (Repenning, 1967), and resembles the posteriorly excavated upper molars of soricid sp. A described above. The tooth, however, cannot be referred to the latter since it is significantly larger than M1 of soricid sp. A, in contrast to the usual condition—smaller P4 than M1—in soricids. CM 29198 appears to represent a third species of shrew at Badwater. The excavation of the posterior border of P4 is similar to that in crocidurines (e.g. *Suncus*, *Crocidura*) and soricines (e.g. *Sorex*). The lingual position of the protocone is closer to the condition on P4 of the former. P4 of limnoecines is unknown (Repenning, 1967).

Prior to this description, the earliest records of soricids were *Domnina thompsoni* from the Chadronian Pipestone Springs locality, Montana (Simpson, 1941), and *Sorex herrlingensis* (Palmowski and Wachendorf, 1966) from an early Oligocene fissure fill near Württemberg. The figured mandible of *S. herrlingensis* (Palmowski and Wachendorf,

Fig. 10. *Domnina* sp. cf. *D. gradata*. (A) CM 23797, Rm1-3, approx. x 17; (B) CM 15014, LP4; (C) 16996, LM1; both approx. x 12.

Fig. 11. Soricid sp. A. (A) CM 15098, Rm1-2; (B) CM 16800, LM1; (C) CM 15113, RM2; all approx. x 12.

Fig. 12. Soricid sp. B. CM 29198, RP4, approx. x 15.

Fig. 13. *Thylacaelurus* sp. cf. *T. montanus*. CM 15061, RM1, approx. x 11.



1966:234) bears p1-4m1-3. The posterior face of p4 is excavated and concave as in heterosoricines and crocidurines (Repenning, 1967). The molars more closely resemble those of heterosoricines in that the hypoflexid notch emerges labially at the level of the external cingulid rather than more dorsally, as in crocidurines. Repenning (1967) did not discuss *S. herrlingensis*, but Thenius (1969) questioned its generic identification. Subsequently, Engesser (1975) correctly removed the species from *Sorex* and referred it to a new European heterosoricine genus, *Quercysorex*.

The earliest occurrence and diversity of shrews at Badwater implies the presence of ancestral soricids in as yet unsampled early and pre-Uintan deposits, and considerably antedates the oldest known record of crocidurines (Burdigalian, Europe), limnoecines (Whitneyan, North America) and soricines (Stampian, Europe). As discussed below, the paleoecological implications of this disjunct distribution are clear: most mid-late Eocene and Oligocene localities preserve similarly restricted environmental situations with, probably, lowland, lake-margin communities (Black, 1967). These do not reflect the diversity of later Eocene and Oligocene life.

Order Dermoptera.

Family uncertain

Thylacaelurus Russell, 1954

Thylacaelurus sp. cf. *T. montanus*

(Fig. 13)

REFERRED SPECIMENS: i: 15124, 15616, 15639, 18193, 18202, 27000; M1: 15061, 15707.

LOCALITIES: 5A, 5 Front, 5 Back.

KNOWN DISTRIBUTION: Uintan, Wyoming; (Chadronian, British Columbia, for *T. montanus*).

DESCRIPTION: Except for their slightly smaller size (L, 1.7; W, 2.0) and the absence of a precingulum, the two isolated upper molars are virtually identical to M1 of *Thylacaelurus montanus* from the early Oligocene Kishenehn deposits of British Columbia, Canada (Russell, 1954). Characteristically, the paracone, paraconule, and protocone are aligned along the anterior margin of the crown, whereas the metacone, metaconule, and hypocone occur along the posterior border. Consequently, these sets of cusps are widely separated by a deep trigon basin that is oriented buccolingually from the labial border of the crown to the internal face of the protocone. The paracone and metacone are quite lingual, leaving a large stylar shelf. Three stylar cusps (two mesostyles and a metastyle) occur along the buccal margin of the crown. The most anterior mesostyle is posterobuccal to the paracone. The posterior mesostyle is anterobuccal to the metacone. The metastyle forms the posterolabial corner of the crown. A postparacrista links the paracone to the anterior mesostyle, and pre- and postmetacristae join the metacone to

the posterior mesostyle and metastyle, respectively. The protocone forms the anterolingual corner of the crown. The conules are large and conical but lack well developed cristae. The hypocone, almost as large as the metaconule, occurs posterolabial to the protocone and is linked to the postprotocrista by a strong crest.

The referred incisors have digitate crowns, with three (one specimen), four (three specimens), or five (one specimen) comb-like projections. CM 15639, an incisor fragment with three lobes, appears to have had four or five when complete. These incisors most closely resemble i3 of the extant dermopteran *Cynocephalus*, and differ from the bilobate lower incisors of *Plagiomene* (Rose, 1973). Although we are reasonably confident in our referral of these incisors to *Thylacaelurus*, they may also belong to the Badwater species of *Nyctitherium*, since digitate incisors have been identified in another genus of this family (Sigé, 1976).

REMARKS: The affinities of *Thylacaelurus* are uncertain. Although Russell (1954) described *T. montanus* as a didelphid marsupial, the species was subsequently identified as a eutherian (McKenna, in Van Valen, 1965), a plagiomenid dermopteran (Van Valen, 1967) and a dimylid-like insectivore (Szalay, 1969). M1 of *Thylacaelurus*, with stylar cusps and connecting cristae, superficially resembles that of *Elpidophorus*, *Plagiomene*, *Planetitherium*, *Remiculus*, *Adapisoriculus*, and didelphid marsupials. In contrast to *Thylacaelurus*, however, M1 of didelphids, *Remiculus*, and *Adapisoriculus* lack a true hypocone, have subcrescentic cusps, smaller conules with internal and external wings, and a medial rather than anterolingual protocone. The stylar cusps and possible reduction of M3 in *Thylacaelurus* are also reminiscent of some talpids and dimylids (see Szalay, 1969), but these resemblances also appear to be convergent when one considers the absence in *Thylacaelurus* of an expanded hypoconal shelf, dilambdodonty, low crescentic conules, and a suite of other characters that unite talpids and dimylids among the soricomorphs (Schmidt-Kittler, 1973).

Rather, the structure of M1-2 of *Thylacaelurus*—the stylar shelf and cusps, the enlarged conules, the anterolingual protocone, and the alignment of the cusps in labiolingual rows on either side of the trigon valley—is characteristic of plagiomenids, recent dermopterans, and the alleged mixodectid *Elpidophorus*. The latter may have been involved in the ancestry of the plagiomenids *Planetitherium* and *Plagiomene* (see Simpson, 1936; Szalay, 1969; Rose, 1973). *Thylacaelurus* appears to be a dermopteran, but not a plagiomenid, since its enlarged premolariform P4 and possible loss or reduction of M3 is apomorphic with regard to the fully molariform P4 and occurrence of M3 in known members of the family. The Badwater record of *Thylacaelurus* is the earliest known occurrence of the genus.

COMMENTS

Two facets of the Badwater late Eocene mammalian assemblage—the alleged relictual occurrences and the earliest known occurrences of taxa—have specific implications regarding our knowledge of middle and late Eocene mammal communities (Black, 1967). These facets are also reflected in the insectivore and dermopteran record. First, the occurrence of *Macrocranium* and a dermopteran at Badwater and their absence from North American middle Eocene and other late Eocene localities parallels the temporally disjunct distribution of *Phenacolemur* (Robinson, 1968a) and neoplagiaulacid multituberculates (Sloan, 1966; Krishtalka and Black, 1975). Second, the Badwater shrews, *Oligoryctes*, *Apternodus*, *Centetodon*, and a variety of rodents have not been recovered elsewhere from pre-Oligocene deposits. These records imply that the Badwater (and Shoddy Springs) sediments represent an otherwise unsampled ecological situation among North American Eocene post-Wasatchian localities. The latter are typically intermontane basin deposits that preserve similar lake margin and associated floodplain facies and correspondingly similar lowland communities. The Badwater assemblage may, in part, reflect an upland community, comprising, at least four groups: multituberculates, a dermopteran, *Phenacolemur*, and *Macrocranium*—small animals that during Bridgerian-Uintan time probably inhabited upland environments that were far from and not preserved in currently sampled Bridgerian-Uintan sediments. We concur with Black (1967) that assemblages recovered from the latter do not represent the actual diversity of middle and late Eocene vertebrates.

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