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## NORTH AMERICAN NYCTITHERIIDAE (MAMMALIA, INSECTIVORA)

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### ABSTRACT

North American Nyctitheriidae comprise the genera *Leptacodon* (*L. tener*, *L. catulus*, new species, and provisionally, *L. munusculum* and *L. packi*), *Nyctitherium* (*N. velox*, *N. serotinum*, and an undescribed species) and *Pontifactor* (*P. bestiola*, *Pontifactor* sp.). "*Leptacodon*" *jepseni* and *Myolestes dasypelix* are removed from the Nyctitheriidae. The former may be an adapisoricid; the latter is a geolabidid. Two distinct groups of nyctitheriids are recognized: one includes *L. tener*, *L. catulus*, *L. packi*, and the species of *Nyctitherium*. The second involves *L. munusculum* and the species of *Pontifactor*. *Saturninia* and *Remiculus* respectively, may be European representatives of the two discrete North American groups of nyctitheriids. *L. tener* may have possessed five upper premolars, with loss occurring at the P3/p3 locus in the evolution of *Nyctitherium*.

### INTRODUCTION

The genera of insectivores that Simpson (1928) first included in the Family Nyctitheriidae were *Nyctitherium*, *Entomacodon*, *Centetodon*, *Myolestes*, and *Protentomodon*. McKenna (1960a) questioned the systematic unity of this group and, instead, employed Heller's (1935) Family Amphilemuridae for *Entomolestes*, *Nyctitherium*, *Sespedectes*, *Amphilemur*, and, tentatively, *Macrocranium* and *Aculeodens*. *Myolestes* and *Centetodon* were subsequently referred to the Geolabidinae (McKenna, 1960b), and *Entomacodon* was shown to comprise material referable to marsupials (McKenna, 1960a) and *Nyctitherium serotinum* (Robinson, 1968). *Proten-*

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*tomodon* was correctly removed from nyctitheres by McKenna (1960a) and Robinson (1968), and considered *Insectivora incertae sedis* until more material could be recovered that would shed light on its affinities.

Van Valen (1967) abandoned the concept of the Amphilemuridae in favor of a Family Adapisoricidae with four subfamilies—Geolabidinae, Nyctitheriinae, Adapisoricinae and Creotarsinae—and an accompanying reshuffling of previous generic allocations.

The Family Nyctitheriidae was resurrected by Robinson (1966, 1968) and McKenna (1968) and strictly defined to include the genera *Leptacodon*, *Nyctitherium*, and *Saturninia*. Robinson (1968) also included the subfamilies Geolabidinae and Micropternodontinae, but these have since been thought to warrant familial status (Butler, 1972). Subsequently, West (1974) described a new genus and species of nyctithere, *Pontifactor bestiola*, from the upper part of the Bridger Formation, Wyoming. Only *Leptacodon*, *Nyctitherium*, and *Pontifactor* are here recognized as North American genera of the Nyctitheriidae.

This study of nyctitheriids is a revision of the second part of a doctoral dissertation (Krishtalka, 1975). The first part dealt with early Tertiary Adapisoricidae and Erinaceidae (Krishtalka, 1976). The material assigned here to the various species of nyctitheriids represents only the specimens examined. All measurements are in millimeters. Capital and lower-case letters: I/i (incisor), C/c (canine), P/p (premolar), M/m (molar), refer to upper and lower teeth.

The recent reclassification of mammals by McKenna (1975) and its corollary *raison d'être* must figure in forthcoming papers dealing with mammalian dentitions and dental homologies. The postcanine dental formula proposed as primitive for tokotheres was dP1/dp1, P2/p2, P3/p3, P4/p4, dP5/dp5, M1/m1, M2/m2, whereby dP5/dp5, M1/m1, M2/m2 were conventionally referred to as M1/m1, M2/m2, M3/m3, respectively. Recent investigations have suggested that five premolars may have occurred in the dermopteran *Plagiomene*, the erinaceid *Litolestes ignotus*, the adapisoricid *Ankylodon* (Schwartz and Krishtalka, 1976; Krishtalka, 1976), and in some plesiadapiform primates (Schwartz and Krishtalka, MS; Schwartz, in press)—groups that also possess three molars. If these identifications are sound, the primitive tokothere post-canine dental complement included five premolars and three molars. The deciduous or permanent nature of each of the five premolars is not certain. Also uncertain are the premolar loci involved in the reduction from five to four and fewer premolars in many tokotheres. Schwartz (in press) has demonstrated that loss of one premolar in plesiadapiforms involves inhibition at the P3/p3 locus. This, however, may not be the case in other tokotheres, specifically, insectivores. Until the homologies are established, the post-incisor complement of nyctitheres is designated here by the conventional C1/c1, P1-4/p1-4, M1-3/m1-3.



The abbreviations used in this paper are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; PU, Princeton University; TTU, Texas Tech University; YPM, Yale Peabody Museum; L, length; W, width; AW, anterior width (width of trigonid); PW, posterior width (width of talonid).

Family Nyctitheriidae Simpson, 1928

*Leptacodon* Matthew and Granger, 1921

*Leptacodon* (Matthew and Granger, 1921), originally referred to the Leptictidae, was provisionally allocated to the Metacodontidae by McKenna (1960a) and then more rigidly defined as a nyctitheriid by both McKenna (1968) and Robinson (1968). As was the case with *Nyctitherium*, much of the confusion concerning the affinity and systematics of *Leptacodon* was due to the inclusion of a number of unrelated species in the genus: the genotype *L. tener* Matthew and Granger, 1921; *L. packi* Jepsen, 1930; *L. ladae* Simpson, 1935; *L. munusculum* Simpson, 1935; *L. jepseni* McKenna, 1960a; and *Diacodon minutus* Jepsen, 1930.

McKenna (1960a) suggested that *L. packi* was a leptictid, that *L. munusculum* and *L. tener* were generically distinct, and that *D. minutus* was referable to *Leptacodon* rather than to the leptictids *Diacodon* or *Palaeictops*. Gazin (1956) had considered *D. minutus* a species of *Palaeictops*. Van Valen (1967) also advocated generic separation of *L. tener*, *L. munusculum*, *L. ladae* and *L. jepseni*. The eventual recognition of *Leptacodon* as a valid nyctitheriid by McKenna (1968) and Robinson (1968) applied only to the genotype, *L. tener*. *L. ladae*, "*L.*" *minutus* and *L. jepseni* are not referable to *Leptacodon*, *sensu stricto*. *L. ladae* is a species of the adapisoricid *McKennatherium*, and "*L.*" *minutus* is probably a North American species of *Adunator* (Krishtalka, 1976). The affinities of *L. jepseni* are described below. *L. packi* and *L. munusculum* are provisionally retained in *Leptacodon*, although they may more properly be referable to *Nyctitherium* and *Pontifactor*, respectively.

*Leptacodon tener* Matthew and Granger, 1921

(Fig. 1; Table 1)

REFERRED SPECIMENS: PU 21395, Rm1-2; PU 21398, Lm1-3.

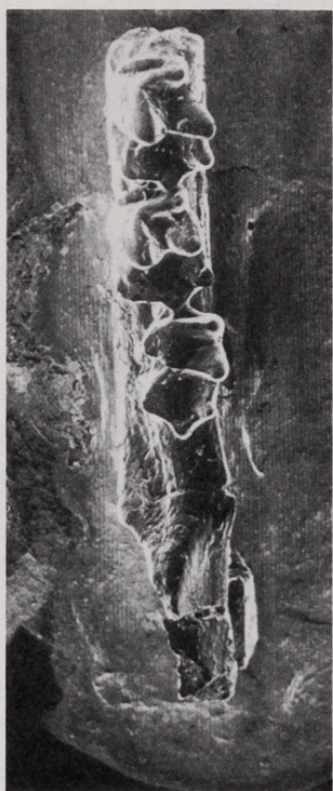
LOCALITY: Cedar Point Quarries, Polecat Bench Formation, Wyoming.

KNOWN DISTRIBUTION: Tiffanian, Colorado, Wyoming, and Alberta.

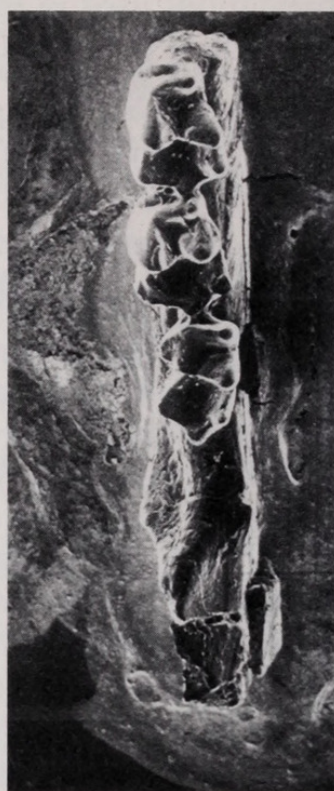
REMARKS: McKenna (1968) has presented a thorough and excellent description of the type material of *L. tener*. The two partial mandibles from the Polecat Bench do not differ significantly from the type.

The upper dentition of the type specimen (AMNH 17179) is important in light of recent suggestions concerning the occurrence of five premolars in a number of early Tertiary mammals: the erinaceid *Litolestes ignotus*,





I  
A



B





the dermopteran *Plagiomene multicuspis* (Schwartz and Krishtalka, 1976; Krishtalka, 1976), the adapisoricid *Ankylodon* (Krishtalka, 1976), and various plesiadapiform and tarsiiform primates (Schwartz, in press; Schwartz and Krishtalka, MS). After examination of AMNH 17179, I concur with McKenna's (1968:5) reconstruction and description of the upper teeth in the crushed rostrum: three molars and six antemolar teeth, the latter labelled A B C D E P4. Tooth A, single rooted, is either an incisor or a canine, probably the latter. Tooth B, also single rooted, has a small heel cusp and appears premolariform. Teeth C, D, and E are double-rooted and are unquestionably premolariform. Thus the five teeth—B, C, D, E, P4—may comprise the upper premolar complement of *Leptacodon tener* and are perhaps homologous with dP1, P2, P3, P4, P5, respectively—the primitive premolar formula of preptotherian mammals (McKenna, 1975). If these identifications are correct, the occurrence of five premolars in *Leptacodon tener* (at least in the upper dentition) defines the primitive condition for Nyctitheriidae. If tooth A is a canine and if AMNH 17179 preserves the entire upper dentition, *L. tener* lacked incisors. Although the presence of incisors has not been demonstrated in nyctitheriids (Robinson, 1968), this may be an artifact of the dearth of nyctitheriid material with completely preserved anterior dentitions. Part of the anterior dentition of *Nyctitherium velox* is present on YPM 14396, partial left mandible with canine, alveolus for p1, and p2-4, m1-2. The presence of four premolars in *Nyctitherium* may be a derived feature with respect to the suggested occurrence of five premolars in *Leptacodon tener*. The dental homologies of the four premolars of *Nyctitherium* are discussed in a later section.

*Leptacodon munusculum* Simpson, 1935  
(Fig. 2; Table 1)

REFERRED SPECIMENS: PU 20026, Rp4-m2; AMNH 39542, Lp3-m3.

LOCALITY: Cedar Point Quarries, Polecat Bench Formation, Wyoming; Gidley Quarry, Fort Union Formation, Montana.

KNOWN DISTRIBUTION: Tiffanian, Wyoming; Torrejonian, Montana.

DESCRIPTION: These specimens closely agree with Simpson's (1935) diagnosis of *L. munusculum* in the following features: p4 is labiolingually compressed, and the talonid is narrow and defined by a straight and parallel entocristid and cristid obliqua. On m1-3 the paraconid is moderately compressed anteroposteriorly, and the talonid does not extend labially beyond the trigonid. The talonid on m3 is somewhat reduced.

REMARKS: Relative to *L. munusculum*, p4 of *L. tener* is less compressed labiolingually and has a wider talonid and a labially convex cristid obliqua. The paraconid on m1-3 of *L. tener* is more nearly cuspsate, the talonid on

←

Fig. 1. *Leptacodon tener*, AMNH 17179, Type, Mason Pocket, Tiffany Formation, Colorado. A. Lm1-3; approx. X 11. B. LP4-M3; approx. X 12.

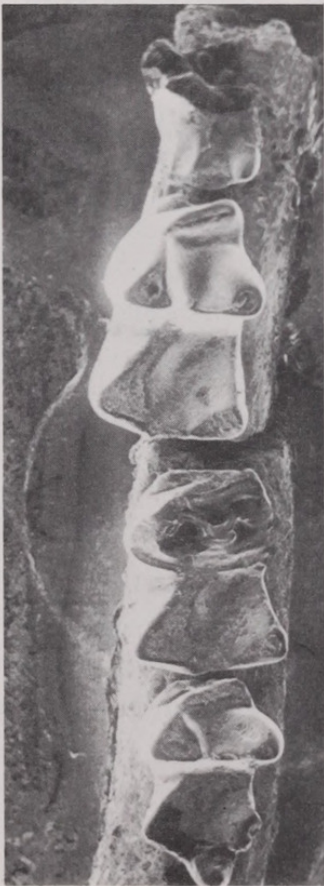




2



3



4





m3 is more elongate, and the talonid on m1-2 extends beyond the labial margin of the trigonid. In terms of these differences, *L. tener* seems more closely related to *Nyctitherium*, whereas *L. munusculum* bears a greater resemblance to *Pontifactor* sp., which is described below. However, remains of an upper dentition that could be confidently ascribed to *L. munusculum* have yet to be reported. Since *Pontifactor* is best defined on the upper dentition, I hesitate to refer *L. munusculum* to that genus, although McKenna (1960a) has advocated removal of *L. munusculum* from *Leptacodon*, an action that may be warranted on the basis of the lower dentition alone. *L. munusculum* is tentatively retained as a species of *Leptacodon* until more material is recovered.

*Leptacodon packi* Jepsen, 1930

(Fig. 3; Table 1)

REFERRED SPECIMENS: PU 14033, Lp4, m2-3; PU 14140, Rp3-m3.

LOCALITY: Silver Coulee beds, Polecat Bench Formation, Wyoming.

KNOWN DISTRIBUTION: Late Tiffanian of Wyoming and Alberta.

DESCRIPTION AND REMARKS: *L. packi* is larger than *L. munusculum* and *L. tener*, but resembles the latter in possessing cuspsate rather than lophid-like paraconids on the molars. Compared to *L. tener*, the trigonid on m1-3 of *L. packi* is less nearly square, the paraconid is somewhat larger, and the hypoconulid is not median, but closer to the entoconid. In these features *L. packi* is structurally intermediate between *L. tener* and *Nyctitherium*. The hypoconulid and entoconid are not quite as twinned on m1-3 of *L. packi* as in *Nyctitherium*, and the hypoflexid notch completely separates the trigonid and the talonid basally. On m1-3 of *Nyctitherium* the labial part of the base between the talonid and trigonid is not interrupted by the hypoflexid notch. The upper dentition, unknown in *L. packi*, is, as described below, quite distinctive in *Nyctitherium*. As was the case with *L. munusculum*-*Pontifactor*, *L. packi* may be more properly identified as a species of *Nyctitherium*, once remains of its upper dentition are recovered.

*Leptacodon catulus*, new species

(Fig. 5; Table 1)

ETYMOLOGY: CATULUS, L., youngest; in reference to the youngest known species of *Leptacodon*.

HOLOTYPE: AMNH 48173, LP3-M3, RP4-M3, Rp4-m3.

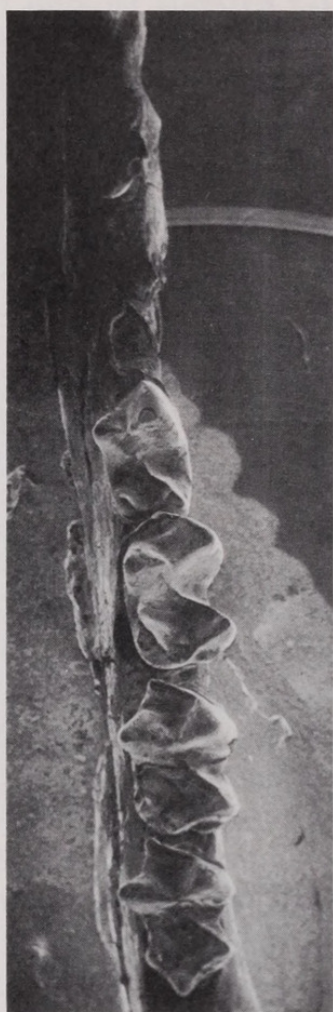
TYPE LOCALITY: Quarry 88, San José Formation, Almagré beds, New Mexico.

Fig. 2. *Leptacodon munusculum*, AMNH 35942, Lp3-m3, Gidley Quarry, Fort Union Formation, Montana; approx. X 11.

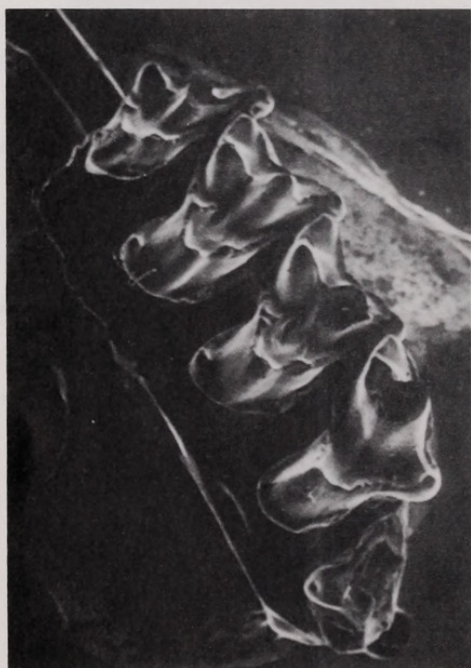
Fig. 3. *Leptacodon packi*, PU 14140, Rp3-m3, Polecat Bench Formation, Wyoming; approx. X 11.5.

Fig. 4. Cf. *Leptacodon* sp., AMNH 59610 and AMNH 59680, Lp4-m3, East Alheit Quarry, Wasatch Formation, Colorado; approx. X 12.





5  
A



B





KNOWN DISTRIBUTION: Wasatchian, New Mexico.

DIAGNOSIS: Late Wasatchian species of *Leptacodon*; size only slightly larger than *L. tener*; P4-M3 virtually identical to *L. tener*; P4 with a more definite lingual cingulum, and tiny hypocone; p4-m1 paraconid greatly reduced; m2-3 paraconid unreduced; hypoflexid deeper than in *L. tener*; cristid obliqua meets trigonid more internally.

DESCRIPTION: *L. catulus* is the youngest known species of *Leptacodon*. p4 is semimolariform and elongate with a well developed protoconid, metaconid, and a basined talonid. The paraconid is a small nubbin that occurs low on the anterior part of the base of the protoconid. The talonid, approximately three-quarters of the width of the trigonid, bears only two cusps, an entoconid and hypoconid. The cristid obliqua is strong, originates from the metaconid portion of the trigonid wall, and extends posterolabially to the hypoconid. As in other species of *Leptacodon*, m1-3 lean slightly lingually and possess open trigonids with well developed and subequal protoconid and metaconid. Characteristically, the paraconid on m1 is reduced to a short, ventrally sloping cristid. On m2-3 the paraconid is fully developed and uncompressed, but smaller than the metaconid or protoconid. The cristid obliqua meets the trigonid wall internal to the ventral notch between the protoconid and metaconid, as is the condition in *Nyctitherium*. However, as in *Leptacodon*, the hypoconulid occurs just lingual to the midline, more nearly medial than in *Nyctitherium*. The talonid is wider than the trigonid on m1, as wide as the trigonid on m2, but narrower and elongated on m3.

In comparable parts of the upper dentition, *L. catulus* is virtually identical to *L. tener* (McKenna, 1968). P4 of *L. catulus* has a slightly stronger posterolingual cingulum with a tiny hypocone, and all upper teeth are slightly more transverse. The dimensions of the upper teeth are P4, 1.4 X 1.7; M1, 1.3 X 1.8; M2, 1.3 X 1.9; M3, 0.9 X 1.7.

REMARKS: *L. catulus* from the Almagre Eocene most closely resembles the Paleocene *L. tener*. The two are basically differentiated by the severe reduction of the paraconid on p4-m1 of *L. catulus*. In the lower dentition, the weak paraconid and the more nearly medial position of the hypoconulid distinguish *L. catulus* from *Nyctitherium*. In addition, p4 of *Nyctitherium* bears three (as opposed to two) talonid cusps, and P4-M2 have a flaring hypoconal shelf and subcrescentic cusps, which are absent in *L. catulus*. *L. catulus* is also distinct from the *L. minusculum*-*Pontifactor* group of nyctitheriids in lacking the anteroposterior compression of the paraconid and trigonid on m1-3 and in the absence of a large hypocone and styler cusps on the upper molars.

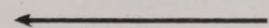


Fig. 5. *Leptacodon catulus*, new species, AMNH 48173, Type, Quarry 88, San José Formation, New Mexico. A. R?p2, p4-m3; approx. X 13. B. LP3-M4; approx. X 12.5.



Cf. *Leptacodon* sp.

(Fig. 4; Table 1)

REFERRED SPECIMENS: AMNH 59610, L1/2p4-m1; AMNH 59625, Rp4-m1; AMNH 59636, Rm1; AMNH 59680, Lm2-3.

LOCALITIES: East Alheit Quarry, Wasatch Formation, Colorado.

KNOWN DISTRIBUTION: Early Wasatchian of Colorado and Wyoming.

DESCRIPTION AND REMARKS: Delson (1971) referred three fragmentary mandibles from Powder River, Wyoming, to cf. *Leptacodon* sp., a species that is much larger than *L. tener* or *L. munusculum*. The material from Four Mile closely resembles this species, but is very fragmentary and does not add appreciably to our knowledge of its generic affinities. The molars do not decrease in size from m1 to m3, the trigonids are open and high, the paraconids are compressed and crestlike, and the talonid basin is deeply rounded with high surrounding walls. The entoconid and hypoconid, strong, sharp cusps, are not worn flat, and the hypoconulid is median. The compression of the paraconid is reminiscent of *L. munusculum*, whereas the open trigonid is closer to the condition in *L. tener*. AMNH 59610 and 59680 are fragments of the same left dentary.

Table 1. Dimensions of lower teeth of *Leptacodon tener*, *L. munusculum*, *L. packi*, *L. catulus* and cf. *Leptacodon*.

	p4		m1			m2			m3		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
<i>L. tener</i>											
PU 21395			1.3	1.1	1.1	1.3	1.1	1.0			
PU 21398			1.3	1.2	1.0	1.3	1.1	1.0	1.2	0.9	0.7
<i>L. munusculum</i>											
PU 20026	1.2	0.8	1.3	0.9	0.9	1.3	0.9	0.9			
AMNH 35942	1.2	0.8	1.2	0.9	0.9	1.2	0.9	0.8	1.1	0.8	0.7
<i>L. packi</i>											
PU 14033	1.5	0.9				1.5	1.2	1.1	1.5	1.0	0.8
PU 14140	1.5	0.9	1.6	1.1	1.1	1.6	1.1	1.0	1.5	1.1	0.8
<i>L. catulus</i>											
AMNH48173-1	1.4	0.8	1.3	0.9	0.9	1.3	1.1	0.9	1.4	1.1	0.9
cf. <i>Leptacodon</i>											
AMNH 59610			2.1	1.5	1.5						
AMNH 59625	2.3	—	2.3	1.5	1.5						
AMNH 59636			2.1	1.4	1.4						
AMNH 59680						1.7	—	1.4	1.8	1.2	1.0



"*Leptacodon*" *jepsoni* McKenna, 1960a

Three partial mandibles comprised the original material described as *L. jepsoni*. Delson (1971) referred additional material to this species, but advocated its removal from the genus *Leptacodon*. Although all the material is too poor to confidently demonstrate the generic status of this species, the type specimen does exhibit features that support Delson's view. In contrast to *Leptacodon* and other nyctitheriids, the paraconid on p4 of "*L.*" *jepsoni* occurs high on the anterior face of the protoconid, almost at the level of the metaconid. The talonid on p4 is short, and the molar hypoconids have become flattened with wear, leaving the entoconids as the highest talonid cusp. The trigonid on m2 is compressed anteroposteriorly, the hypoconulid on m1-2 is reduced, and the hypoflexid is quite shallow.

Among nyctitheriids, the paraconid on p4 is low, projects anteriorly from the anterior part of the base of the protoconid, and the talonid is more elongate. On the molars, the hypoconid is high and does not become flat with wear. The hypoconulid is unreduced in nyctitheriids, the hypoflexid is deep, and the trigonids are higher and uncompressed (Robinson, 1968). Therefore, it appears that "*L.*" *jepsoni* shows greater affinity with Eocene erinaceomorph insectivores (Adapisoricidae and Erinaceidae) than with soricomorphs (Nyctitheriidae, Geolabididae, among others). However, until additional and more complete material of this species is recovered, further speculation on its generic affinities is futile.

*Nyctitherium* Marsh, 1872

McKenna (1960a) correctly noted that a number of disparate forms referred to *Nyctitherium* [*N. curticens*, *N. nitidum*, and Matthew's (1909) referred specimen of *N. celatum*] deserved generic separation. Subsequently, Robinson (in McKenna *et al.*, 1962; 1966; 1968) assigned *N. nitidum* to *Talpavus*, *N. priscum* and *N. curticens* to *Scenopagus*, and synonymized *Nyctilestes serotinum*, *Entomacodon angustidens*, and Matthew's (1909) referred specimen of *N. celatum* with *Nyctitherium serotinum*. Only the latter, AMNH 15103, the referred material of *N. celatum*, should not be included in *N. serotinum*. Rather, as discussed below, it may represent an Early Eocene species of *Pontifactor* (West, 1974), also a nyctitheriid. Thus, Robinson's (1968) review of the genus *Nyctitherium* is, with little exception, still valid and taxonomically sound: two species of *Nyctitherium*, *N. velox* and *N. serotinum*, were recognized and strictly defined. A third was based on a fragmentary lower jaw—the type of *Myolestes dasypelix* Matthew, 1909—which Robinson (1968) considered pathologic and referable to *Nyctitherium*.

Robinson's (1968) diagnosis of *Nyctitherium* included the presence of a single mental foramen below p3. On CM 13724 and CM 13722, partial mandibles of *N. serotinum* from Powder Wash, two foramina occur, below p3 and p2, respectively.



*Nyctitherium serotinum* (Marsh) 1872

(Fig. 6; Tables 2, 4)

REFERRED SPECIMENS: p4, TTU-P- 7001, 7002, 7003, 7004, 7005, 7006, 7007, 7008; m1, TTU-P- 7019, 7018, 7017, 7016, 7020; m2, TTU-P- 7040, 7041, 7042, 7043, 7044; m3, TTU-P- 7045, 7046, 7047, 7048; P4, TTU-P- 7011, 7013, 7014, 7009, 7015, 7010, 7012; M1, TTU-P- 7030, 7034, 7033, 7024, 7028, 7032, 7027, 7029, 7031, 7022, 7025, 7035, 7036, 7023, 7021, 7026; M2, TTU-P- 7038, 7037, 7039; CM 13721, Lp4, m2; CM 13722, Rp4-m2; CM 13724, Rp4, m2-3; CM 13723, Lm1-2; CM 13726, LP4 in partial maxilla; YPM 15259, Rp4-m1; YPM 13611, Lp4-m2.

LOCALITIES: Powder Wash Local Fauna, Green River Formation, Utah; Lone Tree, Bridger Formation (C or D), Wyoming; Bridger Formation (locality unknown), Wyoming.

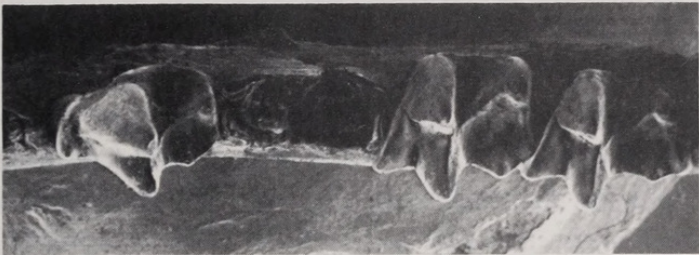
KNOWN DISTRIBUTION: Bridgerian, Wyoming; Early Bridgerian, Utah.

REMARKS: Of all the material assigned by Robinson (1968) to *N. velox*, one specimen, YPM 13611, partial lower jaw with p4-m2 from the upper Bridger beds, lacks an external cingulid on the teeth, and is here referred to *N. serotinum*. Previously described material of *N. velox* and *N. serotinum* does not exhibit much reduction of M3/m3, as compared to the other molars. However, AMNH 12061, from Henry's Fork locality, upper Bridger, displays a greatly reduced m3 (length, 1.2; width, 0.8) compared to m2 (length 1.5; width, 1.1) and is not included in the list of measurements of *Nyctitherium* in Table 2. The lower molars on AMNH 12061 lack external cingulids and, except for the reduced m3, closely resemble *N. serotinum*. This reduction in m3 is tentatively considered part of the variation in *N. serotinum*. On CM 13726, a partial left maxilla with P4 of *N. serotinum*, a diastema occurs anterior to the alveoli for P3 (Fig. 6C). This condition, as Robinson (1968) also noted, is similar to that of *Micropternodus borealis* (Russell, D. A., 1960).

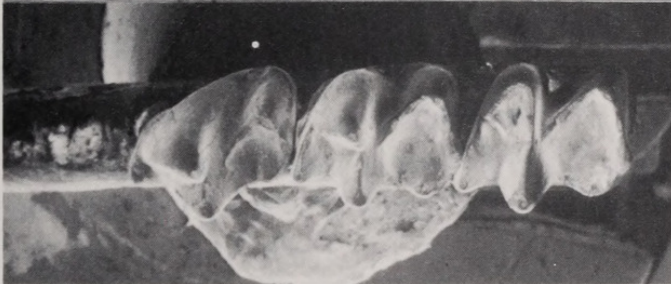
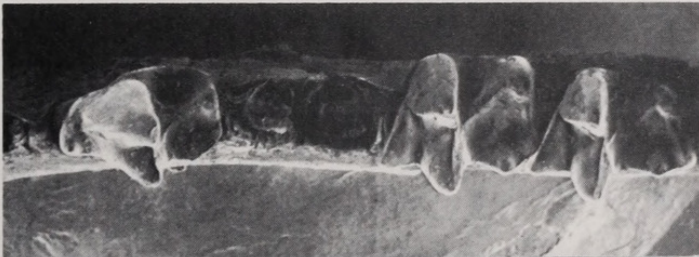
The occurrence of a diastema in *N. serotinum* between the alveoli for P2 and P3 may shed light on the homologies of the premolars in *Nyctitherium*. As discussed above, the upper antemolar dental complement in *Leptacodon tener* may have been a canine (or incisor) followed by five premolars. The occurrence of a canine and four premolars in the lower dentition of *Nyctitherium* is evident on YPM 14396, partial left mandible of *N. velox* (Robinson, 1968). A diastema occurs between p2 and p3 on this specimen (Robinson, 1968: Fig. 1, Plates I, II), and, as noted above, between P2 and P3 of *N. serotinum* (Fig. 6C). If these diastemata are homologous, and if the identification of five premolars in *L. tener* is sound, the loss of a premolar in the evolution of *Nyctitherium* from *Leptacodon* may have occurred behind P2/p2. This would have involved

Fig. 6. *Nyctitherium serotinum*, Powder Wash Locality, Green River Formation, Utah. A. CM 13722, Rp4-m2; approx. X 13. B. CM 13724, Rp4, m2-3; approx. X 12. C. CM 13726, partial left maxilla with P4, showing diastema between alveoli for P2 and P3; approx. X 12.

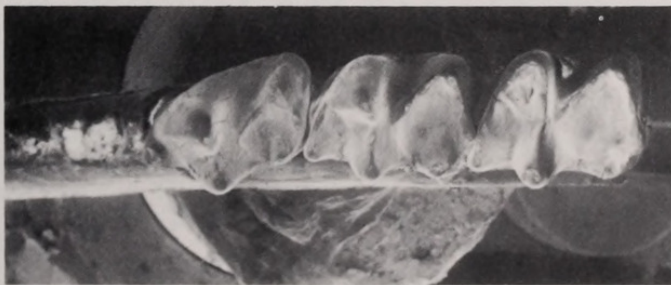




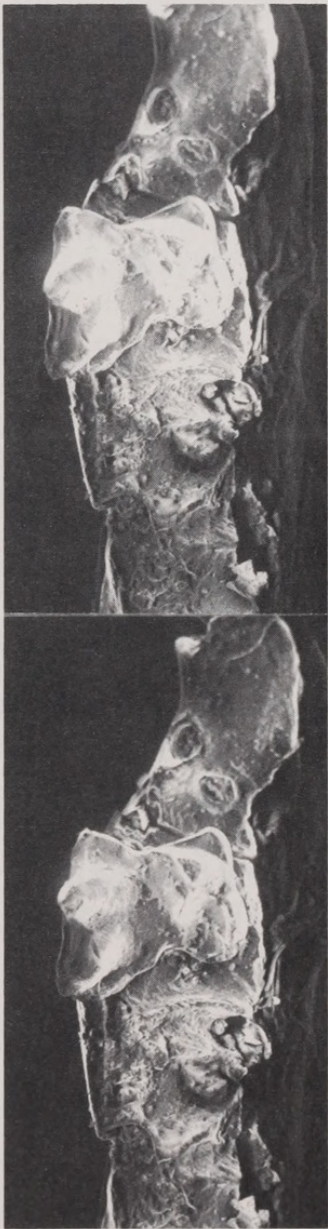
B



6 A



C





inhibition and loss at the P3/p3 locus, a mechanism and site of initial premolar loss that has been observed in *Kennalestes*, *Gypsonictops* (McKenna, 1975), and some plesiadapiform-tarsiiform primates (Schwartz, in press). If this scheme is correct, premolars of *Nyctitherium* are more properly identified as P1/p1 (or dP1/dp1) P2/p2, P4/p4, P5/p5. P1/p1 may be deciduous, as has been suggested for other preptotherian mammals (McKenna, 1975).

The type and only specimen of *N. dasypelix* (Matthew, 1909; Robinson, 1968) is AMNH 11490, type of *Myolestes dasypelix*, partial lower jaw with m1-3 from the early Bridgerian Grizzly Buttes locality, Wyoming. McKenna (1960b) considered *Myolestes dasypelix* (AMNH 11490) and cf. *M. dasypelix* (YPM 13609) more closely related to *Geolabis* than to *Nyctitherium*, and included *Myolestes* and *Geolabis* in the Geolabidinae. Robinson (1968) argued that AMNH 11490 is a pathologic nyctitheriine

Table 2. Dimensions of lower teeth of *Nyctitherium serotinum*.

	p4		L	m1		L	m2		L	m3	
	L	W		AW	PW		AW	PW		AW	PW
YPM 15259	1.7	1.1	1.6	—	1.3						
YPM 13611	1.5	1.1	1.6	—	1.2	1.5	1.2	—			
CM 13721	1.4	1.0				1.5	1.1	1.0			
CM 13722	1.4	1.0	1.5	1.0	1.0	1.6	1.0	1.0			
CM 13723			1.4	1.0	1.0	1.5	1.1	1.0			
CM 13724	1.5	0.9				1.5	1.1	1.0	1.5	1.1	0.8
TTU-P-7008	1.4	0.9									
TTU-P-7002	1.4	0.9									
TTU-P-7006	1.5	0.8									
TTU-P-7005	1.5	1.0									
TTU-P-7004	1.5	1.0									
TTU-P-7003	1.5	1.0									
TTU-P-7007	1.6	1.0									
TTU-P-7019			1.5	1.0	1.0						
TTU-P-7018			1.5	1.1	1.1						
TTU-P-7016			1.5	1.0	1.0						
TTU-P-7017			1.6	1.0	1.0						
TTU-P-7020			1.4	1.1	1.1						
TTU-P-7040						1.5	—	1.0			
TTU-P-7041						1.5	0.9	0.9			
TTU-P-7042						1.5	1.0	1.0			
TTU-P-7043						1.4	1.0	1.0			
TTU-P-7044						1.4	1.0	1.0			
TTU-P-7045									1.3	0.9	0.7
TTU-P-7046									1.5	—	0.8
TTU-P-7047									1.5	0.9	0.7
TTU-P-7048									1.4	1.0	0.8
Mean	1.49	0.98	1.51	1.02	1.08	1.49	1.04	0.99	1.44	0.97	0.75
N.	12	12	9	7	9	10	9	9	5	4	5
SD.	0.09	0.09				0.06					
CV.	6.07	9.13				3.82					



and not a geolabidine “because the paraconids of the molars are not compressed, because the talonid of m3 has three distinct cusps, because the mental foramen does not occur below p4 and because a boss is present on the anterolingual base of the coronoid process” (Robinson, 1968:134). However, on geolabidids the paraconids are also uncompressed, the m3 talonid bears three cusps in a number of species of *Centetodon* (= *Geolabis*, Lillegraven and McKenna, MS), mental foramina in geolabidids variably occur below p2 and p3, and a coronoid boss occurs in three Eocene species of *Centedodon*. AMNH 11490 differs from *Nyctitherium* and agrees with known geolabidids in that the talonid is proportionately shorter, narrower, and much lower than the trigonid on m2, the cristid obliqua is more labial on the posterior wall of the trigonid, and the hypoconulid is more nearly medial on m1-3. AMNH 11490 is here regarded as the type specimen of *M. dasypelix*, a valid genus and species of the Geolabididae.

*Nyctitherium velox* Marsh, 1872  
(Tables 3, 4)

REFERRED SPECIMENS: AMNH 56059, Rm1; AMNH 55658, Lm1 or 2; AMNH 12377, Rm1-2; AMNH 55151, Lm2-3; AMNH 11489, RP4-M1; AMNH 55659, LP4; TTU-P-4047, Lm1-2; YPM 15258, LP4; YPM 14935, Rp4-m2; YPM 16056, LP4-M1; YPM 14946, Rp4; YPM 15257, Lm1-2; YPM 16333, Rm1; YPM 14937, Rm1 or 2; YPM 16057, LM1-2.

LOCALITIES: Hyopsodus Hill, Bridger Formation, Wyoming; Henry’s Fork, Bridger Formation, Wyoming; Lone Tree, Bridger Formation, Wyoming; Huerfano III, Huerfano Formation, Colorado.

KNOWN DISTRIBUTION: Late Bridgerian of Wyoming, Late Wasatchian of Colorado.

REMARKS: Robinson (1968) noted, and I concur, that *N. velox* is best distinguished from *N. serotinum* by the occurrence of a well developed cingulid on p4, m1-3. Upper and lower P4, M1-3 of *N. velox* are also consistently slightly larger than those of *N. serotinum*. AMNH 55151 from Huerfano locality III, tentatively referred to *N. velox* by Robinson (1966),

Table 3. Dimensions of lower teeth of *Nyctitherium velox*.

	p4		m1			m2			m3		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
YPM 14935			—	1.1	1.1	1.7	—	1.1	1.7	1.1	—
YPM 14946	1.9	1.1									
YPM 15257			—	—	1.2	1.7	1.1	1.2			
YPM 16333						1.7	1.2	1.2			
YPM 14937						1.7	1.2	1.2			
AMNH 56059			1.7	1.0	1.1						
AMNH 12377						1.6	1.0	1.1	1.6	1.1	0.9
AMNH 55151						1.6	1.2	1.2	1.5	1.1	—
TTU-P-4047			1.8	1.2	1.2	1.7	1.2	1.2			
Mean			1.75	1.10	1.15	1.67	1.15	1.17	1.60	1.10	



is now definitely assigned to that species.

A third, new, species of *Nyctitherium* is now known from the Late Eocene Badwater local fauna, Wyoming (Setoguchi, M.S. thesis).

Table 4. Dimensions of upper teeth of *Nyctitherium serotinum* and *N. velox*.

	P4		M1		M2		M3	
	L	W	L	W	L	W	L	W
<i>N. serotinum</i>								
TTU-P-7009	1.7	2.0						
TTU-P-7010	1.5	1.7						
TTU-P-7011	1.6	1.8						
TTU-P-7012	1.5	1.8						
TTU-P-7014	1.5	1.8						
TTU-P-7015	1.6	1.9						
TTU-P-7033			1.4	1.8				
TTU-P-7024			1.3	1.7				
TTU-P-7028			1.4	1.7				
TTU-P-7032			1.5	1.9				
TTU-P-7027			1.3	1.7				
TTU-P-7029			—	1.8				
TTU-P-7022			1.4	1.8				
TTU-P-7031			1.4	1.7				
TTU-P-7025			1.4	1.8				
TTU-P-7035			1.4	1.8				
TTU-P-7036			1.5	1.9				
TTU-P-7023			1.3	1.7				
TTU-P-7026			1.4	1.8				
TTU-P-7021			—	1.7				
TTU-P-7037					1.3	1.7		
TTU-P-7038					1.5	1.8		
TTU-P-7039					1.5	1.8		
Mean	1.57	1.83	1.39	1.77	1.43	1.77		
N.	6	6	12	14	3	3		
SD.			0.07	0.07				
CV.			4.85	4.14				
<i>N. velox</i>								
YPM 15056	1.8	2.3	1.7	2.2				
YPM 16057			—	2.0	1.5	2.0		
AMNH 11489	—	2.3	1.6	2.3				
AMNH 55659	1.8	2.2						
Mean	1.80	2.27	1.65	2.17				



*Pontifactor* West, 1974

*Pontifactor*, from the upper part of the Bridger Formation, Wyoming, is based on a number of maxillary fragments and isolated upper molars. Altogether, P4-M3 of *P. bestiola* are known, and are quite distinct from those of *Nyctitherium*: in contrast to the latter, M1-2 of *Pontifactor* have a stylocone, a strong mesostyle and an ectoloph, and lack an expanded hypoconal salient. On P4 of *P. bestiola* the metacone is weak and a hypocone is absent, whereas P4 of *Nyctitherium* has a well developed metacone and a flaring hypoconal shelf. The lower dentition of *P. bestiola* is not known.

*Pontifactor* sp.

(Fig. 7; Table 5)

REFERRED SPECIMENS: AMNH 15103, partial left mandible with dp4-m2, m3 erupting; partial right mandible with m1-2; partial left and right maxillae, with M1-2 (measurements of M1, 1.7 X 2.2; M2, 1.3 X 2.2).

LOCALITY: Willwood Formation, Big Horn Basin, Wyoming.

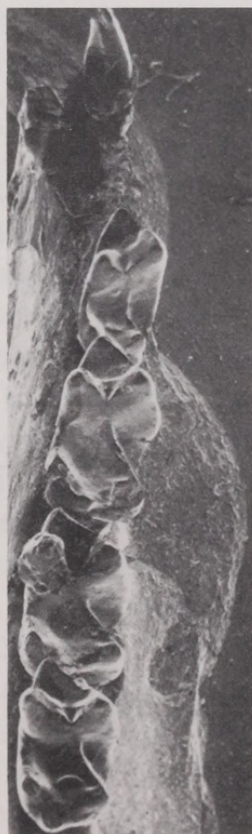
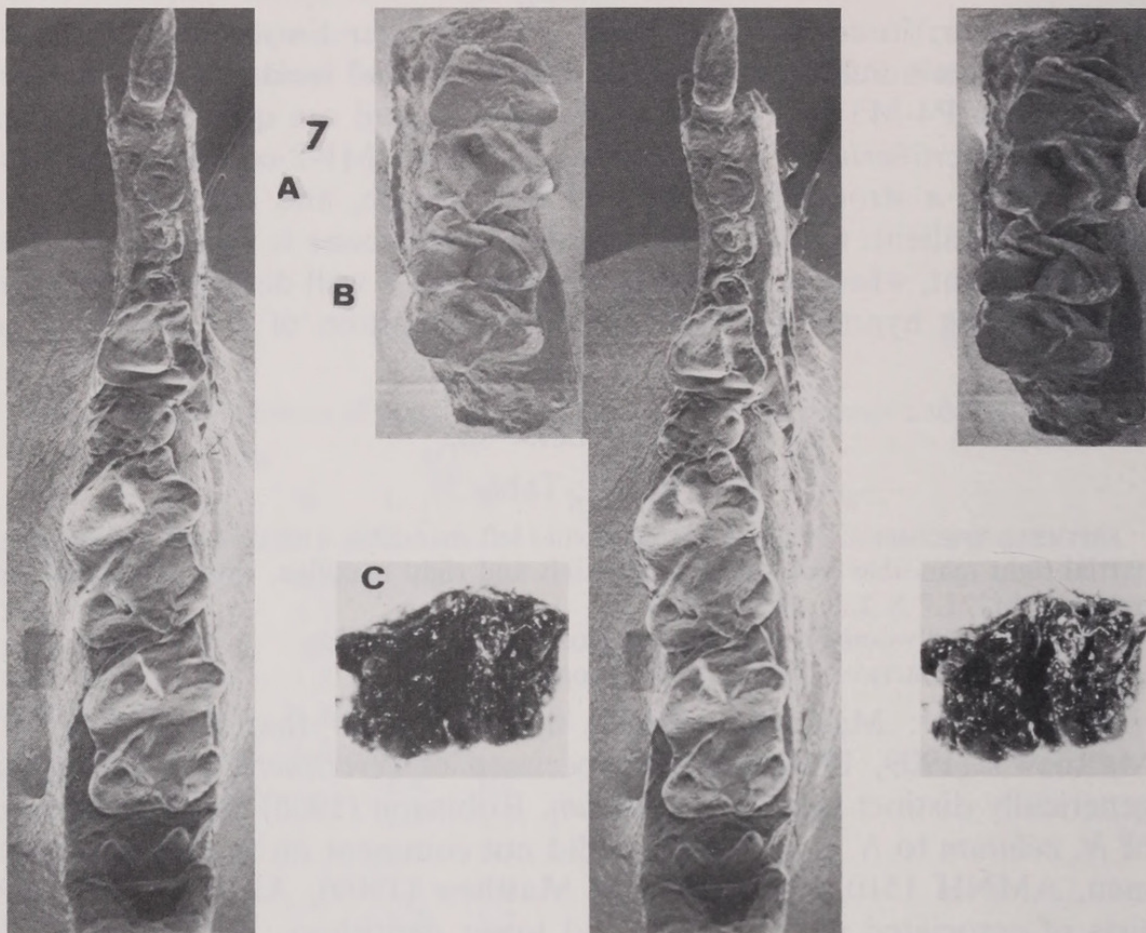
KNOWN DISTRIBUTION: Wasatchian, Wyoming.

DESCRIPTION: McKenna (1960a) first suggested that AMNH 15103, Matthew's (1909, 1918) referred specimen of *Nyctitherium celatum*, was generically distinct from *Nyctitherium*. Robinson (1968) assigned the type of *N. celatum* to *N. serotinum*, but did not comment on the referred specimen, AMNH 15103. According to Matthew (1909), AMNH 15103 consists of associated partial upper and lower dentitions. Both parts of the lower dentition, Ldp4-m2 with m3 erupting, and Rm1-2 do appear to be from the same individual, apparently a juvenile. The right and left M1-2 occlude well with the lower molars and pending recovery of additional material, I accept Matthew's statement of association.

Except for a number of minor differences, M1-2 very closely resemble those of *P. bestiola*: both forms possess prominent subconical to sub-crescentic cusps and conules, a well-developed hypocone, flaring stylar salients, a stylocone, a mesostyle and a W-shaped ectoloph formed by strong centrocristae. Buccally, M2 is shorter than M1 and appears more nearly rectangular in occlusal view. However, on M1-2 of *Pontifactor* sp. the paracone is conical, the metacone is subcrescentic, the stylar shelf is only moderately wide, and the centrocristae are short. In contrast, on M1-2 of *P. bestiola* both the paracone and metacone are subcrescentic, the stylar shelf is broader, the centrocristae are longer, and the anterior part of the parastylar area is depressed below the crown.

West (1974) also noted the similarities between AMNH 15103 and *Pontifactor*, but, without explanation, referred to the former as *N. celatum*. If, as it appears to me, AMNH 15103 represents an Early Eocene species of *Pontifactor*, the preserved dp4-m3 are the first record of the lower dentition. The molars are nyctitheriid-like in that the trigonid and talonid are







distinguished labially by a deep hypoflexid notch, the cusps are tall and spire-like, the talonid is angular and deeply basined, the hypoconid is high and does not become flat with wear, and the hypoconulid is not reduced. In contrast to *Nyctitherium*, the trigonid on m1-2 of *Pontifactor* sp. is anteroposteriorly compressed, the paraconid is lophid-like and flares anterolingually, the hypoconulid is medial, and a mesoconid occurs on the cristid obliqua. In *Nyctitherium*, characteristically, the trigonid on the lower molars is not compressed but open lingually, the paraconid is fully cuspsate, the hypoconulid is twinned with the entoconid, and a mesoconid is absent.

In these respects the lower dentition of *Pontifactor* sp. is closer to that of *Leptacodon munusculum* whereas *Nyctitherium* more nearly resembles *L. tener* and *L. packi*.

REMARKS: Two discrete groups of nyctitheriids appear to be present in the Paleocene and Eocene record of North America: one comprises *Nyctitherium*, *Leptacodon tener*, *L. packi*, and *L. catulus*; the other includes *L. munusculum* and *Pontifactor*. Both groups have a suite of characters that warrant their inclusion in a single family and imply common ancestry. In addition to the diagnostic features listed by Robinson (1968), the lower molars bear sharp, subconical to subcrescentic cusps, angular trigonids and talonids that are separated by a deep hypoflexid notch, a deeply basined talonid which is as wide as or slightly wider than the trigonid, a high hypoconid, and an unreduced hypoconulid. P4, where known, is semimolari-form. M1-2 are not transverse, bear conical to subcrescentic cusps, and large styler shelves and salients, compared to adapisoricids (Krishtalka, 1976).

In *L. tener*, *L. packi*, *L. catulus*, and *Nyctitherium*, the paraconid is not compressed, but fully cuspsate, and the molar trigonids are open lingually. P4-M2 in *Nyctitherium* develop widely expanded hypoconal shelves, weak mesostyles, poor centrocrisae, and do not approach dilambdodonty. In *L. munusculum* and *Pontifactor*, molar paraconids are compressed and lophid-like, and the hypocone remains a restricted cusp. *Pontifactor* develops a strong mesostyle on M1-2, a stylocone, confluent centrocrisae, and a more nearly dilambdodont condition.

The Late Paleocene European genus *Remiculus* (Russell, D.E., 1964; Szalay, 1969) is similar in many respects to *Pontifactor*, a point noted and misinterpreted by West (1974). M1-2 of *R. deutschii* have a mesostyle, strong centrocrisae, subcrescentic cusps, and an anteriorly depressed

Fig. 7. *Pontifactor* sp., AMNH 15103, Willwood Formation, Wyoming. A. L?p1, dp4-m3; approx. X 12. B. Rm1-2; approx. X 10. C. LM1-2; approx. X 7.

Fig. 8. Nyctitheriidae indet., PU 14202, Rp2, p4-m3, Polecat Bench Formation, Wyoming; approx. X 11.



parastylar area. On the lower molars the paraconids are compressed and flare anterolingually, the hypoflexid notches are deep, and the hypoconids are high. The Paleocene *Remiculus* and the Eocene *Saturninia* appear to be European representatives of the two discrete lineages of nyctitheres that also occur in North America. *Remiculus* (and possibly *Cryptotopos* Crochet, 1974) seem allied with *Pontifactor*. *Saturninia*, with an expanded hypoconal shelf on P4-M2 and an absence of dilambdodonty, is more closely related to *Nyctitherium*.

Nyctitheriidae indet.

(Fig. 8; Table 5)

PU 14202, Rp4-m3, from the Silver Coulee Beds, Polecat Bench Formation, Wyoming, seems to represent a new genus of Tiffanian nyctitheriid that has a mosaic of characters in the lower dentition similar to those of the two lineages of nyctitheriids described above. Like *Pontifactor*, the paraconid on m2 is lophid-like and flares anterolingually, and a tiny mesoconid-like thickening occurs on the cristid obliqua. However, as in *Nyctitherium*, the trigonids on m1-3 are uncompressed, the paraconid on m1 is fully cuspsate, and the hypoconulid on m1-2 is close to the entoconid. In contrast to both groups, p4 on PU 14202 is submolariform, with a large, cuspsate paraconid, equal in size and height to the metaconid. The talonid is broad, almost fully molariform and bears three cusps. The resemblances of PU 14202 to the lower dentition of *Nyctitherium* may be shared primitive, whereas the similarities to that of *Pontifactor* appear to be derived.

Table 5. Dimensions of lower teeth of *Pontifactor* sp. and Nyctitheriidae indet.

	p4			m1			m2			m3	
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
<i>Pontifactor</i> sp.											
AMNH 15103											
LDP4-M2	1.3	0.9	1.5	1.4	1.3	1.6	1.4	1.2			
RM1-2			1.6	1.3	1.2	1.6	1.3	1.2			
Nyctitheriidae indet.											
PU 14202	1.3	0.9	1.5	1.1	1.1	1.4	1.2	1.0	1.5	1.1	0.9



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