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PALEOCENE AND EOCENE MARSUPIALS OF NORTH AMERICA

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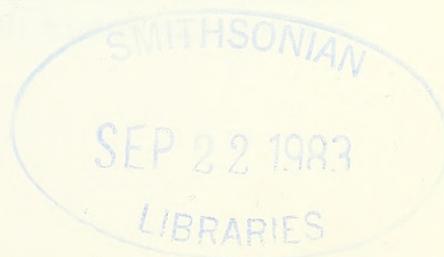
ABSTRACT

North American Paleocene and Eocene marsupials compose two tribes of didelphines. The Didelphini contains five species of *Peratherium* (*P. comstocki*, *P. edwardi*, *P. marsupium*, *P. knighti*, *P. innominatum*). The Peradectini includes six species of *Peradectes* (*P. elegans*, *P. pauli*, *P. protinnominatus*, *P. californicus*, *P. chesteri*, *P. minutus*), two species of *Armintodelphys* (*A. blacki*, *A. dawsoni*), and one species of *Mimoperadectes* (*M. labrus*). Previous allocations of *Alphadon* and *Albertatherium* to the Peradectini, *P. innominatum* to *Peradectes*, *P. protinnominatus* to *P. chesteri*, and the latter to *Herpetotherium* are revised, as are the systematics of all of the species. The two tribes differ in the structure of the entoconid-hypoconulid complex on the lower molars and in the presence or absence of dilambdodonty on the upper molars. The five species of *Peratherium* show virtually no evolutionary change throughout their range in the Eocene. In contrast, the six species of *Peradectes* form a branching lineage that is characterized by cladogenetic speciation and anagenesis from the Paleocene through the Oligocene. *Armintodelphys* and *Mimoperadectes* appear to be early offshoots of that lineage.

INTRODUCTION

Marsupials occur in most early Tertiary North American faunas. The first such record was *Entomacodon minutus* Marsh, 1872, from the Bridger Basin, which was not identified as a marsupial until almost one hundred years after its original description (Robinson, 1968; Krishalka and Stucky, 1983a). Similarly, *Peratherium comstocki* Cope, 1884,

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originally called a creodont, was first recognized as a didelphid by Simpson (1928), who also reviewed the systematics of *Peratherium* (= *Herpetotherium*) *marsupium* (Troxell, 1923), and named *Peratherium innominatum* from material that Matthew (1909b) had assigned to this genus. Matthew (1899, 1909a, 1909b) had debated the marsupial versus insectivore affinities of *E. minutus* (including *Centracodon delicatus* Marsh, 1872) and *P. comstocki* and opted for the latter. This position was colored by the late Nineteenth Century view, taken to its extreme by Wortman (1901), of a close relationship between marsupials, creodonts, and carnivores. Matthew (1909b:335–339) clarified the distinctions between marsupials and allegedly closely related placentals by identifying their “primitive” and “specialized” characteristics; he (p. 321) emphasized the relative importance of derived features in phylogenetic reconstructions. Indeed, Matthew’s discussion, although devoid of cladistic terminology, presages what some current students believe to be the modern innovation in systematics.

In 1921, Matthew and Granger described the first records of North American Paleocene marsupials, *Peradectes elegans* and *Thylacodon pusillus*. In the next 60 years Stock (1936), McGrew (1937, 1959), Gazin (1952, 1956, 1962), McKenna (1960), Bown (1979), and Bown and Rose (1979) added six species of *Peratherium* (*P. californicum*, *P. knighti*, *P. chesteri*, *P. edwardi*, *P. morrisoni*, *P. macgrewi*), two species of *Peradectes* (*P. pauli*, *P. protinnominatus*), and two new genera, *Nanodelphys* and *Mimoperadectes*, each with one species (*N. minutus*, *M. labrus*) to the North American Paleocene and Eocene didelphid record. Most recently, we (Krishtalka and Stucky, 1983a) named a new genus, *Armintodelphys*, with two species (*A. blacki*, *A. dawsoni*), from the early and middle Eocene of Wyoming.

Partial systematic reviews of some of these 19 species in nine genera have occurred only within the last ten years (Setoguchi, 1973, 1975; Bown, 1979, 1982; Lillegraven, 1976; Crochet, 1977, 1979), resulting in a confusing, and often conflicting, shuffling of species among *Peratherium*, *Herpetotherium*, *Peradectes*, and *Nanodelphys*. None of these studies encompassed all Paleocene and Eocene North American didelphids. In the course of describing the marsupials from the Wind River Formation (Krishtalka and Stucky, 1983a) it became apparent that such a study was necessary. Those didelphids recorded from the Wind River Formation (*Peratherium comstocki*, *P. marsupium*, *P. innominatum*; *Peradectes chesteri*; *Armintodelphys blacki*, *A. dawsoni*) were systematically revised. Remaining North American Paleocene and Eocene didelphids are revised here, except for *Thylacodon pusillus*, which is under study elsewhere (see Clemens, 1979; Archibald, 1982). Also included is a summary of the occurrences of these didelphids and a reconstruction of their evolutionary relationships.

Abbreviations used in this paper are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; KU, University of Kansas; LACM, Los Angeles County Museum; MCZ, Museum of Comparative Zoology, Harvard University; PM, Field Museum of Natural History; PU, Princeton University (Museum); TTU-P, Texas Tech University, Paleontology; UCM, University of Colorado Museum; UCMP, University of California Museum of Paleontology; UM, University of Michigan Museum of Paleontology; USNM, U.S. National Museum; UW, University of Wyoming; YPM, Yale Peabody Museum; Fm., Formation; L, length; W, width.

SYSTEMATICS

Family Didelphidae Gray, 1821

Subfamily Didelphinae (Gray, 1821)

Crochet (1979) separated known didelphines into two groups, the Didelphini and Peradectini, based, in part, on diagnostic features of the dentition that Setoguchi (1973) had identified earlier. These features, as well as those identified in another study (Krishtalka and Stucky, 1983a), indicate that members of the Didelphini have lower molars with a tall, spire-like entoconid, a lower, proximal and posterior hypoconulid, and a deep entoconid notch. Their upper molars are dilambdodont, with a lower paracone than metacone, strong conules and stylar cusps, and a posteriorly expanded protoconal base. In contrast, members of the Peradectini have lower molars with subequal and twinned entoconid and hypoconulid, and a weak or vestigial entoconid notch. Their upper molars are not dilambdodont and bear subequal paracone and metacone, a V-shaped protocone, and weak or vestigial stylar cusps and conules.

Both groups differ from known Cretaceous didelphines in having lower molars with shorter talonids and a cristid obliqua that meets the posterior wall of the trigonid labial to the protocristid notch. This implies a common ancestry for the Didelphini and Peradectini from a Cretaceous didelphine. These features, as well as those that are diagnostic of the Peradectini, also imply that *Alphadon* and *Albertatherium* do not belong in that tribe (contra Crochet, 1979).

Tribe Didelphini Crochet, 1979

According to Crochet (1979), *Herpetotherium* is the only North American Tertiary genus in this tribe and includes all North American species formerly referred to *Peratherium*. *H. fugax*, the type species, has a diagnostic anterior dentition (Fox, manuscript; personal communication, 1982). However, the characters of the molar dentition cited by Crochet (1977) in support of this synonymy are variable, at least within the North American Eocene species of Didelphini (Krishtalka and Stucky, 1983a)—species for which the anterior dentition is not known. Accordingly, these species are retained in *Peratherium*.

***Peratherium* Aymard, 1846**

This genus is not known from North American Paleocene horizons. Based on the known material, the five North American Eocene species of *Peratherium* are, in decreasing order of size (Tables 1 and 3), *P. comstocki* Cope, 1884, *P. edwardi* Gazin, 1952, *P. marsupium*, (Troxell, 1923), *P. knighti* McGrew, 1959, and *P. innominatum* Simpson, 1928.

The systematics of three of these species—*P. comstocki*, *P. marsupium*, and *P. innominatum*—were reviewed in detail in a treatment of the marsupials from the Wind River Formation (Krishtalka and Stucky, 1983a), and are briefly summarized here.

***Peratherium comstocki* Cope, 1884**

Referred specimens.—In addition to material referred elsewhere (Cope, 1884; Simpson, 1928, 1968; West, 1982; Krishtalka and Stucky, 1983a), CM 13901 (M₃₋₄), from the Bridger Fm., Twin Buttes, Bridger Basin, Wyoming.

Discussion.—*P. comstocki* is the largest known North American Eocene species of *Peratherium*. The referral of CM 13901 and material from Agua Fria, Texas (West, 1982) extends the known range of this species from the early Wasatchian to the late Bridgerian and perhaps into the earliest Uintan, during which time preserved dentitions of *P. comstocki* show no significant morphological change.

***Peratherium marsupium* (Troxell, 1923)**

Referred specimens.—In addition to material referred elsewhere [Troxell, 1923; McGrew and Sullivan, 1970; West, 1973 (except PM 15864); West and Dawson, 1975 (except CM 23194); Setoguchi, 1975 (except CM 23793, 23803, TTU-P 1375, 1238); Eaton, 1982; West, 1982; Krishtalka and Stucky, 1983a, 1983b], CM 36533 (DP³), TTU-P 5966, CM 29061 (both M¹), CM 15043, 15144, 15668, 15708, 29109, 51345, 53754, 51422 (all M²), CM 28850, 29021 (both M³), CM 15626 (M⁴), CM 55938 (P₃-M₁), CM 55939 (P₃), CM 29045, 55940, 55941 (M₂ or M₃) from localities 5A, 5 Front, 6, Rodent, Wood and 20, Wagon Bed Fm., Wind River Basin, Wyoming.

Discussion.—This species is well-known from middle Wasatchian to Duchesnean faunas of the western interior of North America, and, like *P. comstocki*, undergoes no perceptible changes in preserved parts of the dentition during its geological extent.

***Peratherium innominatum* Simpson, 1928**

Referred specimens.—In addition to material referred elsewhere [Simpson, 1928; Bown, 1979 (as *P. macgrewi*, except UW 10129); Eaton, 1982; Krishtalka and Stucky, 1983a, 1983b], UCMP 44095 (M¹⁻²), CM 42137 (M₂ or M₃), from Sand Quarry, Four Mile area, Wasatch Fm., Colorado; part of UW 9742 (M²), from the Willwood Fm., Bighorn Basin, Wyoming; UCMP 109647 (M³), from the Uintan of California; CM 23851, 23852 (both DP³), CM 15728 (M¹), CM 15083, 23787, 23918, 51354 (all M²), CM 23788, 51237 (both M²⁻³), TTU-P 1349, CM 14644, 15034, 15035, 15049, (all M³), CM 23832, 23893

Table 1.—Dimensions of type specimens of species of Peratherium.

Taxa and catalog no.	P ₃		M ₁		M ₂		M ₃		M ₄	
	L	W	L	W	L	W	L	W	L	W
AMNH 4252					3.15	1.90	3.25	1.70		
					<i>P. comstocki</i>					
USNM 19200							2.95	1.70	2.55	1.50
					<i>P. edwardi</i>					
YPM 13518	1.90	1.00	2.25	1.20	2.70	1.50	2.70	1.50		
					<i>P. marsupium</i>					
YPM 13514 (<i>E. minutus</i>)									2.1	1.1
PU 16115 (<i>P. morrisi</i>)					2.2	1.4	2.3	1.4		
					<i>P. knighti</i>					
AMNH 11493					1.5	1.0	1.5	1.0	1.5	1.0
					<i>P. innominatum</i>					

(both M_4), TTU-P 1360, CM 15676, 15682, 16004, 23935, 23936 (all DP_3), TTU-P 2420, CM 15121, 15132, 15692 (all M_1), TTU-P 2425, 2429, CM 15078, 15102, 15672, 15729, 23844, 23887, 23901, 23906, 23917, 51248 (all M_2 or M_3), CM 23846 (M_4), from localities 5, 5A, 5 Front, 5 Back, 6, Wood and 20, Wagon Bed Fm., Wind River Basin, Wyoming.

Discussion.—Unlike *P. comstocki* and *P. marsupium*, *P. innominatum* has been confused with other didelphines. This species was considered a species of *Peradectes* by Setoguchi (1973), Bown (1982), and Crochet (1979), due, perhaps, to a misinterpretation of the diagnostic (and damaged) features on the type specimen. M_2 on the latter (AMNH 11493) preserves a large, spire-like entoconid, a lower, posterior hypoconulid, and a deep entoconid notch. These features are also evident on the broken M_3 on the type and are diagnostic of *Peratherium* and other Didelphini. *P. innominatum* is closest in size to contemporaneous *Peradectes chesteri*, the type of which has an M_3 with subequal entoconid and hypoconulid and a weak entoconid notch. Upper molars of these two species from the same localities also show the diagnostic features of *Peratherium* and *Peradectes*. Unlike the latter, upper molars of *P. innominatum* are dilambdodont, with a much lower paracone than metacone, prominent styler cusps and conules, and a posterior expansion of the base of the protocone.

Study of the sample of *P. innominatum* from the Wind River Formation (Krishtalka and Stucky, 1983a) and Powder Wash (Krishtalka and Stucky, 1983b) indicates that this species includes the Graybullian *P. macgrewi* Bown, 1979, as a temporal subspecies. Two of Bown's identifications are revised: one of the upper molars in UW 9742 (Bown, 1979, Fig. 40a, center) is dilambdodont and belongs in *P. innominatum* (rather than *P. chesteri*); UW 10129 (Fig. 40c) is not dilambdodont and is transferred to *Peradectes protinnominatus* (from *P. macgrewi*).

Remains of this species have also been identified (Krishtalka and Stucky, 1983a) in the early Eocene Four Mile, middle Eocene Carter Mountain (Eaton, 1982) and late Eocene Badwater samples of didelphids (part of Setoguchi's, 1975, *Peratherium* cf. *P. knighti* and *Nanodelphys* cf. *N. minutus*). Lillegraven's (1976) referred material of *Peratherium* sp. cf. *P. knighti* from the Uintan of San Diego County may include specimens of both *P. knighti* and *P. innominatum*. The range in size of the molars overlaps with that of both species, and the figured upper molars include two morphs: some have a shallow ectoflexus (Lillegraven, 1976, Fig. 1, 2), whereas one (Fig. 3c) has a deep ectoflexus, as is characteristic of *P. knighti* and *P. innominatum*, respectively.

Bown (1982) referred material from the Aycross Formation to *Peradectes* sp. cf. *P. innominatus* on the basis of their similarity to UW 984 from Tabernacle Butte (see McGrew, 1959). UW 984 is identified

here and elsewhere (Krishtalka and Stucky, 1983a) as *Peradectes chesteri*, according to features discussed below; the Aycross material, by implication, may also belong to *P. chesteri*.

According to these observations, the known record of *P. innominatum* extends from the early Wasatchian to the Duchesnean of the western interior of North America, and possibly includes the Uintan of California.

***Peratherium edwardi* Gazin, 1952**

(Fig. 1)

Type.—USNM 19200, partial left dentary with M_{3-4} .

Type locality.—12 miles north of Big Piney, in SW1/4 section 33, T. 32 N, R. 111 W, Sublette County, Wyoming.

Referred specimen.—USNM 19206 (M^{3-4}), from the type locality.

Known distribution.—Late Wasatchian—Green River Basin (Wasatch Fm.), Wyoming.

Discussion.—This poorly known species is intermediate in size between *P. comstocki* and *P. marsupium*. Allocation of this material to the former, as advocated by Setoguchi (1973) and Bown and Rose (1979), is not warranted until a larger sample is available.

***Peratherium knighti* McGrew, 1959**

(Fig. 2)

Entomacodon minutus Marsh, 1872.

Centracodon delicatus Marsh, 1872.

Peratherium knighti McGrew, 1959.

Peratherium morrisi Gazin, 1962.

Type.—AMNH 55684, partial right maxilla with M^{1-3} .

Type locality.—Locality 5, Tabernacle Butte, upper part of Bridger Formation, Wyoming.

Referred specimens.—In addition to material referred elsewhere [McGrew, 1959; West and Dawson, 1973; Bown, 1982; Setoguchi, 1975 (except TTU-P 1237, 1349, 2425, 2429, CM 23787, 23832, 23935, 23936—referred above to *P. innominatum*; TTU-P 5966—referred above to *P. marsupium*)], YPM 13514, partial dentary with M_4 (type of *Entomacodon minutus*), YPM 13508, dentary with $P_{1-3}M_{1-4}$ (type of *Centracodon delicatus*), both from Henry's Fork, Bridger Formation, Bridger Basin, Wyoming; UW 3003 (M_4), UW 2988 (M_{3-4}), from the lower part of the Bridger Fm., Bridger Basin, Wyoming; PU 16115, partial dentary with M_{2-3} (type of *Peratherium morrisi*), from the Cathedral Bluffs tongue of the Wasatch Fm., Washakie Basin, Wyoming; CM 42135 (M_{3-4}), from the type locality; CM 42139 (M_1), UCMP 59131 (M_2 or M_3), from the Wasatch Fm., Four Mile area, Colorado; PM 15864 (M^{2-4}), from the lower part of the Bridger Fm., Green River Basin, Wyoming; CM 23194 (M_2 or M_3), from the Washakie Fm., Sand Wash Basin, Colorado; CM 15600, 15601, 15606, 15656 (all DP³), CM 15030, 15031, 15036, 15037, 15046, 15077, 15081, 15108, 15631, 15670, 23841 (all M^1), CM 55936 ($M^{1,2,3}$), CM 55937 ($M^{2,3}$), CM 15048, 15029, 15097, 15105, 15608, 15614, 15634,

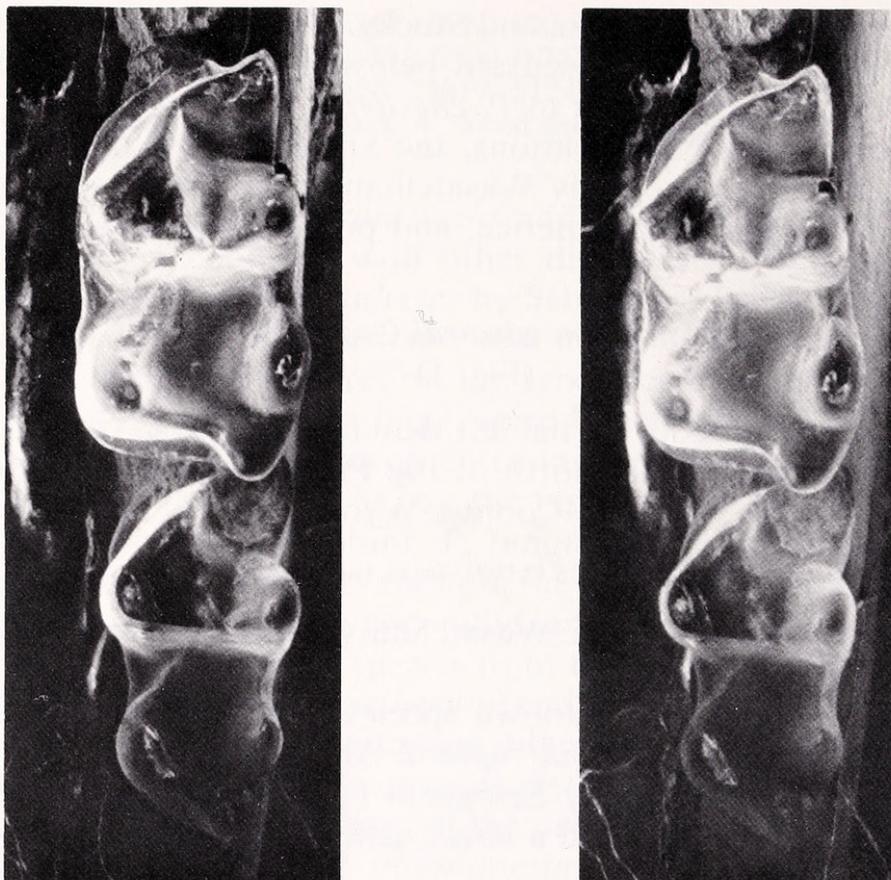


Fig. 1.—*Peratherium edwardi*, USNM 19200, LM₃₋₄, type; approx. $\times 14$.

23803, 23888, 29069 (all M²), CM 15027, 15032, 15050, 15059, 15101, 15118, 29110 (all M³), CM 15033, 15079, 15080, 15143, 15636, 15678, 55963 (all M⁴), CM 15134 (DP₃), CM 14642, 14645, 15028, 15058, 15114, 15119, 15150, 15741, 51202 (all M₁); CM 15040, 15042, 15044, 15057, 15659, 15689, 15710, 15720, 15742, 23894, 23911, 28832, 28893, 29024, 55942, 55964, 55969 (all M₂ or M₃), from localities 5, 5A, 5 Front, 5 Back, 6, Wood and 20, Wagon Bed Fm., Wind River Basin, Wyoming.

Known distribution.—Early Wasatchian—Four Mile area (Wasatch Fm.), Colorado. Bridgerian—Washakie and Green River basins (Cathedral Bluffs tongue of the Wasatch Fm.), Bridger Basin (Bridger Fm.), Green River Basin (upper and lower parts of the Bridger Fm.), Bighorn Basin (Aycross Fm.), Wyoming. Late Bridgerian or Uintan—Sand Wash Basin (Washakie Fm.), Colorado. Uintan and Duchesnean—Wind River Basin (Wagon Bed Fm.), Wyoming.

Emended diagnosis.—Smaller than *P. comstocki*, *P. edwardi*, *P. marsupium*; larger than *P. innominatum*; ectoflexus on M²⁻³ much shallower than in *P. marsupium* and *P. innominatum*.

Discussion.—Three taxa are conspecific with *P. knighti*—*Entomacodon minutus*, *Centracodon delicatus*, and *Peratherium morrissi*. The first two were synonymized by Matthew (1909b) as *E. minutus* (which

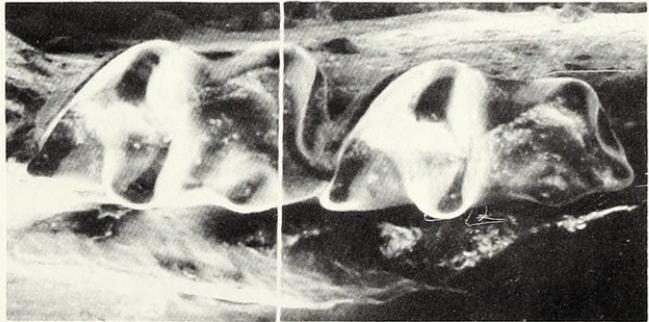
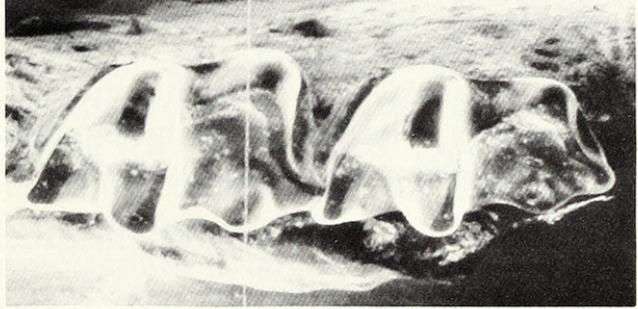
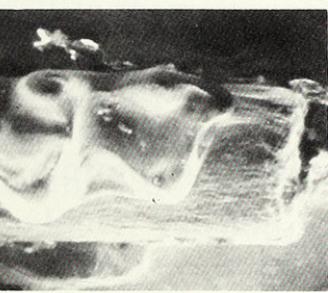
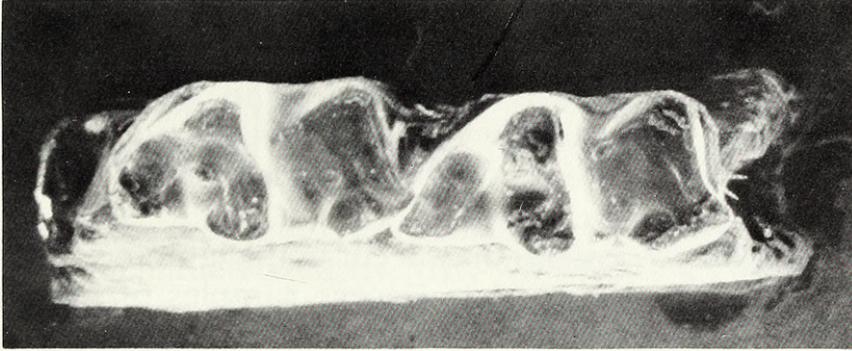
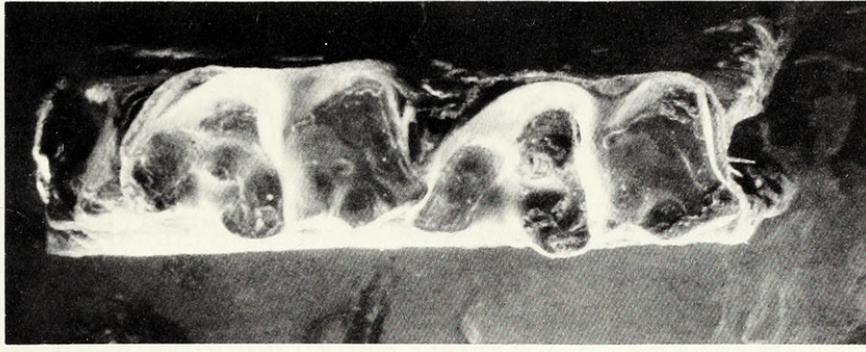


Fig. 2.—*Peratherium knighti*. (A) YPM 13514, M_4 (type of *Entomacodon minutus*); (B) CM 42135, RM_{3-4} (from Tabernacle Butte, the type locality); (C) PU 16115, RM_{2-3} (type of *P. morrisi*); all approx. $\times 15$.

has page priority; Marsh, 1872:214–215), and the types of both were tentatively identified as marsupials by Robinson (1968). The types of *E. minutus* and *P. morrisoni* are indistinguishable from lower dentitions in the hypodigm of *P. knighti* from Tabernacle Butte. *Peratherium* has priority over *Entomacodon*, as does *E. minutus* over *P. knighti*, but the resultant *P. minutum* is preoccupied by *P. minutum* Aymard, 1850. *C. delicatus* is a *nomen oblitum* according to the rules of zoological nomenclature (Art. 23b).

P. knighti is closest in size to the larger *P. marsupium* and the smaller *P. innominatum*, but known samples of these species do not overlap in size. Additionally, M²⁻³ of *P. knighti* have shallower ectoflexi. According to these criteria, we have identified *P. knighti* from material (see "Referred specimens") previously assigned to: *P. marsupium* from the lower part of the Bridger Formation, Green River Basin, Wyoming (West, 1973) and the Washakie Formation, Sand Wash Basin (West and Dawson, 1975); *Peratherium* sp. from Bridger A (McGrew and Sullivan, 1970); as well as from unpublished specimens from the Four Mile fauna, Colorado.

As discussed earlier, *P. knighti* may occur in the Uintan of California (Lillegraven, 1976). Analysis of late Eocene samples of *Peratherium* from Badwater indicates that material previously referred to *Peratherium* cf. *P. knighti* (Setoguchi, 1975) includes specimens of *P. knighti*, *P. innominatum*, and *P. marsupium*.

Based on these synonymies and reidentifications, *P. knighti* is known from the early Wasatchian to the Duchesnean in the western interior of North America, and possibly from the Uintan of California.

Tribe Peradectini Crochet, 1979

North American didelphines included here are *Peradectes*, *Mimoperadectes*, and *Armintodelphys*. *Nanodelphys* is congeneric with *Peradectes* (Crochet, 1978). As discussed under Didelphinae, and Evolutionary Relationships, *Alphadon* and *Albertatherium* lack the diagnostic characters of this tribe and (contra Crochet, 1979) are removed from the Peradectini.

The systematics of one of the species of *Peradectes* (*P. chesteri*) and both species of *Armintodelphys* (*A. blacki* and *A. dawsoni*) were treated elsewhere (Krishtalka and Stucky, 1983a), as part of a description of the didelphines from the Wind River Formation. The systematics of these taxa are briefly summarized here, and additional material is referred to *P. chesteri*.

Peradectes Matthew and Granger, 1921

Three North American species were originally assigned to *Peradectes*—the type species, *P. elegans* Matthew and Granger, 1921; *P.*

pauli Gazin, 1956; and *P. protinnominatus* McKenna, 1960. Subsequently, Setoguchi (1973) and Bown (1979) identified *Peratherium chesteri* Gazin, 1952, and *Peratherium innominatum* Simpson, 1928 as species of *Peradectes*, and *P. protinnominatus* as a junior synonym of *P. chesteri*. Setoguchi (1973) also advocated inclusion of *Peratherium morrisi* in *Peradectes*, and Bown (1979) noted a lack of sufficient morphological distance between *Nanodelphys minutus*, the type species, and *Peradectes chesteri* to warrant generic distinction. Lillegraven (1976) transferred *Peratherium californicum* Stock, 1936, to *Nanodelphys*, and opted for retaining *N. californicus* and *N. minutus* despite an apparent lack of morphological distinction. Crochet (1978) reduced *Nanodelphys* to a subgenus of *Peradectes* in which he included the North American species *P. minutus*, *P. californicus*, *P. innominatus*, and *P. protinnominatus*. *P. elegans* was referred to the subgenus *Peradectes*, *P. pauli* was considered too poorly known to be discussed, and *P. chesteri* was assigned to *Herpetotherium*. Lastly, Clemens (1979) and Archibald (1982) have suggested that *Thylacodon pusillus* is a species of *Peradectes*.

Review of the type and referred material of these taxa indicates that *Peradectes* is characterized by M_{1-3} with short talonids, labial cristid obliquas, and an entoconid and hypoconulid that are low, subequal, and closely appressed; these cusps are separated by a weak entoconid notch and share a common internal talonid wall. On M^{1-3} the paracone and metacone are subequal and not dilambdodont, the styler cusps and conules are weak, and the posterolingual part of the base of the protocone is not expanded. These features are also diagnostic of the Peradectini. Compared to Cretaceous didelphines, the absence of dilambdodonty, and the V-shaped protocone are primitive retentions. Unlike *Mimoperadectes*, the metaconid is larger and higher than the paraconid on M_{1-3} of *Peradectes*; unlike *Armintodelphys*, the entoconid is subequal to the hypoconulid, rather than reduced to a nubbin. Measurements of these taxa are given in Tables 2 and 3.

Systematic conclusions implied by examination of the material are: (1) *Nanodelphys* is congeneric with *Peradectes*; as suggested by Bown (1979) and Crochet (1978), the morphological distinctions between *N. minutus*, the type species, and species of *Peradectes* are of specific magnitude and are minor compared to those that define other genera of didelphines; Crochet's (1978) subgenus *Nanodelphys* has no systematic utility; (2) there are six discernable North American species of *Peradectes*: *P. elegans*, *P. pauli*, *P. protinnominatus*, *P. chesteri* (= *Peratherium chesteri*), *P. californicus* (= *Peratherium californicum* and *Nanodelphys californicus*) and *P. minutus* (= *Nanodelphys minutus*); (3) neither *Peratherium morrisi* nor *P. innominatum* belongs in *Peradectes*; the former is a junior synonym of *Peratherium knighti* and the latter

Table 2.—Dimensions of type and paratype specimens (lower dentition) of species of Peradectes, Armintodelphys, and Mimoperadectes.

Taxa and catalog no.	P ₃		M ₁		M ₂		M ₃		M ₄	
	L	W	L	W	L	W	L	W	L	W
	<i>P. elegans</i>									
AMNH 17376 (right)	1.4	0.7	1.7	1.0	1.7	1.0	1.7	1.0	1.7	1.0
AMNH 17376 (left)	1.4	0.7	1.7	1.0	1.7	1.0	1.7	1.0	1.7	1.0
	<i>P. pauli</i>									
USNM 20879 (type)			1.55	0.80			1.5	1.0	1.5	1.0
USNM 20880 (paratype)						0.90				
	<i>P. protinnominatus</i>									
UCMP 45947 (paratype)			1.55	0.90	1.60	1.05				
UCMP 45948 (paratype)			1.55	0.90	1.60	1.00				
UCMP 45950 (paratype)	1.1	0.6	1.5	0.8						
	<i>P. californicus</i>									
LACM (CIT) 202-1943	1.10	0.55	1.35	0.75	1.50	0.85		0.80		
	<i>P. chesteri</i>									
USNM 19199							1.4	0.9		
	<i>A. blacki</i>									
CM 41159							2.2	1.1	2.2	0.9
	<i>A. dawsoni</i>									
CM 55569							1.5	0.8		
	<i>M. labrus</i>									
UM 66144	2.70	1.45	2.97	1.76	3.07	1.83	3.20	1.77	3.05	1.84

Table 3.—Dimensions of type and paratype specimens (upper dentition) of species of *Peradectes*, *Mimoperadectes*, and *Peratherium*.

Taxa and catalog no.	M ¹		M ²		M ³		M ⁴	
	L	W	L	W	L	W	L	W
<i>Peradectes elegans</i>								
AMNH 17369 (paratype)	1.60	1.50	1.60	1.70	1.40	1.90	1.05	1.95
<i>Peradectes protinnominatus</i>								
UCMP 44077	1.6	1.4	1.5	1.7	1.4	2.0		
<i>Mimoperadectes labrus</i>								
UM 66144	2.84		3.09	3.47	2.94	3.66	2.36	3.26
<i>Peratherium knighti</i>								
AMNH 55684	1.9	1.6	2.05	2.0	2.05	2.2		

is a valid species of *Peratherium* (see above); (4) *Thylacodon pusillus* may not belong in *Peradectes* or the Peradectini.

***Peradectes elegans* Matthew and Granger, 1921**
(Fig. 3)

Type.—AMNH 17376, paired dentaries with RP₁, P₃–M₄ and LP₂–M₄.

Paratype.—AMNH 17369 (M¹⁻⁴).

Type locality.—Mason Pocket, Animas Formation (see Lucas and Ingersoll, 1981), Colorado.

Referred specimens.—In addition to the material referred elsewhere (Simpson, 1935; Gazin, 1956), UCMP 44767 (M₂₋₄), CM 42138 (M₃), from the Wasatch Fm., Sand Quarry, Four Mile area, Colorado; CM 41108 (M₂₋₃), UCM 46216 (M₃₋₄), from the Fort Union Fm., Saddle locality, Bison Basin, Wyoming; AMNH 17199 (M¹⁻²), from the type locality.

Known distribution.—Tiffanian—Bison Basin (Fort Union Fm.), Wyoming; San Juan Basin (Animas Fm.), Colorado. Early Wasatchian—Four Mile area (Wasatch Fm.), Colorado.

Emended diagnosis.—Differs from other species of *Peradectes* as follows: larger size; P₃ more trenchant with longer talonid; P₃ protoconid higher than that of molars; M₁ as large as M₂; M₁₋₄ talonids broader and longer; M₃ talonid broader than trigonid; M¹⁻³ with stronger styler cusps and conules and with uncompressed protocone.

Discussion.—The oldest known material of *P. elegans*, from Bison Basin, includes M₂₋₄ that are broad in proportion to length, with wider talonids than trigonids. Lower molars on the type of *P. elegans* from the Tiffanian Mason Pocket are similar; curiously, RM₃ on the type has a slightly narrower talonid than LM₃. M₁ on the type is as large as

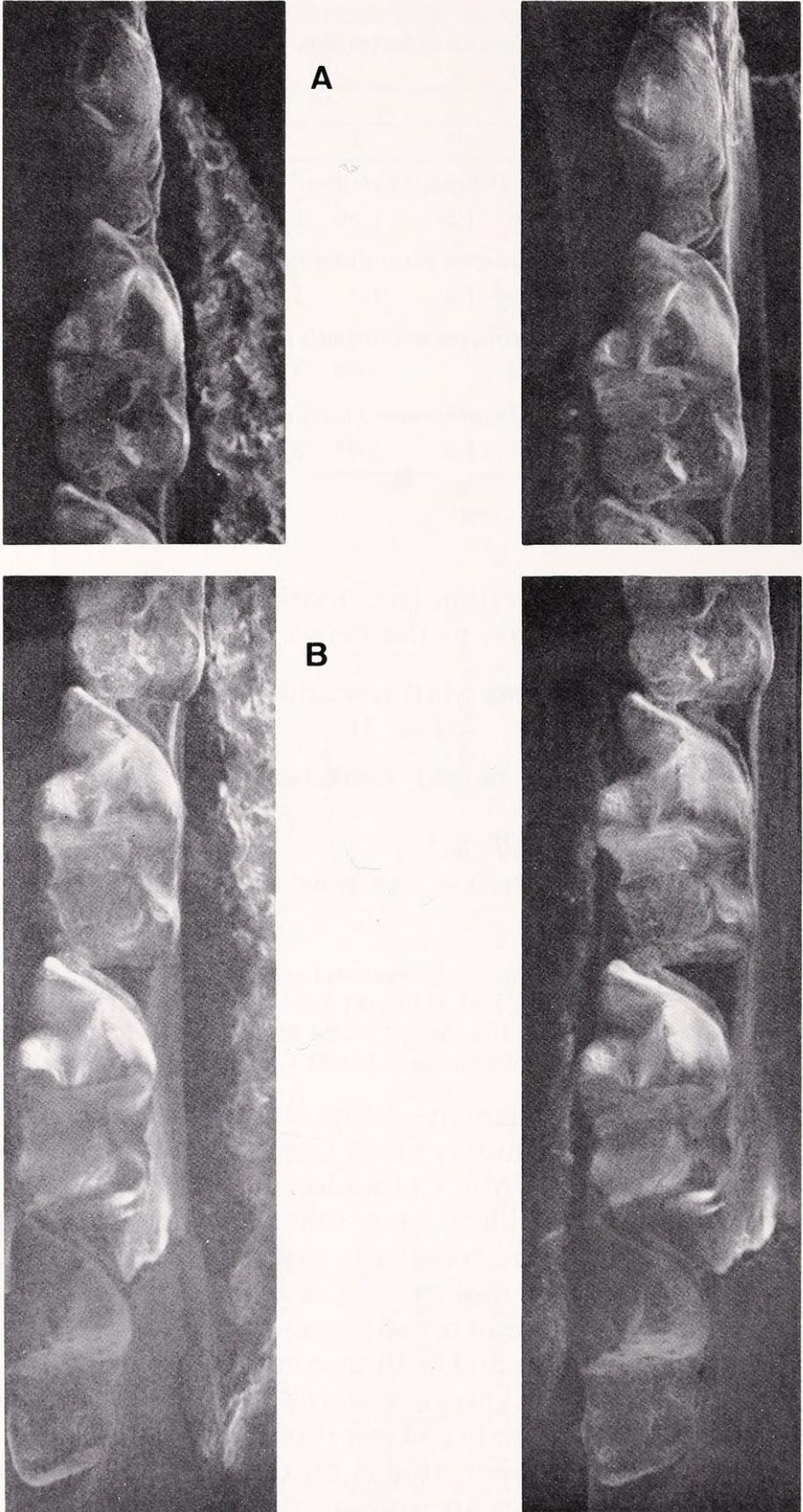


Fig. 3.—*Peradectes elegans*. (A) and (B) AMNH 17376, type, RP_3-M_1 and RM_{2-4} ; $\times 16.5$.

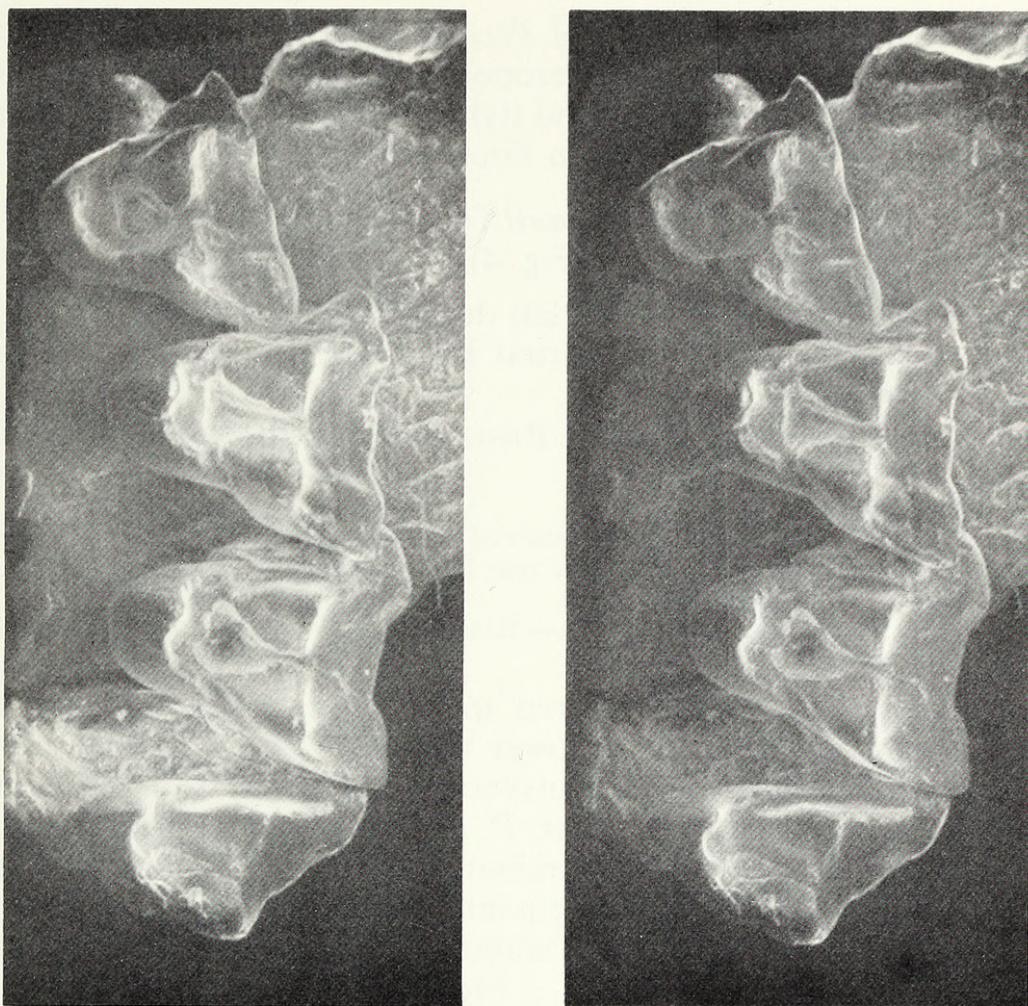


Fig. 3.—*Peradectes elegans*. (C) AMNH 17369, LM¹⁻⁴, paratype; approx. $\times 16.5$.

M_2 . P_3 is trenchant, higher than the molars and has a long talonid. On M_3 the talonid is broader than the trigonid. These characters distinguish the lower dentition of *P. elegans* from that of all other North American species of *Peradectes* and indicate that UCMP 44767, formerly identified as *P. protinnominatus* (McKenna, 1960, Fig. 17c), and CM 42138, both from Four Mile, represent *P. elegans*. M_3 in these specimens has a wider talonid than trigonid; M_{2-4} in UCMP 44767 are indistinguishable from *P. elegans* in size and structure, and the distance between the roots of M_1 implies that M_1 was as large as, if not larger than, M_2 . This material represents the first Wasatchian record of *P. elegans*.

Upper molars of *P. elegans* from Mason Pocket are not transverse, but in occlusal view resemble an equilateral triangle. As noted by Simpson (1935), styler cusps B, C, and D are present although variably developed, the conules are moderately strong and the paracone, slightly lower than the metacone, is higher than the protocone. In contrast, all

other North American species of *Peradectes* have upper molars that are more transverse, with an anteroposteriorly compressed protocone and weaker or vestigial conules and styler cusps C and D. Upper molars of *P. elegans* are not known from Four Mile.

***Peradectes pauli* Gazin, 1956**
(Fig. 4)

Type.—USNM 20879, partial left dentary with M_{3-4} .

Paratype.—USNM 20880, partial left dentary with M_1 and part of M_2 .

Type locality.—Saddle locality, Bison Basin, Fort Union Formation, Wyoming.

Referred specimens.—In addition to material referred elsewhere (Gazin, 1956), CM 41109 (M^3), MCZ 20793 (M^{2-3}), from the type locality.

Known distribution.—Tiffanian—Bison Basin (Fort Union Fm.), Wyoming.

Emended diagnosis.—Compared to *P. elegans*: smaller size; M_1 smaller than M_2 ; M_3 with narrower talonid than trigonid; M_4 with narrower talonid; M^{2-3} more transverse with compressed protocone. Compared to *P. protinnominatus*, *P. chesteri*, *P. californicus*, and *P. minutus*: bases of M_{3-4} more emarginate buccally between trigonid and talonid; M_4 talonid longer than trigonid. Compared to *P. californicus*, *P. chesteri*, and *P. minutus*: wider talonid occlusally on M_{1-3} . Compared to *P. chesteri* and *P. minutus*: M_{1-3} wider in proportion to length; less disparity in L/W ratio from M^2 to M^3 ; less compressed protocone on M^{2-3} ; stronger conules and styler cusps C and D. Compared to *P. minutus*: paracone proportionately higher than protocone and styler cusp B.

Discussion.—Curiously, *P. pauli* has been ignored in recent important studies of early Tertiary didelphines (McKenna, 1960; Setoguchi, 1973; Bown, 1979; Crochet, 1978; Rose, 1981).

In contrast to *P. elegans*, on the type and paratype of *P. pauli* M_1 is smaller than M_2 , M_{3-4} have narrower talonids, and the talonid on M_3 is narrower than the trigonid. As such, *P. pauli* is a distinct species from Bison Basin, where it occurs with *P. elegans* at the Saddle locality.

Analysis of the upper dentition leads to a similar conclusion. CM 41109, an isolated M^3 , and MCZ 20793, M^{2-3} , both from Bison Basin, resemble one another and differ from *P. elegans* in being more transverse, with a narrower, anteroposteriorly compressed protocone and a deeper ectoflexus. Except for slightly larger size, they are closely similar to upper molars of *P. protinnominatus* from Four Mile and the Willwood Formation (see below; McKenna, 1960; Bown, 1979).

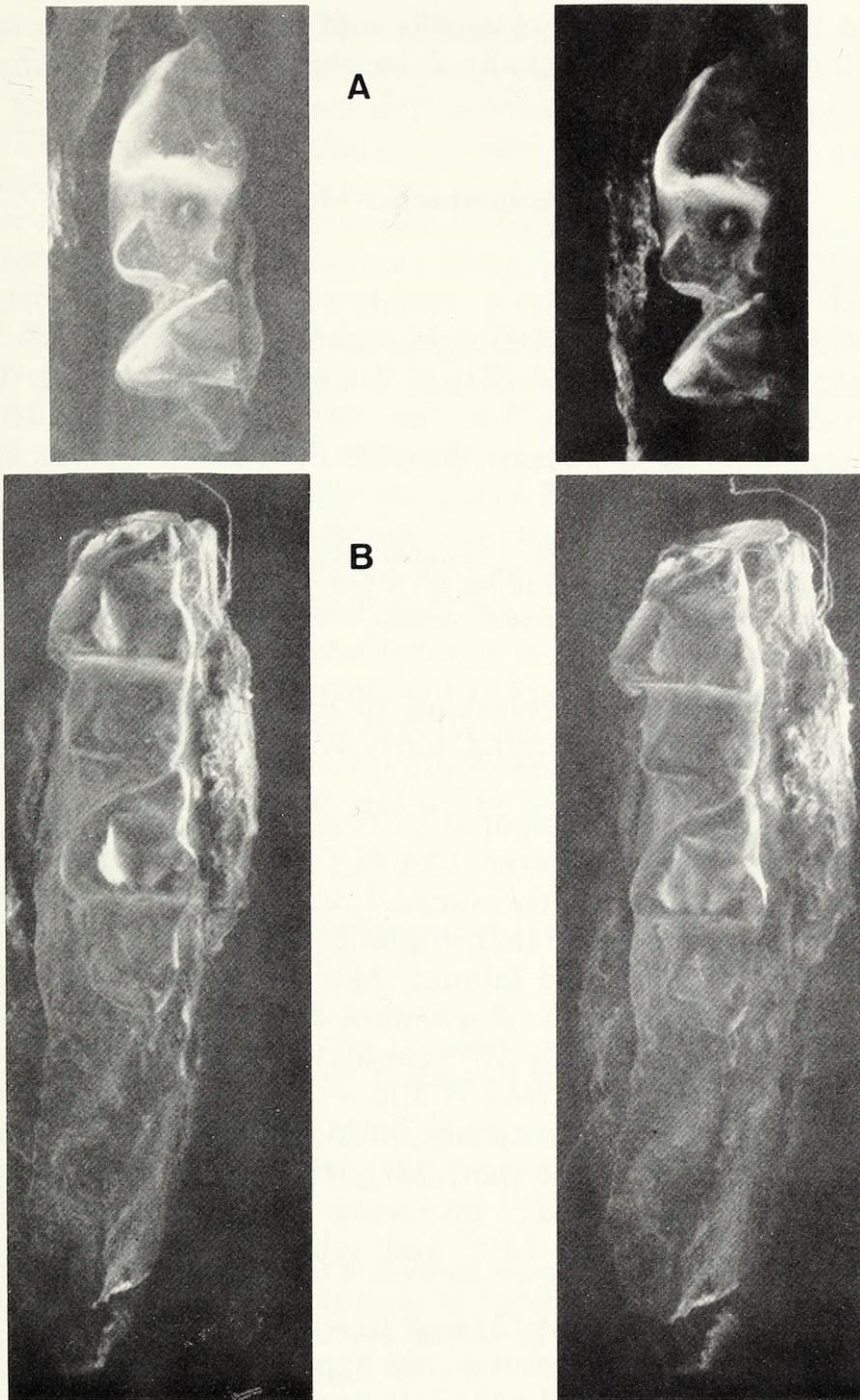


Fig. 4.—*Peradectes pauli*. (A) USNM 20880, LM₁ and trigonid of M₂, paratype; (B) USNM 20879, LM₃₋₄, type; both approx. $\times 16.5$.

P. pauli is suitable morphologically and temporally to be basal to the branching lineage that includes *P. protinnominatus*, *P. californicus*, *P. chesteri*, and *P. minutus*.

***Peradectes protinnominatus* McKenna, 1960**

Peradectes chesteri Bown, 1979.

Peradectes cf. *chesteri* Rose, 1981.

Type.—UCMP 44077, partial right maxilla with M^{1-3} .

Paratypes.—UCMP 45947 (M_{1-2}), UCMP 45948 (M_{1-2}), UCMP 45950 (P_3-M_1).

Type locality.—Alheit Pocket, Wasatch Fm., Four Mile area, Colorado.

Referred specimens.—In addition to material referred elsewhere (McKenna, 1960; Bown, 1979; Rose, 1981), CM 42138 (M_2), UCMP 59132 (M_3), UCMP 59130 (M^3), from the Wasatch Fm., Four Mile area, Colorado; UW 10129 (M^2), from the Willwood Fm., Bighorn Basin, Wyoming.

Known distribution.—Clarkforkian to early Wasatchian—Bighorn Basin (Willwood Fm.), Wyoming. Early Wasatchian—Four Mile area (Wasatch Fm.), Colorado.

Emended diagnosis.—Compared to *P. elegans*: smaller size; P_3 talonid shorter and trigonid lower than M_1 ; M_1 smaller than M_2 ; M^{2-3} more transverse, protocone compressed. Compared to *P. elegans* and *P. pauli*: M_4 talonid shorter than trigonid; M_{3-4} with weaker emargination between trigonid and talonid; M^{2-3} protocone more anterior. Compared to *P. californicus*, *P. chesteri*, and *P. minutus*: M_{1-3} with wider talonid occlusal width; M^{1-3} conules and styler cusps C and D stronger. Compared to *P. chesteri* and *P. minutus*: less disparity in L/W ratio from M^1 to M^3 ; protocone on M^3 less compressed; paracone and metacone on M^{1-3} farther apart; M_{1-3} wider in proportion to length. Compared to *P. minutus*: M^{2-3} protocone less compressed; paracone higher than protocone on M^{1-3} and relatively higher than styler cusp B.

Discussion.—Setoguchi (1973) and Bown (1979) synonymized this species with *P. chesteri*. However, the type of the latter, an M_3 , can only be compared to UCMP 44767, the only specimen with an M_3 in the original material of *P. protinnominatus* from Four Mile (McKenna, 1960). UCMP 44767 is much larger than the type and referred material of *P. chesteri*; it has a wider talonid than trigonid on M_3 , and subequal M_1 and M_2 , and was referred above to *P. elegans*.

In contrast to *P. protinnominatus*, the type and other specimens of *P. chesteri* (see below) have lower molars that lack a buccal emargination between trigonid and talonid, and talonids that have a narrower

occlusal width. As such, UW 9605 and UM 71663, from the Clarkforkian and early Wasatchian, respectively, of the Bighorn Basin, more closely resemble the paratypes of *P. protinnominatus*. Bown (1979) and Rose (1981) reached the same conclusion concerning these specimens (but allied them with *P. chesteri* = *P. protinnominatus*).

Upper molars of *P. protinnominatus* are also distinct from those of *P. chesteri*. Diagnostic differences involve the degree of compression of the protocone on M^3 , the disparity in L/W ratio from M^1 to M^3 , and the development of the conules and styler cusps C and D. As also noted by Bown (1979), upper molars from his Bighorn Basin sample are indistinguishable from the type of *P. protinnominatus*.

Upper molars in UCMP 44095 from Four Mile (McKenna, 1960, Fig. 18a) and one of the upper molars in UW 9742 (Bown, 1979, Fig. 40a, center) are dilambdodont, and are reidentified here and elsewhere (Krishtalka and Stucky, 1983a) as *Peratherium innominatum*. UW 10129, originally identified as *Peratherium macgrewi* (Bown, 1979, Fig. 40c), is not dilambdodont and belongs in *P. protinnominatus*.

P. protinnominatus is intermediate in known dental morphology and temporal occurrence between *P. pauli* and *P. chesteri*. It is also closely related to *P. californicus*, which is more derived in the narrower occlusal width of the molar talonids, and in the weaker styler cusps C and D and conules on M^{1-3} .

Peradectes californicus (Stock, 1936)

Peratherium californicum Stock, 1936.

Nanodelphys cf. *N. minutus* Setoguchi, 1975, in part.

Nanodelphys californicus (Stock, 1936), Lillegraven, 1976.

Peradectes californicum (Stock, 1936), Crochet, 1978.

Type.—LACM (CIT) 202-1943, partial right dentary with P_3 – M_2 .

Type locality.—LACM (CIT) loc. 202, Sespe Fm., Ventura County, California.

Referred specimens.—In addition to material referred elsewhere (Lillegraven, 1976), CM 15664 (M_1), CM 52421, 23845 (both M_3), CM 52417 (M_4), CM 15138, 15612, 51367, 51250, 15611 (all M^1), CM 19748 (M^{2-3}), CM 15671, 15104, 15149 (all M^2), CM 15681 (M^3), from localities 5, 5 Front, 5 Back, 6, 20, Wagon Bed Fm., Wind River Basin, Wyoming.

Known distribution.—Uintan—San Diego County (Friars, Mission Valley, ?Santiago, Sespe Fms.), California. Uintan to Duchesnean—Wind River Basin (Wagon Bed Fm.), Wyoming.

Emended diagnosis.—Compared to *P. elegans*: teeth much smaller; P_3 smaller than M_1 ; M_1 smaller than M_2 ; narrower talonid than trigonid on M_3 ; M^{1-4} more transverse. Compared to *P. elegans* and *P. pauli*: protocone more anterior on M^{1-3} ; shorter talonid than trigonid on M_4 ;

trigonids lower on M_{1-4} . Compared to *P. elegans*, *P. pauli*, and *P. protinnominatus*: P_3 without talonid (not known in *P. pauli*); M_{1-3} talonids with narrower occlusal width; M^{1-3} with weaker conules and stylar cusps C and D. Compared to *P. chesteri* and *P. minutus*: M^2 and M^{2-3} , respectively, less transverse, with a less compressed protocone; M^{2-3} with a shallower ectoflexus and stronger stylar cusps C and D; less disparity in L/W ratio from M^{1-3} .

Discussion.—Lillegraven (1976) recognized that Stock's (1936) type and referred material of *Peratherium californicum* represented an Uintan species of *Nanodelphys* that was morphologically indistinguishable from *Nanodelphys* cf. *N. minutus* from the late Eocene of Badwater (Setoguchi, 1973). He retained *N. californicus* and *N. minutus* on the basis of geographic and temporal disparity. The two species, as understood here, differ morphologically.

Setoguchi (1973) originally recognized two species of *Nanodelphys* from Badwater, *Nanodelphys* cf. *N. minutus* and *Nanodelphys* sp. nov., which he later (Setoguchi, 1975) combined in the former. Crochet (1978) and Bown (1979) independently suggested that *Nanodelphys* and *Peradectes* were congeneric, and Crochet allocated *N. minutus* and *N. californicus* to *Peradectes*.

From our analysis of the Badwater and Oligocene material it appears that *N. minutus* and *N. californicus* are discernable species of *Peradectes*. *P. californicus* includes some of the material that Setoguchi (1973, 1975) assigned to *Nanodelphys* cf. *N. minutus*, whereas Setoguchi's (1973) *Nanodelphys* sp. nov. is referred below to *Peradectes* sp. cf. *P. minutus*. Of Setoguchi's (1975) figured specimens of *Nanodelphys* cf. *N. minutus*, TTU-P 2426 (Fig. 9) is a DP^3 of *Peratherium innominatum* and CM 16007 (Fig. 12) is an M^2 of *Peradectes* sp. cf. *P. minutus*. The remainder are *P. californicus*. Some of his referred specimens (TTU-P 1360, 2420, CM 23846) also represent *Peratherium innominatum*.

In summary, *P. californicus* is known from the Uintan of California, and from the Uintan and Duchesnean of Wyoming where it occurs in lithosympatry with the smaller *Peradectes* sp. cf. *P. minutus* at five of the Badwater late Eocene localities. The *P. californicus* material from Wyoming shows a more restricted range in size than that from California, possibly because of the co-occurrence of the two species at Badwater and the implied character displacement. A larger sample of both species is needed to test this hypothesis.

P. californicus appears to have shared a common ancestry with the *P. chesteri*-*P. minutus* lineage from a *P. protinnominatus*-like peradectine. The first three species are derived in having weaker conules and stylar cusps C and D on the upper molars (see Setoguchi, 1975, Fig. 11, 12; Lillegraven, 1976), and talonids on the lower molars with

narrower occlusal widths between the cristid obliqua and the lingual border. The cristid obliqua runs posteriorly from the trigonid before turning labially to a more internal hypoconid, so that the occlusal width of the talonid is approximately one-half of the basal width. In contrast, other species of *Peradectes* retain the primitive posterolabial orientation of the cristid obliqua, a more buccal hypoconid, and an occlusally wide talonid on the lower molars, as well as stronger conules and stylar cusps C and D on the upper molars. M^3 in *P. chesteri* and M^{2-3} in *P. minutus* (and *Peradectes* sp. cf. *P. minutus*) are more advanced than in *P. californicus* in having a more anteroposteriorly compressed protocone and vestigial or absent stylar cusps C and D. Also, the disparity in L/W ratio from M^1 to M^3 is more marked.

Peradectes chesteri Gazin, 1952

(Fig. 5)

Referred specimens.—In addition to material referred elsewhere (Gazin, 1952; Krishtalka and Stucky, 1983a, 1983b), PM 15682 (M^{3-4}), PM 15866 (M^{2-3}), from Hawk and Fault localities, Bridger Fm., Green River Basin, Wyoming (see West, 1973); UW 984, (P_3 – M_4), from Tabernacle Butte, Bridger Fm., Green River Basin, Wyoming.

Discussion.—The systematics of this species were treated elsewhere (Krishtalka and Stucky, 1983a). *P. chesteri* is known from late Wasatchian to late Bridgerian faunas. Material originally assigned to *P. chesteri* from the Clarkforkian and early Wasatchian of the Bighorn Basin (Bown, 1979; Rose, 1981) was referred above to *P. protinnominatus*.

Compared to *P. elegans*, *P. pauli*, and *P. protinnominatus*, diagnostic and derived features on the type of *P. chesteri*, an M_3 , include an occlusally narrow talonid (the hypoconid is more internal), and an absence of the labial emargination between the trigonid and talonid. These characters are also preserved on UW 984, a partial right dentary with P_3 – M_4 from Tabernacle Butte (see McGrew, 1959; Bown, 1982), and a lower molar from Powder Wash. Upper molars from Powder Wash, the Wind River Formation (Krishtalka and Stucky, 1983a, 1983b), and the Bridger Formation (West, 1973, Pl. 1, Figs. C, D) also bear distinctive features and are referred to *P. chesteri*. The morphology of these specimens indicates that this species is intermediate in molar structure between *P. protinnominatus* and *P. minutus*. *P. chesteri* has the basic features of the former, but is more derived in that: there is a greater disparity in L/W ratio from M^1 to M^3 , so that M^1 is longer than wide, M^2 is more nearly equilateral, and M^3 is very transverse; the paracone and protocone are relatively lower and higher, respectively, and the paracone and metacone are closer to one another; the conules and stylar cusps C and D are vestigial or absent, and the protocone is

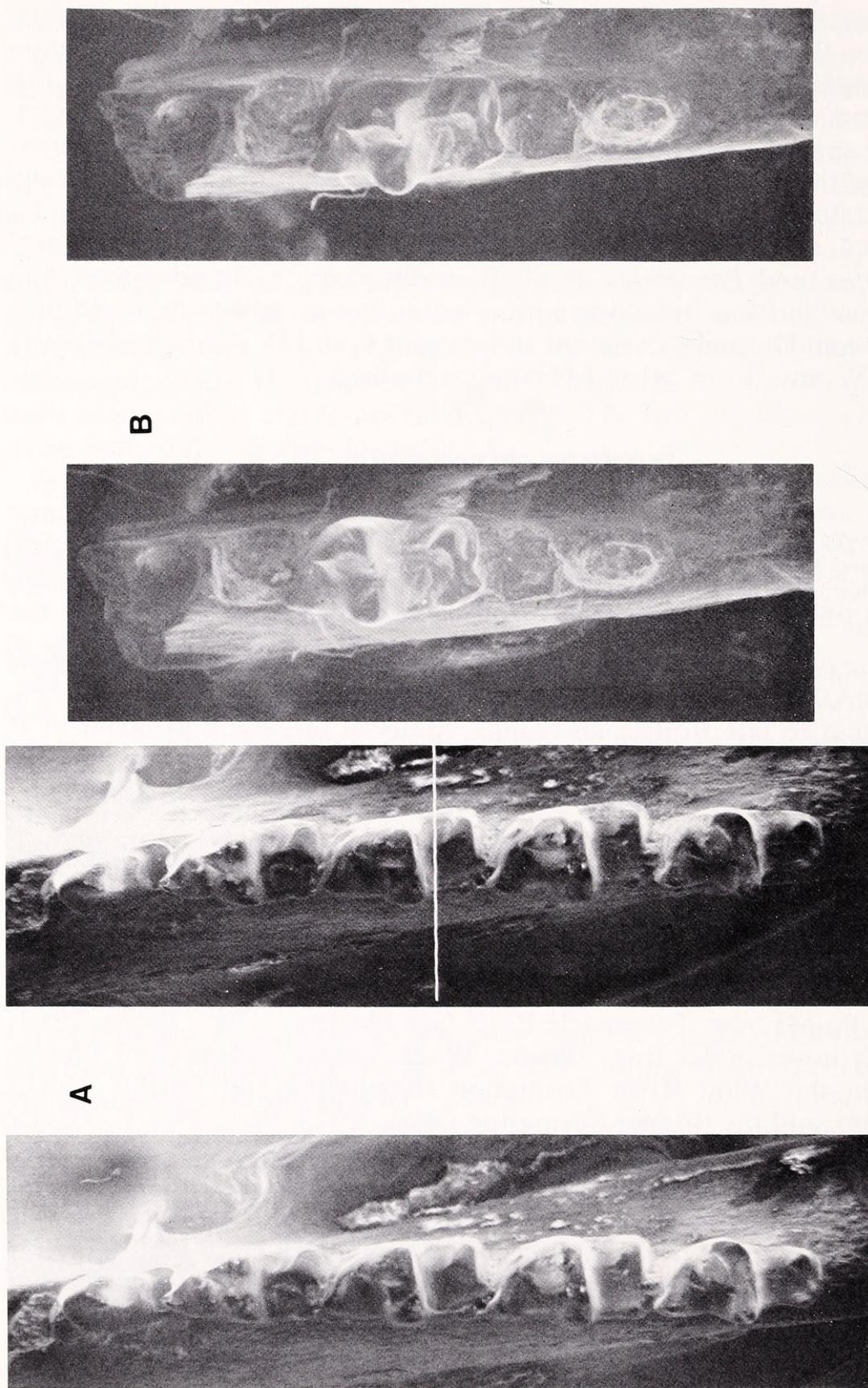


Fig. 5.—*Peradectes chesteri*. (A) UW 984, RP₃-M₄, approx. × 14; (B) USNM 19199, RM₃, type, approx. × 17.

more compressed anteroposteriorly on M^3 ; the lower molars are narrower in proportion to length, the talonids are narrower occlusally, and the buccal part of the base between the trigonids and talonids is not emarginate. These features are further modified in *P. minutus*: the protocone on M^{2-3} is more compressed anteroposteriorly and the paracone is reduced in height to that of the protocone and almost to that of stylar cusp B. On the type of *P. chesteri* a large gap occurs between the alveolus for the posterior root of M_4 and the ascending ramus of the dentary. This gap is absent from lower jaws of *P. minutus*, indicating a shortening of the jaw in the latter. *P. chesteri* is divergent from *P. californicus* in having a more compressed protocone on M^3 , greater disparity in L/W ratio from M^1 to M^3 , and in lacking conules and stylar cusps C and D. Their inferred common ancestry was discussed above.

Peradectes* sp. cf. *P. minutus

Nanodelphys sp. nov. Setoguchi, 1973.

Nanodelphys cf. *N. minutus* Setoguchi, 1975, in part.

Referred specimens.—CM 15091, 15628, 15687, 51369 (all M^1), CM 16007, 15094 (both M^2), CM 15047, 15618 (both M^3), CM 18216 (DP_3), CM 52415 (M_1), CM 15016, 15006, 15087, 15082, 29484, 52413, 52416 (all M_2), CM 15666, 15685, 23843, 23847, 52418 (all M_3), from localities 5, 5A, 5 Front, 5 Back, 6, Wood, 20, Badwater Creek area, Wagon Bed Fm., Wind River Basin, Wyoming.

Discussion.—Setoguchi (1973) was correct in recognizing the occurrence of two peradectines at the late Eocene Badwater localities. For reasons not given, he later (1975) emended this conclusion and combined the two species as *Nanodelphys* cf. *N. minutus*. The latter is a composite of two taxa, one of which is *P. californicus* (see above). The remaining part of the sample represents a primitive variant of *P. minutus*, which is here given tentative taxonomic recognition. The few M^2 s and M^3 s are somewhat less transverse than those of *P. minutus* and have a somewhat higher paracone in relation to the protocone and stylar cusp B. Also, parts of the dentition that preserve other diagnostic features of *P. minutus* (the short talonid on M_4 ; loss of the gap between M_4 and the ascending ramus of the dentary) are not represented in the Badwater sample. As such, it seems prudent to distinguish this material from *P. minutus* until more conclusive evidence for referral to the latter is available.

Peradectes sp. cf. *P. minutus* occurs with *P. californicus* at five of the Badwater localities. Teeth of the former are smaller, M^{2-3} are more transverse and have more compressed protocones, and, as a result, the disparity in L/W ratio from M^{1-3} is greater. Also, M_{1-3} are narrower in proportion to length. Although these two species differ in size at Badwater, their combined range in size is encompassed by the samples of *P. californicus* from the Uintan of California. As discussed above,

this may be an example of character displacement in lithosympatric species, but larger samples are needed to test this inference.

Peradectes minutus (McGrew, 1937)

When McGrew (1937) named the Orellan *Nanodelphys minutus* the Tiffanian *P. elegans* was the only known species of *Peradectes*. Large differences in size and morphology implied generic distinction. However, the morphology of other species of *Peradectes* recovered since then from Paleocene and Eocene horizons indicates that *N. minutus* is the most derived species of a branching lineage that includes *P. pauli*, *P. protinnominatus*, and *P. chesteri* (and *Peradectes* sp. cf. *P. minutus*). Its advanced dentition appears to be the result of incremental and cumulative changes in that lineage, and generic distinction is no longer warranted. Crochet (1978) and Bown (1979) reached a similar conclusion.

Earlier suggestions by Galbreath (1953) and Setoguchi (1973) that "*N.*" *minutus* may be conspecific with *Peratherium huntii* are in error. Cope (1884) and Galbreath (1953) noted the large size of the entoconid on the type of *P. huntii*—a diagnostic feature of the Didelphini—and, partly on this basis, Hough (1961) allocated *P. huntii* to *Herpetotherium fugax*.

P. minutus is most closely related to *P. chesteri*. However, M³ and especially M² are more transverse, with a more highly compressed protocone. On M¹⁻³ the reduced paracone and the protocone are subequal in height and slightly higher than an enlarged stylar cusp B (see McGrew, 1937, Fig. 3; Setoguchi, 1978, Fig. 7A). *P. minutus* also lacks the gap on the mandible between M₄ and the ascending ramus that is evident on the type of *P. chesteri* (Fig. 5).

P. minutus is known from Oligocene horizons of the western interior of North America. Late Eocene material that Setoguchi (1975) referred to *Nanodelphys* cf. *N. minutus* was assigned above to *Peradectes* sp. cf. *P. minutus*, *P. californicus*, and *Peratherium innominatum*. As discussed above, recognition of *Peradectes* sp. cf. *P. minutus* is tentative. It has most of the derived features of *P. minutus* and, with recovery of additional material, may prove to be conspecific with the latter.

Setoguchi's (1978) sample of "*Nanodelphys* new species" from the Orellan of Badwater is also a composite of numerous taxa. Much of the material represents a small species of *Peratherium* or *Herpetotherium*, which explains his attribution of dilambdodonty to this species. Of the specimens he referred, only CM 19802, 19804, 21697, 33557, 33570, 33574, 33577, 33582, 33589, 33590, 33595, 33598, 33600, 33613, 33619, 33621, 33625, 33628, 33631, 33632, 33642, 33647 belong to the Peradectini, and specifically *P. minutus*. To these should also be added CM 33599 (M¹⁻³) and KU 16611 (M¹⁻³).

Armintodelphys Krishtalka and Stucky, 1983

The two species in this genus—*A. blacki* and *A. dawsoni*—are known from the late Wasatchian to early Bridgerian and from the early Bridgerian, respectively, of the Wind River Formation. *A. dawsoni* is also known from the early Bridgerian Powder Wash locality, Utah (Krishtalka and Stucky, 1983*b*). The systematics of the two species were treated in detail elsewhere (Krishtalka and Stucky, 1983*a*). Briefly, *Armintodelphys* is derived over other North American Peradectini in having M_{2-4} with a reduced, nubbin-like entoconid that is smaller and lower than the hypoconulid, and M_2 with a narrower talonid than trigonid. Otherwise, the two species most closely resemble *P. pauli* in retaining high molar trigonids, long talonids, a buccal emargination between the trigonids and talonids, a longer talonid than trigonid on M_4 , and a narrower talonid than trigonid on M_3 . More derived species of *Peradectes* have an M_4 with a shorter talonid than trigonid, as well as other advanced features. Accordingly, *Armintodelphys* may have evolved from or shared a common ancestry with *P. pauli*.

An M^2 from Powder Wash, tentatively referred to *A. dawsoni* (Krishtalka and Stucky, 1983*b*), differs from that of known species of *Peradectes* in having a weak, compressed protocone, an enlarged styler cusp C, more closely approximated paracone and metacone, and expanded styler salients. As in other Peradectini, the M^2 is not dilambdodont.

Mimoperadectes Bown and Rose, 1979

The only described species in this genus, *M. labrus*, occurs in early Wasatchian faunas from the Bighorn and Powder River basins. Apart from being the largest known species in the Peradectini, *M. labrus* is specialized in having a paraconid on M_{2-4} that is larger and higher than the metaconid. It shares with species of *Peradectes* the morphology of a low, subequal, and closely appressed entoconid and hypoconulid on the lower molars. It differs from all species of *Peradectes* except *P. elegans* in retaining an M_1 that is as large as M_2 , an M^3 that is not transverse, and M^{2-3} with comparatively strong conules and styler cusps C and D, and an uncompressed protocone. As such, *Mimoperadectes* most closely resembles *P. elegans*, but is more derived in having an M_3 with a narrower talonid than trigonid. These features imply that *Mimoperadectes* originated in common with *P. pauli* from a Paleocene species of *Peradectes* that had developed the narrow M_3 talonid. As Bown and Rose (1979) noted, the enlarged paraconid on the lower molars is convergent on the condition in stagodontid marsupials. Unlike the latter, *M. labrus* lacks the enlarged, specialized posterior premolars, and compressed trigonids on the lower molars.

EVOLUTIONARY RELATIONSHIPS

The depiction of relationships (Fig. 6) among *Peratherium*, *Herpetotherium*, *Peradectes*, *Mimoperadectes*, and *Armintodelphys* is based on current thought (Clemens, 1966, 1968, 1979; Fox, 1979) that an *Alphadon*-like dentition represents the primitive condition among didelphines. Accordingly, the following molar characters are primitive for Tertiary North American didelphines: on M_{1-3} , the talonid is equal in width to, but much longer than, the trigonid; the cristid obliqua meets the posterior wall of the trigonid medially, below the ventral apex of the protocristid; the entoconid is high and conical; the hypoconulid is subequal or lower than, and posterior or posterolabial to, the entoconid; the entoconid notch is moderate or large; the metaconid is larger than the paraconid; on M_4 , the talonid is much longer than the trigonid; on M^{1-3} , the paracone and metacone are subequal; the centrocrista is straight (not dilambdodont) or weakly directed toward the styler shelf (incipiently dilambdodont); the styler cusps and conules are well developed.

In comparison, Tertiary North American didelphines are advanced dentally in having a shortened talonid on M_{1-3} and a more labial cristid obliqua on the lower molars (Fig. 6, node 1)—features that imply their common ancestry. Dental characters among these genera suggest a subsequent divergent radiation: on the one hand, members of the Didelphini—*Peratherium* and *Herpetotherium*—retain one variant of the primitive *Alphadon*-like hypoconulid-entoconid complex, but are specialized in having dilambdodont M^{1-3} , with a reduced paracone in comparison to the metacone and a reduced ectoflexus (Fig. 6, node 2). On the other hand, members of the Peradectini—*Peradectes*, *Mimoperadectes*, *Armintodelphys*—appear united by a different suite of derived features: on M_{1-3} , a reduced entoconid and hypoconulid that are closely appressed, subequal, and separated by a weak entoconid notch, and arise from a common internal talonid wall; on M^{1-3} , reduced styler cusps and conules (Fig. 6, node 3). These genera retain the primitive, non-dilambdodont, structure of the upper molars.

Although the common ancestry of the Didelphini and Peradectini is implied by their possession of a shorter talonid and a labial cristid obliqua on M_{1-3} , their origin is difficult to decipher. The derived characters of each group appear to be variable among the species of *Alphadon* (see Clemens, 1966; Lillegraven, 1969; Fox, 1971, 1979). For example, published figures of the dentition indicate that dilambdodonty does not occur among species of *Alphadon*. However, incipient dilambdodonty, where the centrocrista or just the premetacrista is directed toward the styler shelf, is evident on some upper molars of *A. marshi*, *A. lulli*, *A. rhaister*, and *A. russelli*. Some species of *Alphadon*

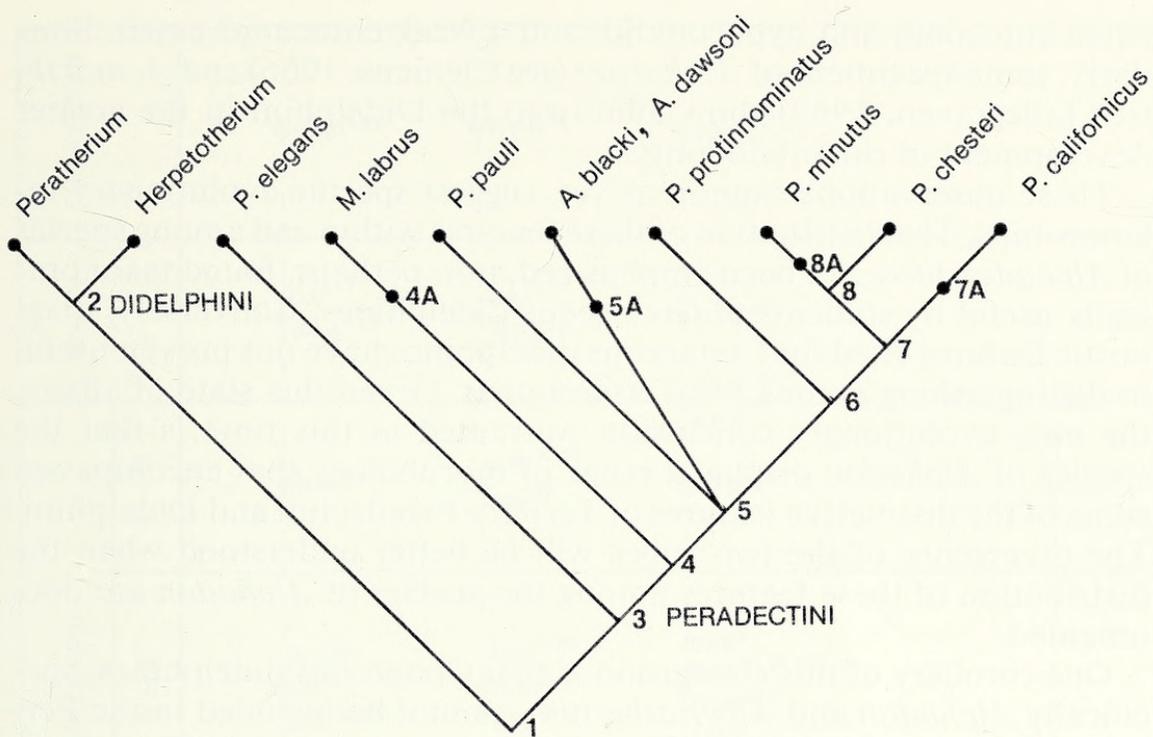


Fig. 6.—Relationships among Paleocene and Eocene North American marsupials. Node 1: shorter talonid on M_{1-3} ; cristid obliqua meets trigonid labially, below protoconid on M_{1-3} ; Node 2: M^{1-3} dilambdodont, paracone much lower than metacone and ectoflexus reduced; on M_{1-3} , entoconid taller and spire-like, hypoconulid much lower and posterior, entoconid notch very deep; Node 3: on M_{1-3} , reduced entoconid and hypoconulid subequal, closely appressed and share common internal talonid wall; entoconid notch weak; on M^{1-3} , styler cusps C and D and conules reduced; Node 4: M_3 talonid narrower (basally) than trigonid; Node 4A: large size, M_{2-4} paraconid larger and higher than metaconid; Node 5: M_1 smaller than M_2 ; M^{2-3} more transverse, with moderately compressed protocone; Node 5A: M_{2-4} entoconid and entoconid notch vestigial; M_2 talonid narrower (basally) than trigonid; Node 6: M_4 talonid shorter than trigonid; P_3 with shorter talonid; P_3 lower than M_1 ; protocone more anterior on M^{1-3} ; Node 7: M_{1-3} talonids with narrower occlusal width (hypoconid more internal, cristid obliqua runs posteriorly from trigonid); M^{1-3} with reduced conules and styler cusps C and D; Node 7A: P_3 talonid lost; Node 8: greater disparity in L/W ratio from M^1 to M^3 ; conules and styler cusps C and D vestigial; M^3 more transverse with a more highly compressed protocone; loss of labial emargination between trigonid and talonid on M_{1-3} ; M_{1-3} narrower in proportion to length; Node 8A: M^{1-3} paracone reduced to height of protocone and almost to that of enlarged styler cusp B; M^3 and especially M^2 more transverse, with a more highly compressed protocone; loss of gap between M_4 and ascending ramus (shortening of jaw).

appear to have a tall entoconid, a lower and posterior hypoconulid, and a strong entoconid notch on some of the lower molars. Others have a subequal entoconid and hypoconulid and a weak entoconid notch. Compared to other species of *Alphadon*, *A. russelli* (Fox, 1979) seems to most closely resemble the Peradectini in having M_{2-3} with short talonids, a labial cristid obliqua, closely appressed, low and sub-

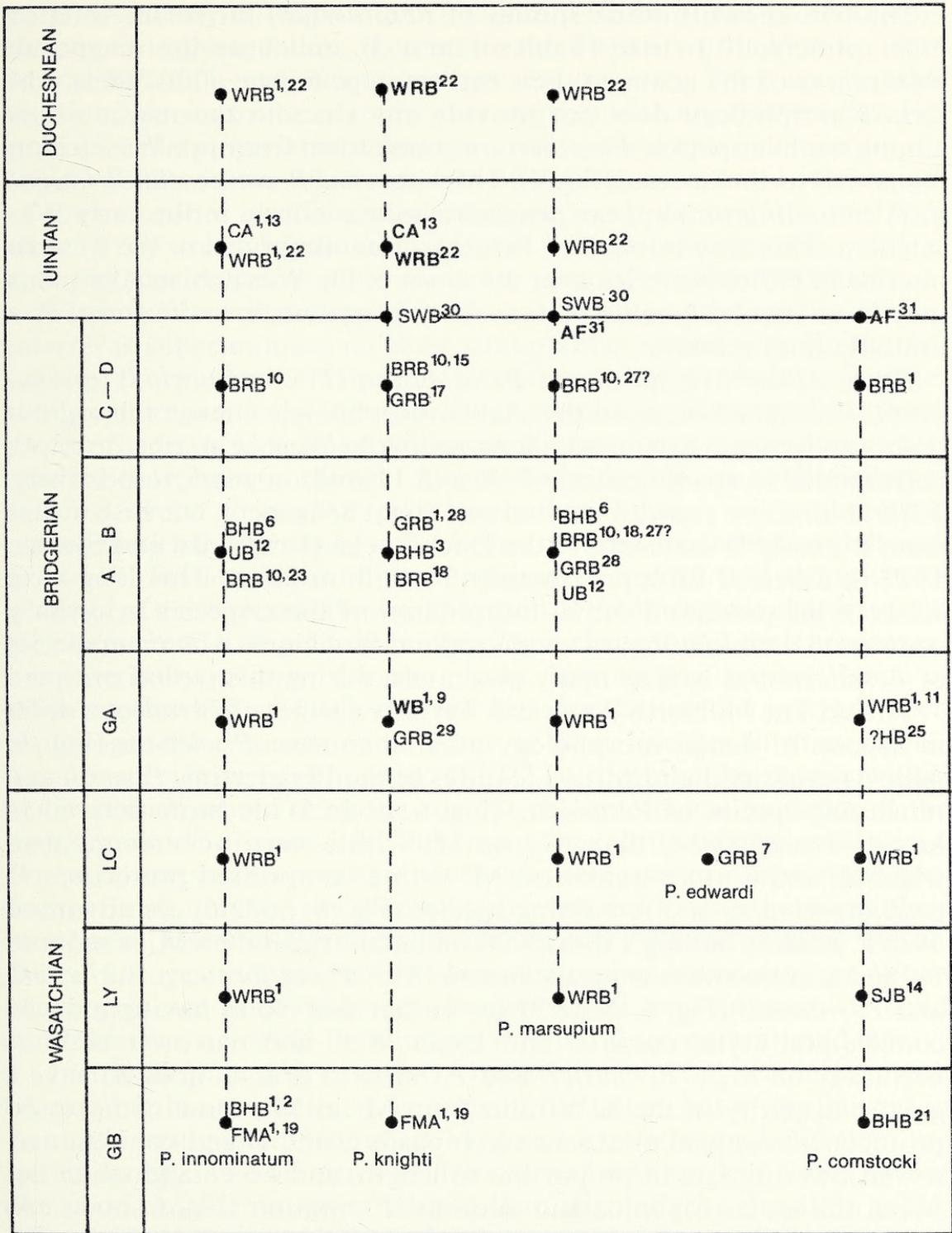
equal entoconid and hypoconulid, and a weak entoconid notch. Similarly, some specimens of *A. rhaister* (see Clemens, 1966) and *A. marshi* (see Lillegraven, 1969) show affinity to the Didelphini in the greater development of dilambdodonty.

These observations cannot, as yet, suggest specific evolutionary relationships. The distribution of these features within and among species of *Alphadon* have not been emphasized, nor, perhaps, found taxonomically useful by students of Cretaceous didelphines. Conversely, diagnostic features cited for Cretaceous didelphines have not proven useful in distinguishing among the Tertiary ones. Given this state of affairs, the only evolutionary conclusion warranted at this time is that the species of *Alphadon* display a range of morphology that encompasses some of the distinctive features of Tertiary Peradectini and Didelphini. The divergence of the two tribes will be better understood when the distribution of these features among the species of *Alphadon* are documented.

One corollary of this conclusion is that Cretaceous didelphines, specifically *Alphadon* and *Albertatherium*, cannot be included in the Peradectini (contra Crochet, 1979) or Didelphini; none of the Cretaceous species has, as yet, been demonstrated to have the suite of diagnostic and derived features of either tribe. A second is that *Thylacodon pusillus* may not be a species of *Peradectes* nor the Peradectini, if figures of *Peradectes* cf. *P. pusillus* (Archibald, 1982, Figs. 42, 43), from the Puercan of Montana, accurately represent the morphology of the species. They indicate that M^1 and M^2 have large styler cusps C and D, and M_{1-3} have elongated talonids, very high trigonids, large entoconids, and deep entoconid notches. None of the figured specimens exhibits the derived features of *Peradectes* or the Peradectini. A third corollary is that the common supposition of an ancestral-descendant relationship between *Peradectes* and *Peratherium* (Clemens, 1968) is unsupported; at its earliest appearance *Peradectes* (ss) is too derived in features of the lower dentition.

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Fig. 7.—Occurrences of North American Eocene species of *Peratherium*. Distance between ages and subages (GB—Graybullian; LY—Lysitean; LC—Lostcabinian; GA—Gardnerbuttean), and placement of occurrences (black dots) are diagrammatic. Letter abbreviations denote areas of occurrences; numbers refer to original sources for identifications and occurrences. AF—Agua Fria; BHB—Bighorn Basin; BRB—Bridger Basin; BSB—Bison Basin; CA—California; FMA—Four Mile area; GRB—Green River Basin; HB—Huerfano Basin; PRB—Powder River Basin; SJB—San Juan Basin; SWB—Sand Wash Basin; WB—Washakie Basin; WRB—Wind River Basin; UB—Uinta Basin. 1—this paper, Krishtalka and Stucky, 1983a; 2—Bown, 1979; 3—Bown, 1982; 4—Bown and Rose, 1979; 5—Delson, 1971; 6—Eaton, 1982; 7—Gazin, 1952; 8—Gazin, 1956;



9—Gazin, 1962; 10—Gazin, 1976; 11—Guthrie, 1971; 12—Krishtalka and Stucky, 1983*b*; 13—Lillegraven, 1976; 14—Lucas et al., 1981; 15—Marsh, 1872; 16—Matthew and Granger, 1921; 17—McGrew, 1959; 18—McGrew and Sullivan, 1970; 19—McKenna, 1960; 20—Rose, 1981; 21—Schankler, 1980; 22—Setoguchi, 1973, 1975; 23—Simpson, 1928; 24—Simpson, 1935; 25—Simpson, 1968; 26—Stock, 1936; 27—Troxell, 1923; 28—West, 1973; 29—West and Dawson, 1973; 30—West and Dawson, 1975; 31—West, 1982.

The five known Eocene species of *Peratherium* in North America differ principally in size (Tables 1 and 3), and bear the diagnostic trademarks of the genus at their earliest appearance. Thus, their preserved morphology does not provide any clues to the relationships among the five species. *Peratherium* is unknown from pre-Wasatchian faunas in North America (Fig. 7). Three species (*P. comstocki*, *P. knighti*, *P. innominatum*) appear penecontemporaneously in the early Wasatchian. This may imply that *Peratherium* immigrated to the western interior of North America near the onset of the Wasatchian. If so, this may have involved one species, with subsequent diversification, or a multiple immigration.

Three of the five species of *Peratherium* (*P. comstocki*, *P. marsupium*, *P. knighti*) show no detectable morphologic change throughout their stratigraphic extent, which according to West et al. (manuscript), corresponds to approximately 7, 9, and 11 million years, respectively. *P. innominatum* shows a gradual and slight anagenetic increase in size from the early Wasatchian to the Duchesnean (Krishtalka and Stucky, 1983a), a period of approximately 11 million years. This long-term stasis in the preserved dental morphology of these species is in sharp contrast to the evolutionary tempo and mode of North American species of *Peradectes*, as well as many placentals, during this period of time.

The six known North American Tertiary species of *Peradectes* differ in aspects of dental morphology other than size. *P. elegans* (Fig. 6, node 3) exhibits the primitive features of the Peradectini. *P. pauli* and remaining species of *Peradectes* (Fig. 6, node 5) are more derived in having a smaller M_1 than M_2 , an M_3 with a narrower talonid than trigonid, and a more transverse M^3 with a compressed protocone. *P. protinnominatus* and remaining species (Fig. 6, node 6) are advanced over *P. pauli* in having a shorter talonid than trigonid on M_4 , a reduced P_3 , and a more anterior protocone on M^{1-3} . *P. californicus*, *P. chesteri*, and *P. minutus* (Fig. 6, node 7) are further derived in having reduced conules and styelar cusps C and D on M^{1-3} , and narrower talonids occlusally on M_{1-3} . *P. chesteri* and *P. minutus* (Fig. 6, node 8) have a greater disparity in the L/W ratio from M^1 to M^3 , more compressed protocones, vestigial or absent styelar cusps C and D and conules, narrower lower molars in proportion to length, and no emargination between the molar trigonids and talonids. *P. minutus* (Fig. 6, node 8A) seems most advanced in the hypertrophy of styelar cusp B, the reduction in height of the paracone, and the severe compression of the protocone on the upper molars.

In summary, the primitive features of the Peradectini, expressed in *P. elegans*, are modified in *P. pauli* and, in turn, in *P. protinnominatus*, *P. californicus*, *P. chesteri*, and *P. minutus*. The major and discrete modifications are: reduction of P_3 , M_1 , the molar talonids, and the

conules and styler cusps C and D; compression of the protocone on the upper molars; and an increase in the disparity of L/W ratio from M^1 to M^3 . Other modifications are less discrete. They are variable within a species to the point of near overlap with another species. For example, the progressive reduction in the buccal emargination on the lower molars, in the relative height of the trigonids, and in the height of the paracones on the upper molars appear to be part of a morphocline. They are valuable as diagnostic criteria (and are only used as such) in species that express disparate parts of that morphocline.

When the reconstruction of relationships among the species of *Peradectes* is superimposed on their stratigraphic record (Fig. 8), the polarity of morphologic change is consistent with the increasingly younger temporal occurrence of these species. Accordingly, these species appear to form a branching lineage that is characterized by speciation and gradual morphologic change. An ancestral-descendent relationship is implied in the *P. pauli*-*P. protinnominatus* lineage, with subsequent cladogenetic divergence of a *P. chesteri*-*P. minutus* lineage and *P. californicus*. Juxtaposition of the stratigraphic record and dental morphology of these species implies that each of the lineages is characterized by incremental and gradual morphologic change, and the appearance, anagenetically, of new, discrete phena, here termed species. None of these species has uniquely derived features that would preclude such a phylogenetic reconstruction. None of these lineages form an evolutionary species (sensu Simpson, 1961). To combine the species within them as such would deny the current paleontological evidence of the appearance of discrete and incremental evolutionary novelties in a temporal succession of progressively younger species. Gaps in the geologic record (and in our knowledge) of these species between their successive first and last occurrences are not evidence against the inferred lineages, nor evidence for an alternative interpretation. When those gaps are filled, that new evidence will lend support, demand modification, or refute the lineages inferred from current evidence.

Armintodelphys (Fig. 6, node 5A) may have evolved in common with *P. pauli*; it has the derived features of the latter, but is specialized in having a vestigial entoconid on M_{2-4} and a narrower talonid than trigonid on M_2 . The affinities of *Mimoperadectes* are less clear. Except for an M_3 with a narrower talonid than trigonid, the dentition of *M. labrus* (Fig. 6, node 4A) most closely resembles that of *P. elegans*, and lacks the derived features of other species of *Peradectes*. It may have evolved in common with *P. pauli* from a Paleocene species of *Peradectes* with a reduced talonid on M_3 . *M. labrus* is specialized in its large size, and in having a larger paraconid than metaconid on M_{2-4} .

The fossil record of North American early Tertiary didelphines reveals contrasting evolutionary histories. Species of the Didelphini ap-

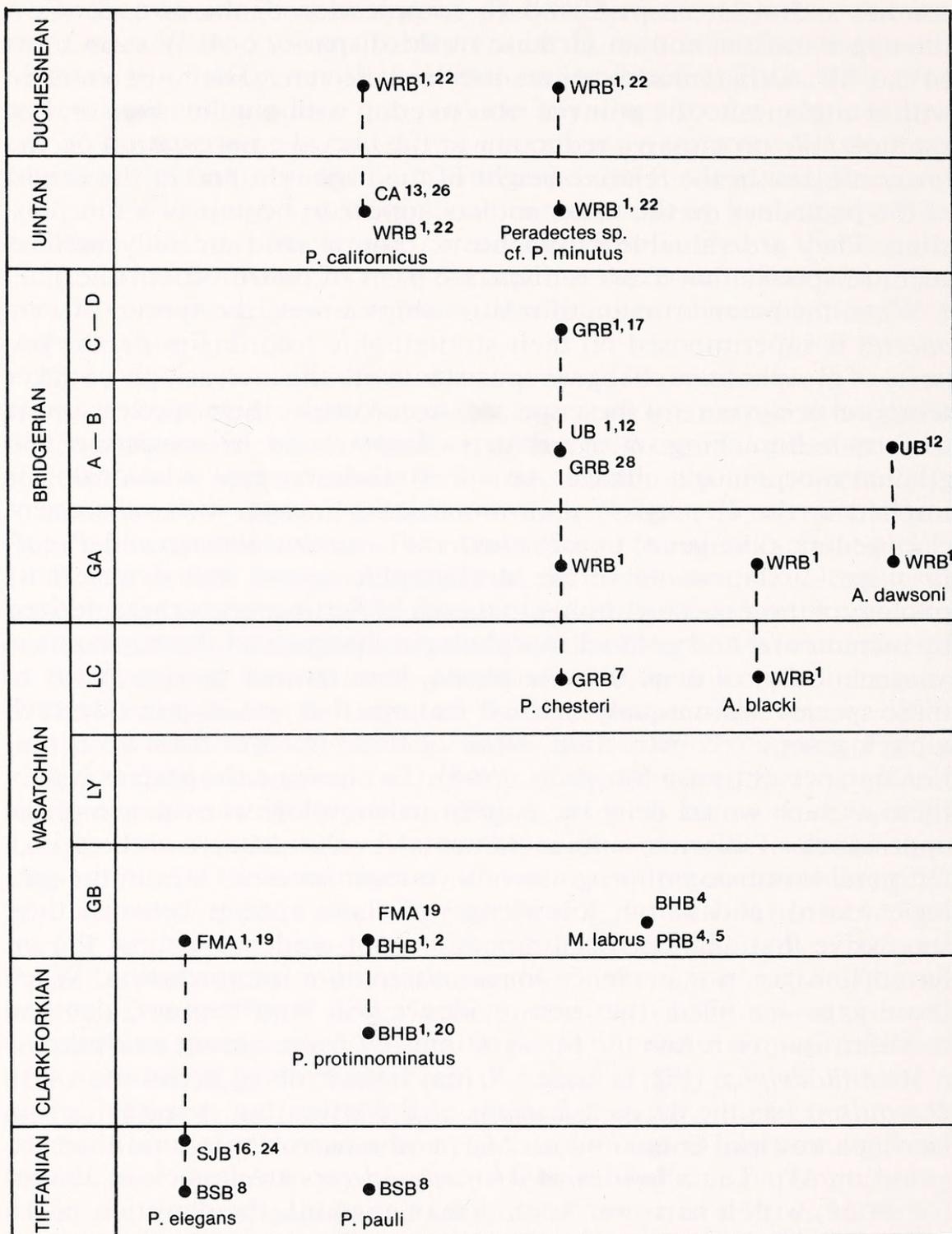


Fig. 8.—Occurrences of North American Paleocene and Eocene species of Peradectini. For explanation of symbols see legend for Fig. 7.

pear abruptly and penecontemporaneously, and remain virtually unchanged throughout their temporal extent. Among the Peradectini, species of *Peradectes* appear sequentially, exhibit cumulative modifications, and apparently form a branching lineage that is characterized by anagenesis and cladogenesis. *Armintodelphys* and *Mimoperadectes*, are offshoots of that lineage.

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