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AND EARLY EOCENE PALAEOORYCTINAE (MAMMALIA, INSECTIVORA)  
FROM THE CLARKS FORK AND BIGHORN BASINS, WYOMING**

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Philip D. Gingerich, Director

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SYSTEMATICS AND PHYLOGENY OF LATE PALEOCENE  
AND EARLY EOCENE PALAEOORYCTINAE (MAMMALIA, INSECTIVORA)  
FROM THE CLARKS FORK AND BIGHORN BASINS, WYOMING

BY

JONATHAN I. BLOCH<sup>1,2</sup>, ROSS SECORD<sup>1,3</sup>, AND PHILIP D. GINGERICH<sup>1</sup>

*Abstract*— New specimens of *Palaeoryctes punctatus* from the middle Clarkforkian of the Clarks Fork Basin include a left dentary preserving the crowns of I<sub>1</sub>-C<sub>1</sub>, P<sub>3</sub>, and M<sub>1-2</sub>, with alveoli for P<sub>2</sub>, P<sub>4</sub>, and M<sub>3</sub>. The lower dental formula, previously unknown for this species, is 3.1.3.3. A maxillary fragment preserves the crowns of a broken P<sub>4</sub>, complete M<sub>1</sub>, and a broken M<sub>2</sub>. Specimens previously referred to *Palaeoryctes* cf. *P. punctatus* and cf. *Palaeoryctes* sp. from the late Tiffanian are morphologically distinct and here included in a new species, *Palaeoryctes jepseni*. The holotype of *P. jepseni* is from Y2K Quarry, and additional specimens are known from Divide, Princeton, and Schaff quarries.

We describe a new genus and species, *Otteryctes winkleri*, from the middle Wasatchian of the Bighorn Basin. The holotype includes nearly complete upper and lower dentitions, with a dental formula of 3.1.3.3 / 3.1.3.3. *Otteryctes winkleri* is similar to the earlier Eocene *Eoryctes melanus* in having ossified tubes marking the course of the stapedia and promontory branches of the internal carotid artery through the middle ear, rather than the smooth promontory found in Paleocene *Palaeoryctes puercensis*. *O. winkleri* differs from *E. melanus* in the structure of P<sub>4</sub>, in lower molar shape, and in being larger. The body weight of *O. winkleri* was about 80 grams, estimated from cranial length (ca. 36 mm), which is about 55% greater than the weight estimated for *E. melanus*.

The phylogeny of palaeoryctines can be approached stratophenetically, cladistically, and stratocladistically. Our cladistic analysis of seven North American palaeoryctine species using 32 morphological characteristics yielded four equally-parsimonious cladograms. A stratocladistic analysis of the same morphological data yielded a better-resolved phylogeny with two overall most-parsimonious phylogenetic trees associated with a single cladogram. This result, which is more congruent with a traditional stratophenetic interpretation, suggests that *Palaeoryctes jepseni* from the late Tiffanian gave rise to *Palaeoryctes punctatus* in the latest Tiffanian or earliest Clarkforkian, and that *P. punctatus* gave rise in turn to a more derived *Eoryctes-Otteryctes* clade in the latest Clarkforkian or early Wasatchian.

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## INTRODUCTION

Palaeoryctidae are a group of insectivorous mammals of uncertain phylogenetic affinities known from early Paleocene through early Eocene times in North America. Palaeoryctine palaeoryctids, the subfamily group of interest here, are thought to have been mole-like burrowing species (Van Valen, 1966), but postcranial remains are few and inadequate to confirm this. Palaeoryctids are distinctive dentally in that they have closely appressed paracones and metacones on the upper molars and somewhat reduced talonids on the lower molars. This configuration has been termed 'zalambdodont' by some authors (e.g., Matthew, 1913; Thewissen and Gingerich, 1989). Asher et al. (2002) suggested, however, that the term should be reserved for those forms in which the metacone on the upper molars and the talonid basin on the lower molars are very reduced or absent, as is seen in extant tenrecs and extinct apternodontid insectivores. The term 'protozalambdodont' (Novacek, 1976) might then be more appropriate in describing the condition seen in palaeoryctids and some other anatomically similar mammalian groups such as extinct Geolabididae (Bloch et al., 1998).

This study reflects many years of collecting in the Clarks Fork and Bighorn basins. Palaeoryctines are rare, but often well preserved when found. Previous reports included description of *Aptoryctes ivyi* (Gingerich, 1982), *Eoryctes melanus* (Thewissen and Gingerich, 1989), and notice in an abstract of the new taxa described and named here (Bloch and Gingerich, 1997).

In this paper we describe a new dentary and a maxillary fragment of *Palaeoryctes punctatus* Van Valen (1966) from the middle Clarkforkian of the Clarks Fork Basin. The dentary was found in a freshwater limestone at UM locality SC-62 (for a discussion of the taphonomy and preparation techniques of freshwater limestones see: Gingerich, 1987; Bloch, 2001; Bloch and Bowen, 2001; Bloch and Boyer, 2001; Bowen and Bloch, 2002). The maxillary fragment is from Holly's Microsite (UM locality SC-188), a mudstone quarry and wash site. These specimens double the known sample of *P. punctatus* and are the most complete specimens recovered from the type area (see Rose, 1981). We name a new species, *Palaeoryctes jepseni*, from the late Tiffanian of the Clarks Fork Basin, based on new specimens from Y2K Quarry that can now be shown to be different from *P. punctatus*. *Palaeoryctes jepseni* is interpreted to include specimens from Princeton and Schaff quarries that were previously referred to *Palaeoryctes* sp. and cf. *Palaeoryctes* sp. by Rose (1981), and to *Palaeoryctes* cf. *P. punctatus* by Gingerich (1982). We describe a new genus and species of early Eocene age, *Ottoryctes winkleri*, based on a partial skull with a nearly complete upper and lower dentition from the middle Wasatchian of the central Bighorn Basin. Finally, we present new hypotheses of phylogeny for North American Paleocene-Eocene Palaeoryctinae based on stratophenetic, cladistic, and stratocladistic analyses of known specimens.

## SYSTEMATIC POSITION AND CLASSIFICATION OF PALAEORYCTIDAE

The systematic position of Palaeoryctidae is uncertain despite decades of study. When *Palaeoryctes* was named, Matthew (1913) followed Gill (1872) in considering it to belong in a section of Insectivora termed Zalambdodonta. Winge (1917) and Simpson (1931) placed *Palaeoryctes* in a family-group Palaeoryctae or Palaeoryctidae, and later Simpson (1945) classified Palaeoryctidae in the superfamily Tenrecoidea, order Insectivora. McDowell (1958) argued for close affinity to *Deltatheridium*. Following this, Van Valen (1966) included the subfamilies Deltatheridiinae, Palaeoryctinae, and Micropternodontinae in Palaeoryctidae, and classified these in the order Deltatheridia. Romer (1966) and Butler (1972) classified Palaeoryctidae in Proteutheria. Butler (1972) removed micropternodontines from Palaeoryctidae, and Butler and Kielan-Jaworowska (1973) removed deltatheridiines. Later McKenna (1975) classified Palaeoryctidae in the order

Kennalestida; Szalay (1977) included Palaeoryctidae in Leptictimorpha; and Novacek (1976), Kielan-Jaworowska (1981), and Bown and Schankler (1982) included Palaeoryctidae in Proteutheria. Gingerich (1982) and Thewissen and Gingerich (1989) classified Palaeoryctidae in Insectivora, and McKenna et al. (1984) placed Palaeoryctidae in Soricomorpha. Other authors have argued, however, that Palaeoryctidae are not directly related to Lipotyphla (including Soricomorpha; e.g., McDowell, 1958; Van Valen, 1966, 1967; Lillegraven, 1969; Szalay, 1977; Butler, 1988).

Palaeoryctinae (= Palaeoryctidae of Kellner and McKenna, 1996, and McKenna and Bell, 1997) has included *Palaeoryctes* with four species (*P. puercensis* Matthew, 1913; *P. punctatus* Van Valen, 1966; *P. minimus* Gheerbrant, 1992; and *P. cruoris* Gunnell, 1994), *Pararyctes* with one species (*P. pattersoni* Van Valen, 1966), *Aptoryctes* with one species (*A. ivyi* Gingerich, 1982), *Eoryctes* with one species (*E. melanus* Thewissen and Gingerich, 1989), and, questionably, *Thelysia* with one species (*T. artemia* Gingerich, 1982). Kellner and McKenna (1996) proposed that *Thelysia* and *Pararyctes* are not palaeoryctids, but rather Pantolestidae and “Eutheria incertae sedis,” respectively. Subsequently, McKenna and Bell (1997) included Palaeoryctidae (sensu stricto), Pantolestidae (including *Thelysia*), and *Pararyctes* in the Order Cimolesta.

In this study we follow a modified version of the subfamily Palaeoryctinae, including species referred to *Aptoryctes*, *Eoryctes*, *Palaeoryctes*, and the new genus *Ottoryctes*, that is similar in its taxonomic composition to the Palaeoryctidae of McKenna and Bell (1997). We do not follow McKenna and Bell in restricting the family Palaeoryctidae to these taxa as we believe, given our current state of phylogenetic resolution, that excluding taxa like *Pararyctes* that appear closely similar will only complicate later phylogenetic studies and classification. We follow Thewissen and Gingerich (1989) in including palaeoryctids in Insectivora (sensu Novacek, 1986) in order to recognize (as they did) a close relationship between taxa included in Palaeoryctidae, Leptictidae, and Lipotyphla. This broad classification is supported by recent phylogenetic hypotheses based on cladistic analyses published by Asher et al. (2002), in which ‘Lipotyphla’ is paraphyletic with respect to a number of fossil taxa, including the palaeoryctids *Eoryctes* and *Pararyctes*.

## LOCALITIES AND BIOSTRATIGRAPHY

Localities yielding specimens studied here are shown in Figure 1. Most University of Michigan localities in the Clarks Fork Basin and vicinity, prefaced SC for Sand Coulee in the following text, are also shown on maps in Rose (1981) and Gingerich and Klitz (1985). Others, prefaced FG, are in the Foster Gulch area in the northern Bighorn Basin. Graybull River localities in the central Bighorn Basin, prefaced GR, are shown on maps in Bown et al. (1994). Biostratigraphic zonation is discussed in Gingerich (1975, 1983, 2001), Rose (1981), Archibald et al. (1987), Lofgren et al. (2004), and Robinson et al. (2004). Stratigraphic levels for specimens from Polecat Bench and vicinity in the Clarks Fork and northern Bighorn basins are provided in Gingerich (2001).

## DENTAL TERMINOLOGY AND MEASUREMENTS

Dental terminology follows Van Valen (1966) and Szalay (1969). All measurements were made using a calibrated ocular micrometer fitted to the lens of a Leica StereoZoom-4 microscope. Length and width of lower teeth were measured parallel and perpendicular to the long axis of the dentary, with the buccal side of the trigonid in an upright position. Length and width of upper teeth were measured parallel and perpendicular to the buccal edge of the tooth. Measurements reported here are maximum tooth dimensions, not distances between interproximal wear facets.

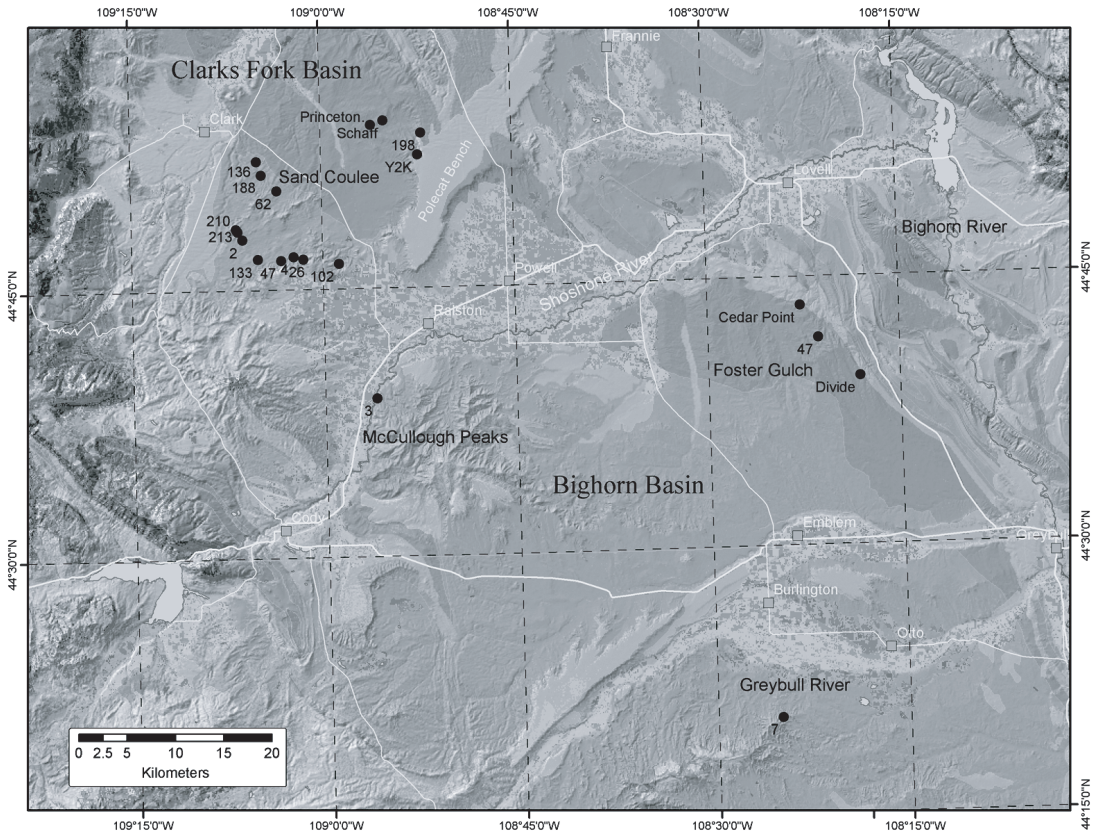


FIG. 1 — Geographic distribution of palaeoryctine specimens studied here, shown on a shaded relief map of the Bighorn and Clarks Fork basins of northwestern Wyoming. Numbered localities are in the Foster Gulch (abbreviated FG), Greybull River (GR), McCullough Peaks (MP), and Sand Coulee (SC) areas, respectively.

#### INSTITUTIONAL ABBREVIATIONS

- AMNH — Division of Paleontology, American Museum of Natural History, New York  
 UM — Museum of Paleontology, University of Michigan, Ann Arbor  
 UW — University of Wyoming, Collection of Fossil Vertebrates, Laramie  
 YPM-PU — Princeton University collection, Yale Peabody Museum, New Haven  
 ZPAL — Institute of Paleobiology, Polish Academy of Sciences, Warsaw

#### SYSTEMATIC PALEONTOLOGY

Superorder INSECTIVORA, sensu Novacek, 1986  
 Order LIPOTYPHILA?  
 Family PALAEORYCTIDAE Winge, 1917  
 Subfamily PALAEORYCTINAE Winge, 1917

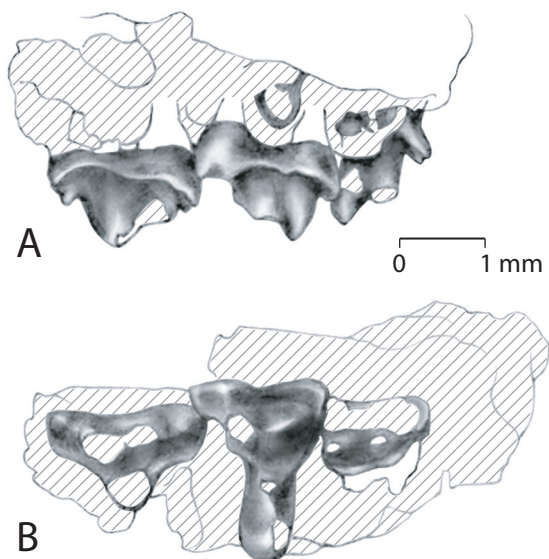


FIG. 2 — Partial upper dentition (UM 77025) of *Palaeoryctes punctatus* from SC-188 (Cf-2) in the Clarks Fork Basin. Drawings show a fragmentary left maxilla with crowns of a broken P<sup>4</sup>, complete M<sup>1</sup>, and a broken M<sup>2</sup> in lateral (A) and occlusal (B) views. Note that the M<sup>1</sup> and M<sup>2</sup> are of similar length.

*Palaeoryctes* Matthew, 1913

*Palaeoryctes punctatus* Van Valen, 1966

Figs. 2-3

*Holotype*.— AMNH 15850, right maxillary fragment with broken M<sup>1-3</sup>; right dentary fragment with broken P<sub>4</sub>-M<sub>2</sub> and intact M<sup>3</sup>; distal end of left humerus, and proximal end of ulna.

*Type locality*.— ‘Blue beds’ at the head of Big Sand Coulee (Van Valen, 1966). Rose (1981: 36) stated that “it now seems probable that this specimen is from ... the vicinity of locality SC-102.” Locality SC-102 is late Clarkforkian (Cf-3) in age.

*Referred specimens*.— Middle Clarkforkian (*Plesiadapis cookei* zone, Cf-2): UM 69232, R dent. M<sub>1</sub>, broken M<sub>2</sub> (SC-136, surface; described in Rose, 1981); 77025, L max. broken P<sup>4</sup>, M<sup>1</sup>, and the buccal edge of a broken M<sup>2</sup> (SC-188, quarry); 82674, L dent. I<sub>1</sub>-C<sub>1</sub>, P<sub>2</sub>, M<sub>1-2</sub> (SC-62, limestone).

*Age and distribution*.— Middle to late Clarkforkian land-mammal age (*Plesiadapis cookei* zone, Cf-2, and *Phenacodus-Ectocion* zone, Cf-3).

*Description and comparison*.— UM 77025 (Fig. 2), a left maxillary fragment, is the only specimen other than the holotype that preserves the morphology of the upper teeth of *Palaeoryctes punctatus*. The buccal half of P<sup>4</sup>, previously unknown for *Palaeoryctes punctatus*, is comparable to that of other palaeoryctids in having a stylocone, a strong parastyle that is transversely wide, and a strong metastyle. The P<sup>4</sup> is longer than M<sup>1</sup> (Table 1). Like the M<sup>1</sup>, the P<sup>4</sup> has a moderate ectoflexus. Interpretation of the lingual aspect of P<sup>4</sup> is difficult. While breaks in this area strongly indicate that the protocone is either partly or completely broken away, it is unclear how far lingually the crown would have extended. It is possible that not much of the crown is missing. In this case, the P<sup>4</sup> of *P. punctatus* would be notably narrower buccolingually than that of any other known palaeoryctid and thus might be a diagnostic characteristic of the species. Alternatively, the protocone could have extended much farther lingually than preserved in the specimen. While it is

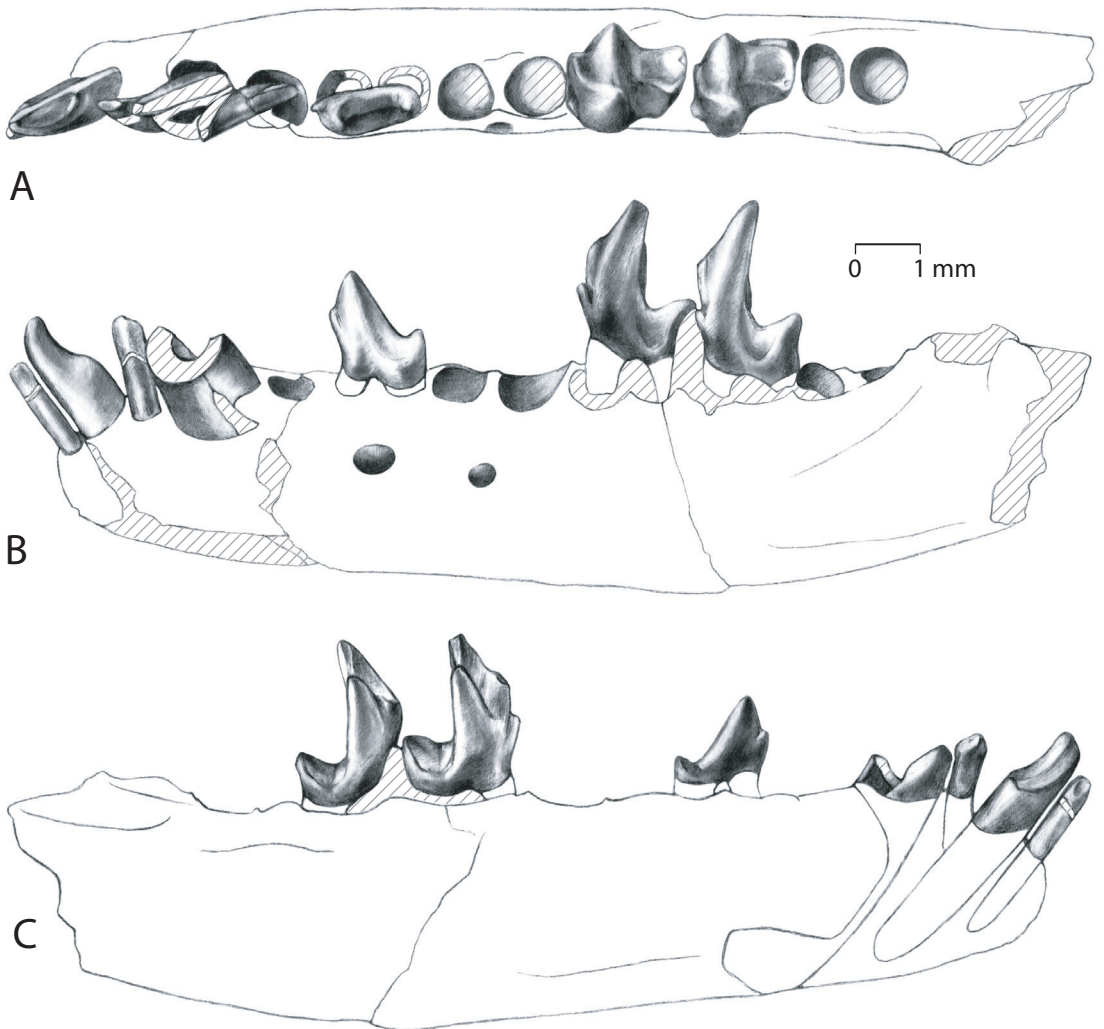


FIG. 3 — Partial lower dentition (UM 82674) of *Palaeoryctes punctatus* from SC-62 (Cf-2) in the Clarks Fork Basin. Drawings show occlusal (A), buccal (B), and lingual (C) views of a left dentary with I<sub>1</sub>-C<sub>1</sub> (broken base of crown), P<sub>3</sub>, and M<sub>1-2</sub>. Note that the postvallid of M<sub>1</sub> is transversely oriented and that the dentary has a mental foramen between the anterior and posterior roots of P<sub>4</sub>.

difficult to see exactly where the specimen is broken (in other words, it looks like a nearly complete crown) this is still likely to be the best interpretation. This interpretation would then be in agreement with the expected morphology of P<sub>4</sub> in *Palaeoryctes* based on comparison of that tooth in other species (e.g., *Palaeoryctes jepseni* n. sp.; see next section).

The size and morphology of M<sup>1-2</sup> are similar in UM 77025 and in the holotype of *P. punctatus*, as far as comparisons can be made in broken specimens, although M<sup>1</sup> in the latter is slightly larger and has a narrower shelf with a more reduced ectoflexus such that the buccal edge of the tooth is almost straight (Van Valen, 1966). M<sup>1</sup> of UM 77025 has a somewhat deeper ectoflexus than that of the holotype, making it more like other species of *Palaeoryctes* in this respect. We attribute the differences to intraspecific variation.

UM 82674 (Fig. 3), a left dentary, is the third, and most complete dentary of *Palaeoryctes punctatus* to be collected from the type area and includes the first known anterior teeth for the



TABLE 1 — Tooth crown and dentary measurements of *Palaeoryctes punctatus*. L, greatest anteroposterior dimension of tooth; W, greatest transverse dimension of tooth; AW, greatest transverse dimension of trigonid; PW, greatest transverse dimension of talonid. Depth of dentary was measured on the buccal side of the dentary below the anterior root of M<sub>1</sub>. Asterisk indicates estimate on a broken or worn specimen. Cf-2 and Cf-3 are zones within the Clarkforkian land-mammal age. All measurements are in mm.

Tooth position	AMNH 15850 (holotype) SC-102 Cf-3	UM 69232 SC-136 Cf-2	UM 77025 SC-188 Cf-2	UM 82674 SC-62 Cf-2
<i>Upper dentition</i>				
P <sup>4</sup> L	—	—	1.78	—
W	—	—	—	—
M <sup>1</sup> L	1.93	—	1.68	—
W	—	—	2.15	—
M <sup>2</sup> L	1.75	—	1.50*	—
W	—	—	—	—
M <sup>3</sup> L	—	—	—	—
W	—	—	—	—
<i>Lower dentition</i>				
P <sub>3</sub> L	—	—	—	1.48
W	—	—	—	0.68
P <sub>4</sub> L	1.43*	—	—	—
W	0.70*	—	—	—
M <sub>1</sub> L	1.98	—	—	1.90
AW	—	—	—	1.35
PW	—	—	—	1.00
M <sub>2</sub> L	1.88*	1.70	—	1.68
AW	—	1.16	—	1.43
PW	—	0.92	—	0.93
M <sub>3</sub> L	1.65	1.60	—	—
AW	—	—	—	—
PW	—	0.86	—	—
<i>Depth of dentary</i>	2.95*	—	—	3.00

species. The I<sub>1</sub> is very small, somewhat procumbent, and weakly spatulate at the tip of the crown. The I<sub>2</sub> is relatively large, procumbent, and caniniform. The I<sub>3</sub> is a small, vertically oriented, peg-like tooth. The canine is broken, but was relatively robust and inclined anteriorly.

The alveolus of P<sub>2</sub> is partly crushed, but this tooth was single-rooted and the sole alveolus is larger than those of P<sub>3</sub>. The anterior roots of P<sub>3</sub> and M<sub>1</sub> are notably smaller than their alveoli. The crown of a double-rooted P<sub>3</sub>, previously unknown for *Palaeoryctes punctatus*, is small, with a high, moderately compressed protoconid and a trenchant heel that culminates in a distinct posterior cusp. It has an anterior cusp about one-third of the way down the anterior flank of the protoconid. The alveolus of a double-rooted P<sub>4</sub> indicates that it held a large tooth, about 1.5 times the length of P<sub>3</sub>.

The lower molars have very high trigonids, low and shelf-like paraconids, and narrow talonids with a high hypoconid. Meaningful comparison of  $M_1$  between UM 82674 and the holotype is hampered by the very damaged nature of the latter. While they are the same length, the trigonid of the holotype appears to be less anteroposteriorly compressed than that of UM 82674. The second molar ( $M_2$ ) of this specimen is similar in size to that of the holotype (as far as comparison is possible) and is nearly identical in size and morphology to that of the only other referred specimen (UM 69232; Rose, 1981). Furthermore, UM 82674 is similar to both Torrejonian *Palaeoryctes puercensis* (Matthew, 1913) and Tiffanian *Palaeoryctes jepseni* n. sp., in having a distinct mental foramen on the buccal side of the dentary below  $P_4$ . The holotype of *P. punctatus* appears to lack a mental foramen below  $P_4$  (Van Valen, 1966), although this is difficult to assess with confidence. These differences could be interpreted as being significant enough to merit specific separation, but we provisionally consider them to be the result of intraspecific variability in *P. punctatus*, pending the discovery of more specimens.

*Discussion*.—Simpson (1937) wrote that “for the purposes of future comparison, it may be recorded that Amer. Mus. No. 15850 is suggestive of *Nyctitherium* but certainly belongs to no described species and is probably of a new genus. It is inadequate as a type and is therefore not named or described” (Simpson, 1937: 4). Undaunted by the quality of the specimen, Van Valen (1966) based a new species *Palaeoryctes punctatus* on AMNH 15850, the only specimen known at the time. Another Clarkforkian specimen (UM 69232), consisting of an  $M_2$  and a fragment of  $M_3$ , was referred to *P. punctatus* by Rose (1981), based on similarity in morphology to the holotype “as far as the two can be compared” (Rose, 1981, p. 36). Subsequently, Tiffanian palaeoryctids of similar size were tentatively referred to cf. *Palaeoryctes* (Rose, 1981) and to *Palaeoryctes* cf. *punctatus* (Gingerich, 1982). This was principally because of the lack of diagnostic characteristics in the holotype of *P. punctatus*. Discovery of more complete specimens of *P. punctatus* from the vicinity of the type locality allows for a more detailed evaluation of the taxonomic assignment of the Tiffanian specimens (see below).

Van Valen (1966) described a number of differences between the holotypes of *Palaeoryctes punctatus* and *P. puercensis*. Relevant to the discussion here, he noted that *P. punctatus* had (compared to *P. puercensis*): (1) about one-third larger body size; (2) a more pronounced and less vertical anterior cingulum on  $M_1$ ; (3) a more pronounced and no less vertical anterior cingulum on  $M_2$ ; (4) a more anteriorly extended paralophid on  $M_{1-2}$ ; (5) a postvallid of  $M_1$  that was slightly oblique (not strictly transverse); (6) a little higher and slightly more reduced paraconid on  $M_2$ ; (7) a relatively deeper mandible; (8) no mental foramen below the posterior root of  $P_4$ ; (9) no space between the ascending ramus and  $M_3$ ; (10) an  $M^1$  metacone more distinct from the paracone; (11) a longer  $M^{1-2}$  relative to length of paracone; and (12) a somewhat narrower stylar area with a reduced ectoflexus.

Contrary to Van Valen’s (1966) diagnosis, based on UM 82674, we note that in both *Palaeoryctes punctatus* and *P. puercensis*: (1) the anterior cingulum on  $M_1$  is similar in size and orientation; (2) the postvallid of  $M_1$  is transverse (not oblique); (3) the dentary has a mental foramen below the posterior root of  $P_4$ ; and (4)  $M^{1-2}$  are of similar length relative to length of the paracone.

The new specimens do support many of Van Valen’s (1966) points about *Palaeoryctes punctatus* (compared to *P. puercensis*), including that: (1) it is about 36% larger (based on  $M_1$  area); (2) the anterior cingulum on  $M_2$  is slightly more pronounced and no less vertical; (3) the paralophid on  $M_{1-2}$  is more anteriorly extended; (4) the paraconid on  $M_2$  is slightly higher and more reduced; (5) the mandible is deeper (49%) relative to body size; (6) there is very little space between the ascending ramus and  $M_3$  (however, note that this character is highly variable between specimens of the closely related species *P. jepseni*; see below); (7) the  $M^1$  metacone is slightly more distinct from the paracone; and (8) there is a somewhat narrower stylar area with a reduced ectoflexus. Thus, while some of Van Valen’s (1966) original diagnostic characteristics are not supported with an increased sample size, *P. punctatus* clearly has features setting it apart from the earlier *P. puercensis*, and should be retained as a separate species.

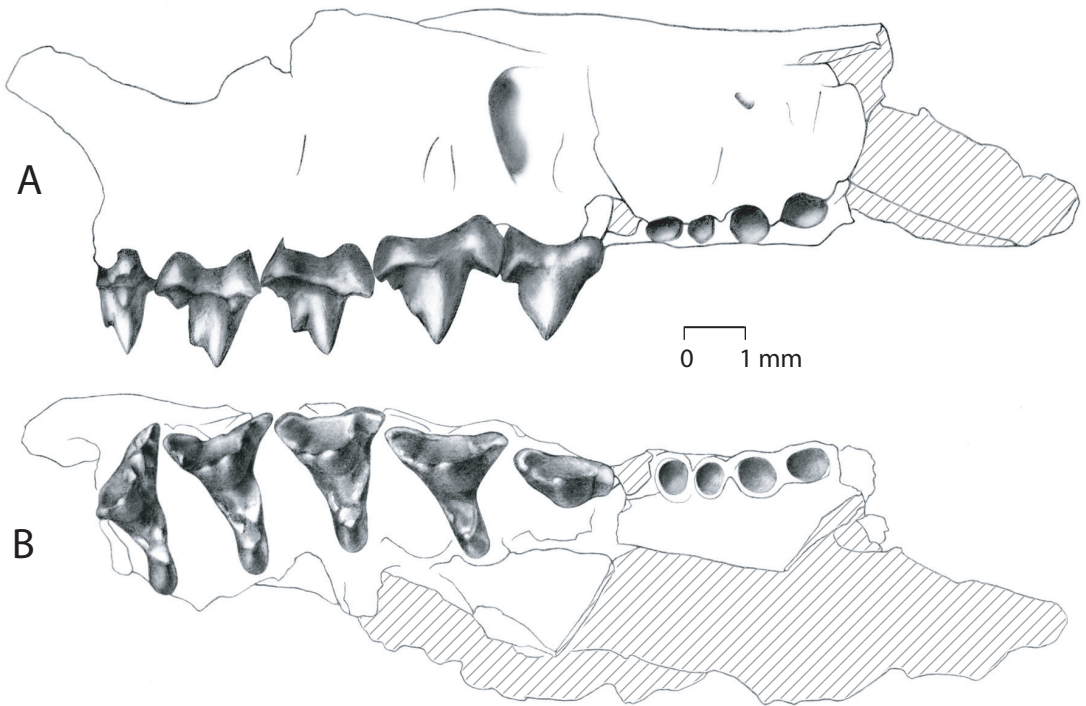


FIG. 4 — Partial upper dentition (UM 109458) of *Palaeoryctes jepseni* from Y2K Quarry (Ti-5) in the Clarks Fork Basin. Drawings show lateral (A) and occlusal (B) views of a left maxilla with alveoli for C<sup>1</sup>-P<sup>2</sup> and complete crowns of P<sup>3</sup>-M<sup>3</sup>. Note the absence of a protocone on P<sup>3</sup>.

***Palaeoryctes jepseni*, new species**

Figs. 4-7

*Palaeoryctes* sp., Rose, 1981, p. 36.

Cf. *Palaeoryctes* sp., Rose, 1981, p. 156-157.

*Palaeoryctes* cf. *punctatus*, Gingerich, 1982, p. 43.

*Holotype*.— UM 109156, right dentary with P<sub>3</sub>-M<sub>3</sub>, and alveoli for C<sub>1</sub> (posterior part) and P<sub>2</sub>.

*Type locality*.— Y2K Quarry within SC-389, Fort Union Formation, west side of Polecat Bench, Clarks Fork Basin, Park County, Wyoming (Secord et al., 2002). Y2K Quarry is late Tiffanian in age (Gingerich, 2001, 2003; Secord, 2002; Secord et al., 2002), in the *Plesiadapis simonsi* lineage zone (Ti-5b).

*Referred specimens*.— **Divide Quarry** (FG-46; middle Tiffanian, Ti-4): UM 83232, R dent. P<sub>3,4</sub>; 83272, R M<sub>2</sub>; 83273, L P<sub>4</sub>; 87043, R dent. M<sub>1</sub>. **Princeton Quarry** (in SC-187, late Tiffanian, Ti-5): YPM-PU 13958, L max. P<sup>3</sup>-M<sup>1</sup>, broken M<sup>2</sup>, R max. with alveolus for P<sup>3</sup>, P<sup>4</sup>-M<sup>2</sup>, broken M<sup>3</sup>; 14122, L max. P<sup>4</sup>-M<sup>3</sup>; 17806, L and R dents., broken I<sub>2</sub>, alveolus for I<sub>3</sub>, broken C<sub>1</sub>-P<sub>2</sub>, complete P<sub>4</sub>-M<sub>3</sub>. **Schaff Quarry** (in SC-421, Ti-5): YPM-PU 19394, L dent. broken C<sub>1</sub>, complete P<sub>2</sub>-M<sub>3</sub>. **Y2K Quarry** (type locality, see above; Ti-5): UM 109319, L max. M<sup>1</sup>; 109420, L M<sub>1</sub>; 109424, R M<sub>3</sub> (badly etched); 109434, L dent. C<sub>1</sub>-M<sub>1</sub>; 109458, R max. P<sup>3</sup>-M<sup>3</sup>, alveoli for C<sup>1</sup>-P<sup>2</sup>; 109506, L dP<sup>4</sup>(?), 109549, L M<sub>2</sub>; 109847, L M<sub>1</sub>.

TABLE 2 — Measurements of upper cheek teeth of *Palaeonyctes jepseni*, new species. Specimens are from Princeton Quarry and Y2K Quarry in the *Plestiadapis fordinatus* zone (T1-5). Abbreviations as in Table 1. All measurements are in mm.

Tooth position	UM 109319 Y2K	UM 109458 Y2K	UM 109506 Y2K	UM 109549 Y2K	UM 109584 Y2K	YPM-PU 13958 Princeton	YPM-PU 14122 Princeton
<i>Upper dentition</i>							
dp4 L	—	—	2.05	—	—	—	—
dp4 W	—	—	2.10	—	—	—	—
P3 L	—	1.70	—	—	—	1.76	—
P3 W	—	0.85	—	—	—	1.09	—
P4 L	—	2.08	—	—	1.90	2.14	1.98
P4 W	—	2.25	—	—	1.98	2.10	2.08
M1 L	1.83	1.88	—	—	—	2.03	1.97
M1 W	2.50	2.45	—	—	—	2.60	2.62
M2 L	—	1.95	—	1.90	—	1.88	1.80
M2 W	—	2.60	—	2.80	—	2.96	2.94
M3 L	—	1.45	—	—	—	1.17*	1.07
M3 W	—	2.85	—	—	—	3.00*	3.12

*Age and distribution.*— Middle and late Tiffanian of western North America (*Plesiadapis churchilli* zone, Ti-4; *Plesiadapis fodinatus* zone, Ti-5; and *P. simonsi* zone, Ti-5b). Species is not known outside the Clarks Fork and northern Bighorn basins.

*Diagnosis.*— Differs from all other species in having a reduced protocone on P<sup>3</sup>. Further differs from Torrejonian *Palaeoryctes puercensis* in having: a larger body size; a more expanded paraconid on P<sub>4</sub>; a larger M<sub>3</sub> relative to the other molars; a P<sup>3</sup> with three roots, distinct anterior and posterior basal cusps, and a distinct metacone; a P<sup>4</sup> protocone that is not sharply connate; an M<sup>1-2</sup> enlarged metastylar area; and a metacone smaller than the paracone. Further differs from Tiffanian *Palaeoryctes cruoris* in having: a smaller body size; P<sub>3,4</sub> protoconid more compressed buccolingually; P<sub>3</sub> talonid unbasined; P<sub>4</sub> talonid basin reduced to narrow groove; lower molars with higher trigonids, and narrower talonids; a P<sup>3</sup> metacone present; a wider P<sup>4</sup>; and M<sup>1-2</sup> with a deeper ectoflexus, and a smaller metacone. Further differs from Clarkforkian *Palaeoryctes punctatus* in having: a more gracile canine; a more vertically oriented and acutely shaped protoconid on P<sub>3</sub>; a deeper notch separating the protoconid and metaconid on the lower molars; and in lacking a mental foramen below P<sub>3</sub>.

*Description.*— The most complete upper dentition of *Palaeoryctes jepseni* is from the type locality of the species, Y2K Quarry. This specimen (UM 109458; Fig. 4) is a right maxilla with P<sup>3</sup>-M<sup>3</sup> and alveoli for C<sup>1</sup>-P<sup>2</sup>. Other specimens preserving aspects of the upper dentition (YPM-PU 14122, YPM-PU 13958) referred to *P. jepseni* are also known from Princeton Quarry (Table 2).

The posterior third of a shallow embrasure pit, which would have occluded with C<sub>1</sub>, is present in the front edge of the maxilla in UM 109458. Behind the embrasure pit are four alveoli interpreted here as having contained the roots of a large double-rooted C<sup>1</sup> and a double rooted P<sup>2</sup>.

P<sup>3</sup> of *Palaeoryctes jepseni* is known from two specimens (UM 109458 and YPM-PU 13958). The crown is continuous with three distinct roots, and seems to be somewhat more variable in width than length (Table 2). The anterior and lingual roots are of equal diameter and considerably smaller than the posterior root. Related to the variable width of the crown, the lingual root in YPM-PU 13958 (Princeton Quarry) projects lingually past the main body of the crown, and is capped by a flat surface. In contrast, the lingual root in UM 109458 (Y2K Quarry) is below the main body of the crown and the lingual wall above it is steep. In the latter only a weak posterolingual cingulum is present, which extends from just above the lingual root posteriorly two-thirds the distance of the posterolingual margin. The lingual root is positioned more buccally in UM 109458. The crown of P<sup>3</sup> is triangular in outline with a tall paracone in the center and a rapidly descending centrocrista extending posteriorly to a variably expressed metacone (Fig. 4). In UM 109458, there is only a slight bulge of enamel in the position of the metacone. The centrocrista is continuous with the metacrista and forms a sharp blade that is separated from a distinct metastyle by a carnassial notch. In YPM-PU 13958, the metacone is much stronger and forms a distinct cusp. Variability in expression of this cusp might be explained, to some degree, by wear. This does not appear to be the case, however, because the teeth of YPM-PU 13958 appear to be more worn (signs of apical wear) than those of UM 109458. In YPM-PU 13958 a moderate cuspule is present on the anterior edge of the buccal margin of P<sup>3</sup>. This area is broken in UM 109458, but one also appears to have been present. A very small cingulum, continuous with the metastyle, is present on the edge of the crown, buccal to the metacone.

P<sup>4</sup> of *Palaeoryctes jepseni* is known from four specimens. All are three-rooted and generally consistent in morphology and size (Table 2). The crown of P<sup>4</sup> is transversely wide with a weak ectoflexus. It is semi-molariform, and has a small metacone closely appressed to a large paracone. In lateral view the P<sup>4</sup> is equal in height to M<sup>1</sup>, and slightly taller than P<sup>3</sup> (Fig. 4A). The metacone in P<sup>4</sup> is variably expressed, and is present only as a bulge of enamel in UM 109458, but as a more distinct cusp in other specimens from both Y2K and Princeton quarries. A distinct carnassial notch is present on a blade-like metacrista, at the base of the metacone. A relatively broad, buccally-sloping, metastylar shelf extends anteriorly away from a small metastyle toward the midline of the crown. A very distinct anteriorly-positioned parastyle is present, with a small ridge sweeping down from its apex to form a tiny, strongly sloping, posterolingual fossa. The crown of P<sup>4</sup> lacks a paraconule, but has a moderate swelling in the position of the metaconule about midway along the

TABLE 3 — Tooth crown and dentary measurements of lower cheek teeth of *Palaeoryctes jepseni*, new species. Specimens are from Divide Quarry in the *Plestiadapis churchhili* zone (Ti-4), and from Princeton Quarry, Schaff Quarry, and Y2K Quarry in the *Plestiadapis fodinatus* zone (Ti-5). Abbreviations as in Figure 1. All measurements are in mm.

Tooth position	UM 83232 Divide Ti-4	UM 83272 Divide Ti-4	UM 83273 Divide Ti-4	UM 87043 Divide Ti-4	UM 109156 (holotype) Y2K Ti-5	UM 109420 Y2K Ti-5	UM 109424 Y2K Ti-5	UM 109434 Y2K Ti-5	UM 109847 Y2K Ti-5	YPM-PU 17806 Princeton Ti-5	YPM-PU 19394 Schaff Ti-5
<i>Lower dentition</i>											
P <sub>2</sub> L	—	—	—	—	—	—	—	1.13	—	—	1.15
W	—	—	—	—	—	—	—	0.60	—	—	0.63
P <sub>3</sub> L	1.48	—	—	—	1.43	—	—	1.60	—	1.53	1.54
W	0.65	—	—	—	0.68	—	—	0.70	—	0.63	0.66
P <sub>4</sub> L	1.90	—	1.70*	—	1.85	—	—	1.85	—	1.80	1.96
W	0.90	—	0.88	—	0.89	—	—	0.88	—	0.85	0.91
M <sub>1</sub> L	—	—	—	2.00*	1.68	1.75*	—	1.75	1.73	1.78	1.64
AW	—	—	—	1.18*	1.20	1.25	—	1.23	1.33	1.35	1.40
PW	—	—	—	1.03	1.00	1.03*	—	1.05	1.08	1.05	—
M <sub>2</sub> L	—	1.80	—	—	1.88	—	—	—	—	1.93	1.90
AW	—	1.41	—	—	1.38	—	—	—	—	1.45	1.35
PW	—	1.10	—	—	0.93	—	—	—	—	1.08	1.05
M <sub>3</sub> L	—	—	—	—	1.75	—	1.47*	—	—	1.84	1.76
AW	—	—	—	—	1.25	—	1.15	—	—	1.38	1.20
PW	—	—	—	—	0.75	—	0.75	—	—	0.88	0.88
<i>Depth of dentary</i>	2.85*	—	—	—	2.50	—	—	2.70	—	2.60	2.50

posterior side of a narrow profossa. The protocone is tall and sharp. There are no pre- or postcingula on P<sup>4</sup>.

M<sup>1</sup> of *Palaoryctes jepseni* is known from four specimens, and is somewhat variable in morphology and size (Table 2). The crown of M<sup>1</sup> has a strong paracone and closely appressed metacone (the two cusps are joined for almost the whole height of the metacone and about two-thirds of the height of the paracone) and is similar in morphology to that of P<sup>4</sup>, although transversely narrower. A distinct carnassial notch is present on a blade-like metacrista, at the base of the metacone on M<sup>1</sup>. From the notch, the metacrista extends posteriorly to a metastyle. The metastylar lobe and blade-like metacrista of M<sup>1</sup> are larger and longer, respectively, than those of P<sup>4</sup>. The stylar shelf is more developed in M<sup>1</sup> than P<sup>4</sup>, with the ectocingulum continuous along the buccal margin of the crown. The ectoflexus in M<sup>1</sup> is deep, compared to P<sup>4</sup>, although the degree of this increased depth is somewhat variable between specimens. A paracrista extends from the base of the paracone and intersects the ectocingulum at a distinct stylocone on M<sup>1</sup>. Anterior to the stylocone is a distinct parastyle that wraps around and articulates with the buccal face of the metastyle of P<sup>4</sup>. The crown of M<sup>1</sup> has a distinct paraconule and metaconule about mid-way along either side of a narrow profossa which culminates lingually in a tall and sharp protocone. No pre- or postcingula are present on the crown of M<sup>1</sup>.

M<sup>2</sup> of *Palaoryctes jepseni* is known from four specimens and, as in M<sup>1</sup>, there is a moderate amount of variability in morphology and size (Table 2). The crown of M<sup>2</sup> is transversely narrower than that of M<sup>1</sup>, and has a distinctly deeper ectoflexus. It is similar in all other details to that of M<sup>1</sup>.

M<sup>3</sup> of *Palaoryctes jepseni* is known from three specimens, all of which are similar in size and morphology (Table 2). The crown of M<sup>3</sup> differs from those of other molars in being transversely narrower and in having a greatly reduced metacone and no metastylar lobe. The parastylar lobe is larger than that of the other molars, but it is more buccally oriented, and it is parallel to the buccolingual dimension of the crown. The paracone of M<sup>3</sup> is lower than those of M<sup>1-2</sup>. While M<sup>3</sup> has a distinct paraconule, it has no metaconule. Otherwise, the crown of M<sup>3</sup> is similar in all other details to that of M<sup>1-2</sup>.

The most complete dentaries of *Palaoryctes jepseni* are from Princeton, Schaff, and Y2K quarries, and more fragmentary dentaries are known from Divide Quarry (Table 3). The type specimen from Y2K Quarry preserves the complete crown of P<sub>3</sub>-M<sub>3</sub> (Fig. 5), while some of the more anterior teeth are known in dentaries from Schaff and Princeton quarries (Figs. 6-7).

No specimen of *Palaoryctes jepseni* preserves I<sub>1</sub>. An alveolus for a large, single-rooted I<sub>2</sub> is, however, preserved in the dentary of *P. jepseni* from Schaff quarry (YPM-PU 19394; Fig. 6A). The crown of I<sub>2</sub> (YPM-PU 17806) is procumbent and caniniform, with a pointed tip and a central anteroposteriorly directed rib bordered medially and laterally by smaller crests. The crown of I<sub>2</sub> terminates posteriorly with a small basal cuspule. An alveolus for a tiny single-rooted I<sub>3</sub> is preserved in YPM-PU 19394 (Fig. 6A), and part of the simple and peg-like crown of I<sub>3</sub> is preserved in YPM-PU 17806.

No specimens preserve a complete crown of the C<sub>1</sub> of *P. jepseni*, but several preserve single roots with partial crowns (Figs. 6-7). The crown of C<sub>1</sub> was probably high and somewhat buccolingually compressed, forming a long and slender caniniform tooth.

The crown of a single-rooted P<sub>2</sub> of *Palaoryctes jepseni* is preserved in two specimens that are nearly identical in comparable morphology and size (Table 3). The P<sub>2</sub> is high crowned (at its apex, equal in height to that of P<sub>3</sub>) and has a low flat talonid heel with an incipient cuspule centrally oriented. While it does have an anterior bulge of enamel, it has no anterior cuspule (Fig. 6).

P<sub>3</sub> of *Palaoryctes jepseni* is preserved in five specimens, all of which are fairly similar in morphology and size (Table 3). The crown of the double-rooted P<sub>3</sub> is short, relative to P<sub>4</sub>, with a high, moderately compressed protoconid and a trenchant heel that culminates in a distinct posterior cusp. It has an anterior cusp about one-third down the anterior flank of the protoconid.

P<sub>4</sub> of *Palaoryctes jepseni* is preserved in six specimens and is moderately variable in morphology and size (Table 3). The crown of the double-rooted P<sub>4</sub> is higher than that of P<sub>3</sub> and about equal to that of M<sub>1</sub>. In general, the morphology of P<sub>3</sub> is similar to that of P<sub>4</sub> with most of the crown consisting of a tall and narrow protoconid. A low, very distinct cusp is present on the anterior face

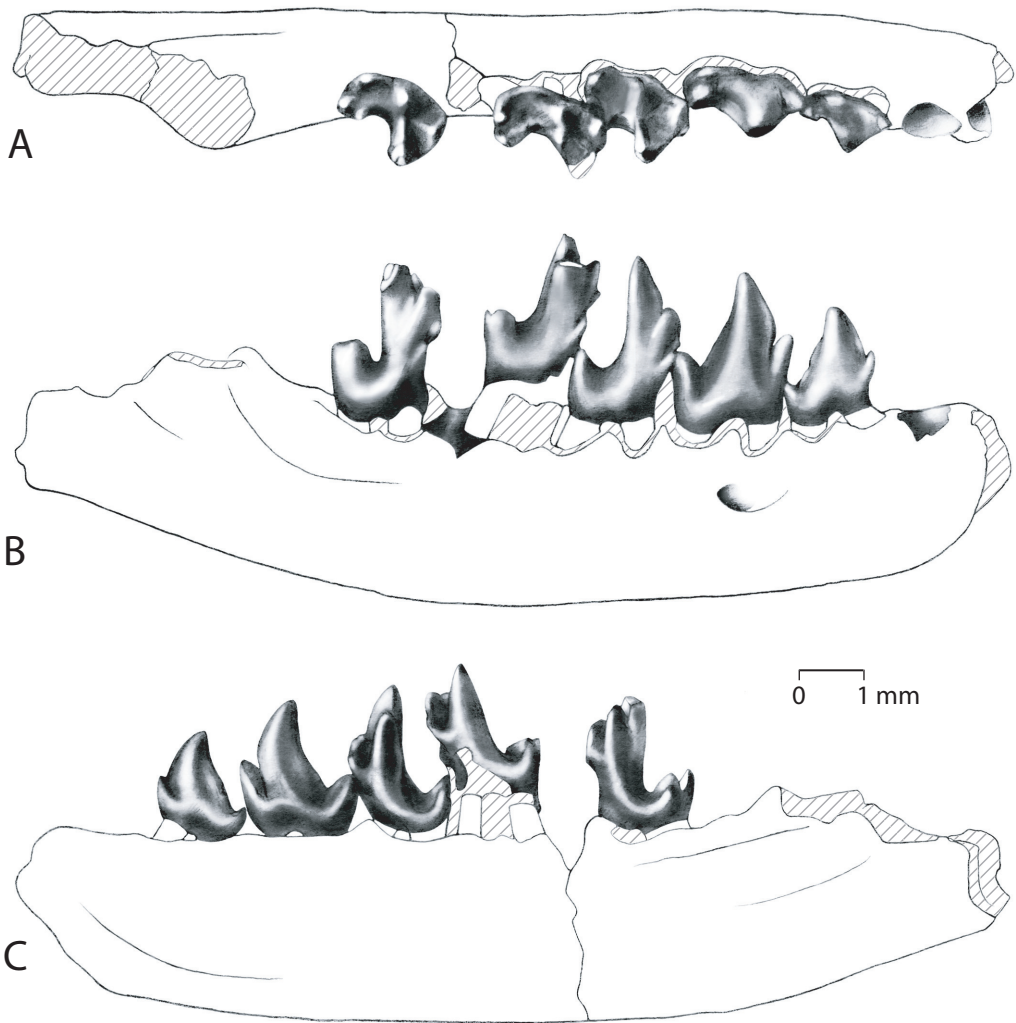


FIG. 5 — Partial lower dentition (UM 109156; holotype) of *Palaeoryctes jepseni* from Y2K Quarry (Ti-5) in the Clarks Fork Basin. Drawings show occlusal (A), buccal (B), and lingual (C) views of a right dentary with an alveolus for a single-rooted  $P_2$  and crowns of  $P_3$ - $M_3$ . Note the vertically oriented and acute protoconid on  $P_3$  and the mental foramen below  $P_4$ .

of the protoconid and a posterior cusp is present at the terminus of an elongated, blade-like, unbasined talonid.

$M_1$  of *Palaeoryctes jepseni* is preserved in seven specimens, all of which are fairly consistent in morphology. The  $M_{1-2}$  are the highest-crowned teeth in the dentary. As is typical for other palaeoryctines for which the tooth is known, the crown of  $M_1$  has a very tall anteroposteriorly-compressed trigonid with a narrow and short talonid. The highest cusp of the trigonid is the protoconid that is connected to a subequal metaconid by a notched protolophid. The paraconid is expanded into a buccolingual loph on the front of the trigonid. A buccal cingulum is present on the anterior face of the trigonid, the apical terminus of which articulates with the tip of the blade-like talonid of  $P_4$ . The narrow talonid of  $M_1$  is separated from the trigonid by a deep hypoflexid. The cristid obliqua intersects the base of the postvallid below the protocristid notch. A narrow,



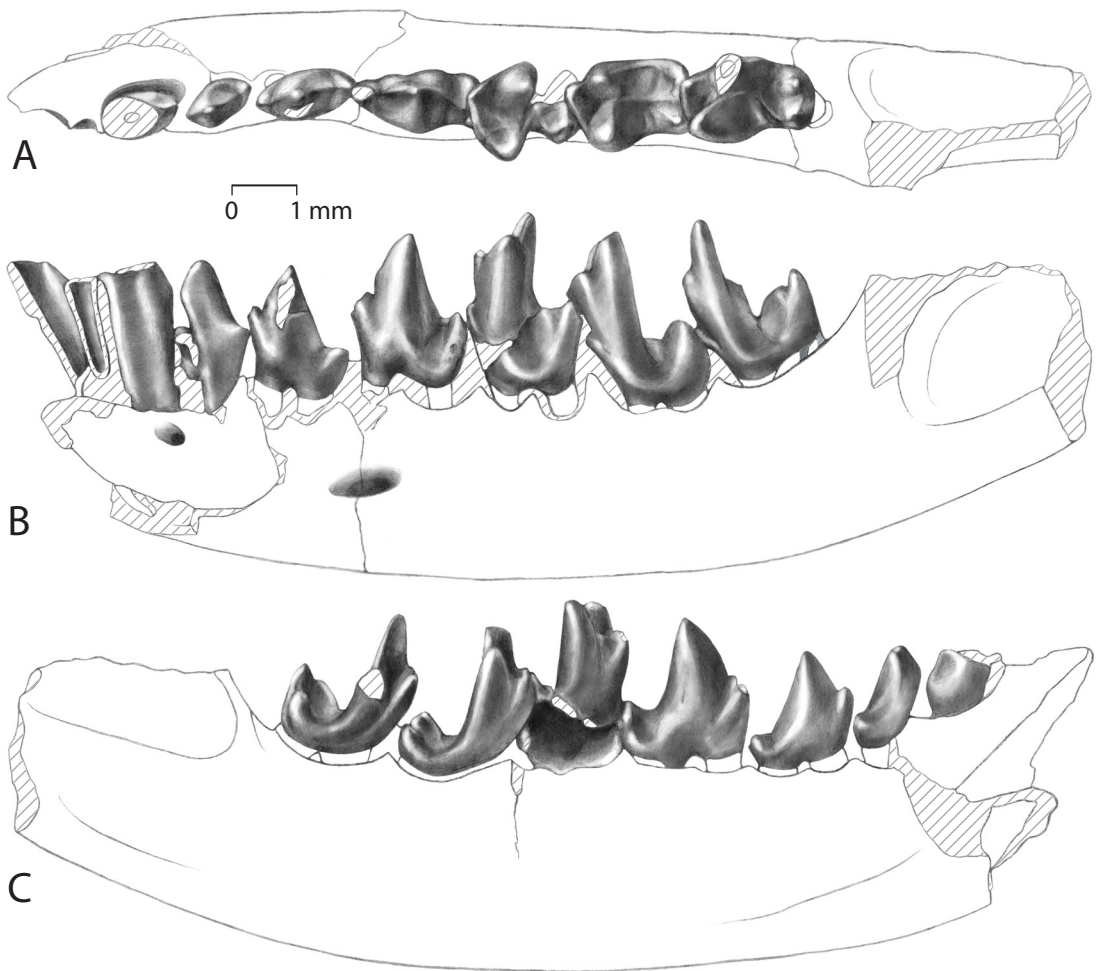


FIG. 6 — Partial lower dentition (YPM-PU 19394) of *Palaeoryctes jepseni* from Schaff Quarry (Ti-5) in the Clarks Fork Basin. Drawings show occlusal (A), buccal (B), and lingual (C) views of a left dentary, with alveoli for  $I_{2,3}$  and crowns of  $C_1$ - $M_3$ . Note the gracile canine (crown partly missing).

buccally-sloping basin descends the occlusal surface of the talonid from closely appressed hypoconid and hypoconulid cusps. The twinned (proximal) hypoconid-hypoconulid cusps are relatively weak and are mostly merged with the sharp rim of the steeply sloping talonid basin. The entoconid is more distinct and positioned lingually on the talonid.

$M_2$  of *Palaeoryctes jepseni* is preserved in four specimens. The morphology of the crown of  $M_2$  is similar in most respects to that of  $M_1$ , but differs in having a slightly more anteroposteriorly-compressed trigonid.

$M_3$  of *Palaeoryctes jepseni* is preserved in four specimens. The trigonid of  $M_3$  is slightly lower than in  $M_2$ , but is otherwise nearly identical. The talonid of  $M_3$  differs from that of  $M_{1,2}$  in having a narrower and more elongate basin with an enlarged hypoconulid that is a greater distance from the hypoconid.

The dentary, known from six specimens, is remarkably uniform in depth (Table 3). Mental foramina are positioned below  $P_4$  and below the  $C_1$ - $P_2$  junction. No mental foramen is present

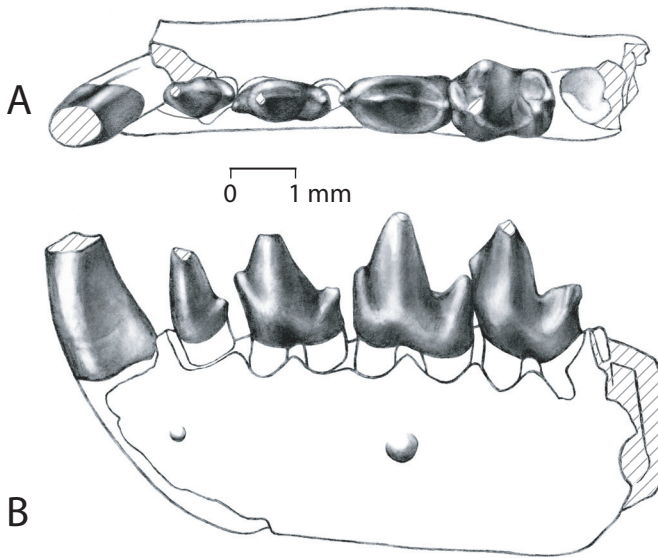


FIG. 7 — Partial lower dentition (UM 109434) of *Palaeoryctes jepseni* from Y2K Quarry (Ti-5) in the Clarks Fork Basin. Drawings show occlusal (A) and buccal (B) views of a left dentary with crowns of  $C_1$ - $M_1$ . Note the moderate-sized canine, the vertically oriented and acute protoconid on  $P_3$ , and the mental foramen below  $P_4$ .

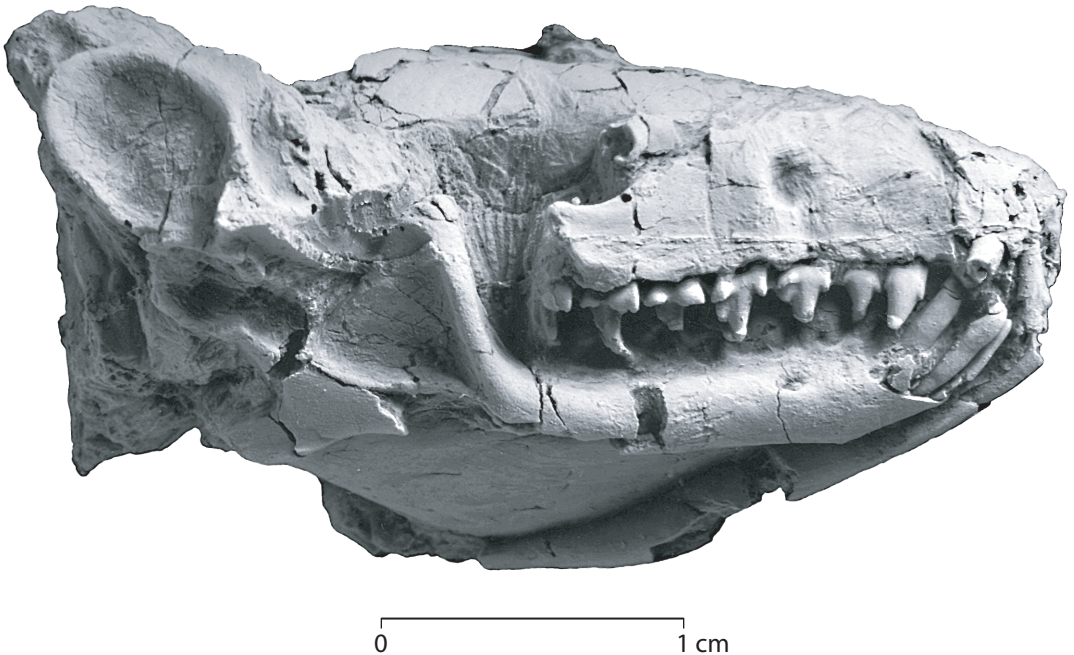


FIG. 8 — Lateral view of the holotype of *Ottoryctes winkleri*, UM 72624, from locality GR-7 (Wa-5; middle Wasatchian) in the Bighorn Basin. The specimen includes much of the skull and both dentaries. When originally found the mandibular teeth were in occlusion with the maxillary teeth, as shown here.

below P<sub>3</sub>. In some specimens (e.g., those from Y2K and Princeton quarries) there is a space between the talonid of M<sub>3</sub> and the ascending ramus, while in others (e.g., YPM-PU 19394 from Schaff Quarry), there is very little space behind the M<sub>3</sub>.

*Discussion.*— New specimens of *Palaeoryctes punctatus* of Clarkforkian age demonstrate that *Palaeoryctes jepseni* n. sp., from the late Tiffanian, is morphologically distinct. It is very possible that, with further study, questionably identified specimens conferred to species of *Palaeoryctes* from Tiffanian localities outside of the Bighorn Basin (e.g., those described by Holtzman, 1978; Winterfeld, 1982; Gunnell, 1994; Erickson, 1999) might also be referable to *P. jepseni*.

### **Ottoryctes**, new genus

*Type species.*— *Ottoryctes winkleri*, new species.

*Included species.*— Genotype only.

*Diagnosis.*— Differs from all other palaeoryctines for which the morphology is known in having distinct anterior and posterior accessory cuspules on C<sup>1</sup>, a very reduced metacone on M<sup>3</sup>, and a distinctly narrow and pointed protoconid on P<sub>4</sub>. Further differs from *Eoryctes* in having a smaller C<sub>1</sub> (Figs. 11-13, 15), an anterior cuspule on P<sub>3</sub>, and more expanded talonids on M<sub>1-3</sub>. Further differs from *Palaeoryctes* (e.g., *P. puercensis*) in having a double-rooted P<sup>2</sup>, a P<sup>3</sup> that lacks a protocone, a C<sub>1</sub> that is larger than P<sub>2</sub>, and a blade-like unbasined talonid on P<sub>4</sub>. Further differs from *Aptoryctes* in having a double-rooted C<sup>1</sup>, a double-rooted P<sup>2</sup>, and a metacone on P<sup>4</sup>.

*Etymology.*— Named for Otto, a townsite on the Graybull River near the type locality, and in turn for Otto Franc von Lichtenstein who founded the Pitchfork Ranch on the Graybull River in 1878. Greek *oryctes* (masc.), digger, a common root for palaeoryctid names.

### **Ottoryctes winkleri**, new species

Figs. 8-14

*Holotype.*— UM 72624: cranium with right C<sup>1</sup>-M<sup>3</sup>, roots of right I<sup>2-3</sup>, left C<sup>1</sup>-M<sup>3</sup>, roots of left I<sup>1-2</sup>, and part of the alveolus for left I<sup>3</sup>; mandible with left C<sub>1</sub>-M<sub>3</sub>, the root of left I<sub>2</sub>, alveolus for left I<sub>3</sub>; right C<sub>1</sub>-M<sub>3</sub>, root of right I<sub>1</sub>, complete I<sub>2</sub>, and alveolus for right I<sub>3</sub>.

*Type locality.*— University of Michigan locality GR-7 in the Willwood Formation of the northern Bighorn Basin, NE 1/4, Section 5, T50N, R96W, Bighorn County, Wyoming.

*Age and distribution.*— Middle Wasatchian land-mammal age (Wa-5; early Eocene). Species is known only from the Bighorn Basin, Wyoming.

*Diagnosis.*— As for genus.

*Etymology.*— Named for Dr. Dale A. Winkler who found the type specimen, in recognition of his many contributions to vertebrate paleontology.

*Description.*— The holotype and only known specimen of *Ottoryctes winkleri* includes much of the skull and both dentaries (Figs. 8-14). When originally found, the dentaries were in occlusion with the maxillary teeth (Fig. 8). They were removed during preparation to expose the crowns of the teeth (Figs. 9, 11-13). We interpret the dental formula as 3.1.3.3/3.1.3.3. Measurements of preserved teeth are listed in Table 4.

The skull is about 36 mm long, giving *Ottoryctes winkleri* an estimated body mass of 80 g, which is about 55% larger than that of *E. melanus* (skull length ca. 32 mm; estimated body mass ca. 51 g; Thewissen and Gingerich, 1989). In most details, the skull of *Ottoryctes* is similar to that of *Eoryctes* described by Thewissen and Gingerich (1989) and the cranial descriptions below are based on that study.

The dorsal surface of the cranium is similar to that of *Eoryctes* in having a single sagittal crest on the midline and in lacking complete zygomatic arches (as far as can be determined). As in *Eoryctes*, the tympanic cavity of *Ottoryctes* is enlarged, although it does not appear to have extended as far rostrally. Also like the cranium of *Eoryctes*, a large epitympanic recess is present posterior to the mandibular fossa.

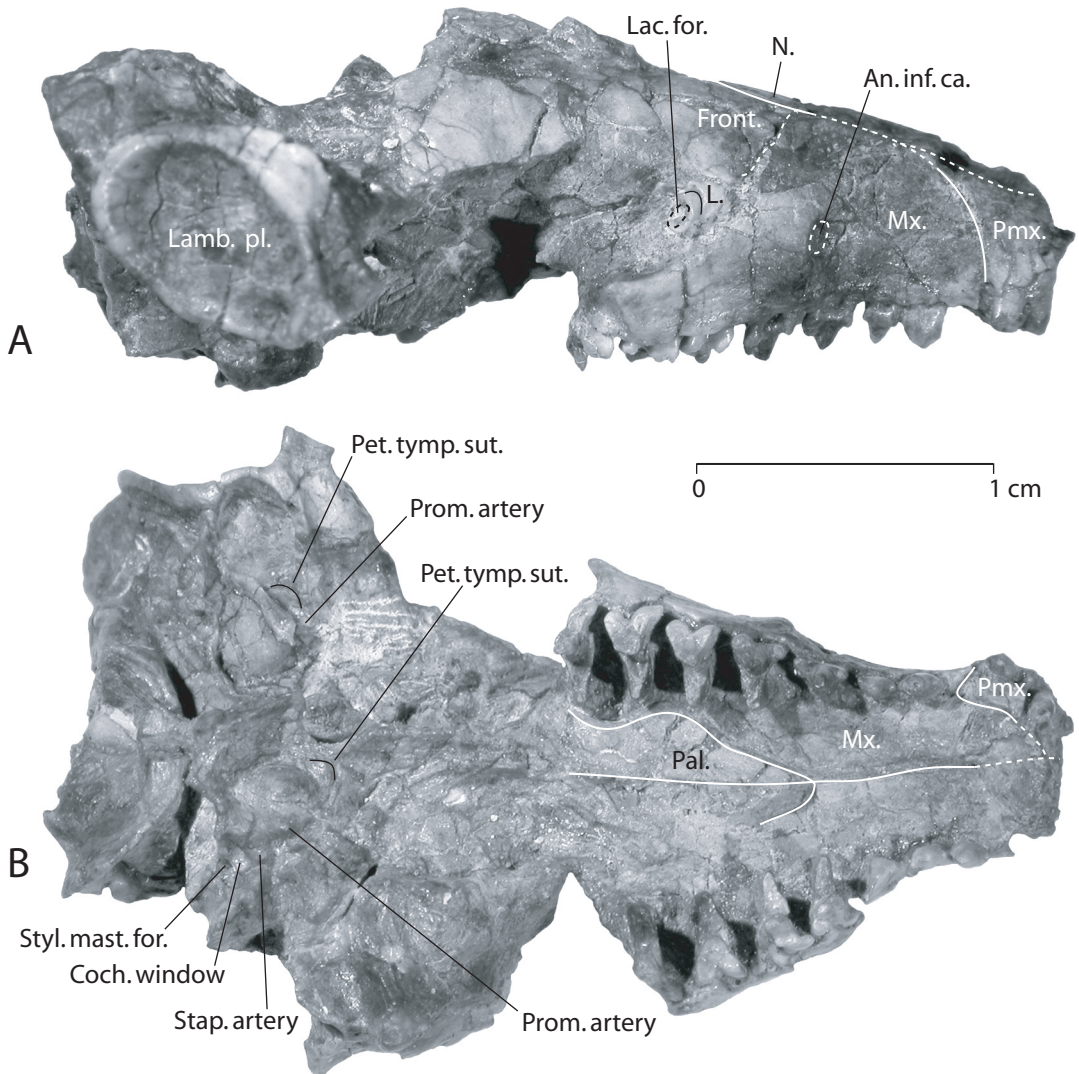


FIG. 9 — Skull of the holotype of *Ottoryctes winkleri*, UM 72624, from locality GR-7 (Wa-5; middle Wasatchian) in the Bighorn Basin. Labeled photographs in right lateral (A) and ventral (B) views. Abbreviations: *An. inf. ca.*, anterior opening of the infraorbital canal; *Coch. window*, cochlear window; *Front.*, frontal; *Lac. for.*, lacrimal foramen; *Lamb. pl.*, lambdoidal plate of squamosal; *Mx.*, maxilla; *N.*, nasal; *Pal.*, palatine; *Pet. tym. sut.*, possible suture between the petrosal and tympanic (see discussion in Thewissen and Gingerich, 1989); *Pmx.*, premaxilla; *Pal.*, palatine; *Prom. artery*, canal for the promontorial branch of the internal carotid artery; *Stap. artery*, canal for the stapedial branch of the internal carotid artery; *Styl. mast. for.*, stylomastoid foramen.

The posterior tips are the only part of the nasals preserved in UM 72624, but it is clear that they were similar to those of *Eoryctes* in that they tapered posteriorly, had a broad contact with the frontal, and no contact with the lacrimal. For the most part, the frontal and parietal of UM 72624 are either badly broken or missing, although a small portion of the frontal-parietal suture appears to be preserved in the middle of the left orbit, indicating that it would have been in a similar position to that of *Eoryctes*.

TABLE 4 — Tooth crown and dentary measurements of *Ottoryctes winkleri*, UM 72624 (holotype), from locality GR-7 of middle Wasatchian age (Wa-5) in the central Bighorn Basin. Abbreviations as in Table 1. All measurements are in mm. Measurements of some anterior teeth are given in the text.

Tooth position	Left side			Right side		
	L	W/AW	PW	L	W/AW	PW
<i>Upper dentition</i>						
P <sup>2</sup>	1.41	0.79	—	1.36	0.73	—
P <sup>3</sup>	1.93	1.36	—	1.96	1.31	—
P <sup>4</sup>	1.94	2.76	—	2.02	2.61	—
M <sup>1</sup>	—	2.94	—	2.00	2.88	—
M <sup>2</sup>	—	3.15	—	2.04	3.40	—
M <sup>3</sup>	1.56	—	—	1.43	—	—
<i>Lower dentition</i>						
P <sub>2</sub>	1.13	0.68	—	1.23	0.76	—
P <sub>3</sub>	1.86	0.92	—	1.82	0.92	—
P <sub>4</sub>	2.04	1.04	—	2.17	1.16	—
M <sub>1</sub>	2.14	1.60	1.35	2.06	1.71	1.48
M <sub>2</sub>	1.92	1.90	1.45	2.00	1.91	1.44
M <sub>3</sub>	2.26	1.92	1.11	2.15	1.94	1.08
<i>Depth of dentary</i>	3.16			3.15		

The maxilla contacts the premaxilla anteriorly, and the nasal, frontal, and lacrimal bones posteriorly (Fig. 9A). As is the case in *Eoryctes*, the maxillary-frontal suture runs medio-orally from the lacrimal to the nasal. The infraorbital canal, as in *Eoryctes*, runs from above P<sup>4</sup> to above M<sup>2</sup> and is relatively large anteriorly, with a height of 1.9 mm and a width of 1.1 mm. The zygomatic process is very small, and the zygomatic arch would probably have been incomplete, much the same as those of *Eoryctes*. In palatal view (Fig. 9B), the maxilla contacts the premaxilla anteriorly and the palatine posteriorly. As in *Eoryctes*, the palatine extends anteriorly as far as P<sup>3</sup>. The lacrimal foramen is well preserved. The lacrimal clearly would have contacted both the frontal and maxillary bones, although the boundaries of these contacts are somewhat obscured by breaks in the specimen.

The squamosal of *Ottoryctes* is dominated in lateral view by a very large lambdoid plate (Fig. 9A). This has also been noted in apternodontid insectivores (Asher et al., 2002) and in *Eoryctes* (Thewissen and Gingerich, 1989).

The promontorium of the petrosal is large and rounded, with bony tubes for the promontory and stapedial branches of the internal carotid artery present on its posterolateral side (Fig. 9B), as in *Eoryctes* (Thewissen and Gingerich, 1989). This is unlike the condition in *Palaeryctes puercensis*, which has a smooth promontory.

C<sup>1</sup>-M<sup>3</sup> and the roots of I<sup>2-3</sup> are preserved on the right side of UM 72624, while C<sup>1</sup>-M<sup>3</sup>, the roots of I<sup>1-2</sup>, and part of the alveolus for I<sup>3</sup> are preserved on the left side (Figs. 10-11). A fragment of the root of what we interpret to be the left I<sup>1</sup> is displaced and situated anterolingual to the root of the left I<sup>2</sup>. The I<sup>1</sup> root was about 0.56 mm long and 0.42 mm wide. The root of the right I<sup>2</sup> is twisted and slightly displaced anteriorly (as a result of posthumous deformation). I<sup>2</sup> was distinctly larger than I<sup>1</sup>, about 0.95 mm long and 0.73 mm wide. The left I<sup>2</sup> is also displaced anteriorly, and its buccal side is sheared away, exposing the pulp cavity. The root of the right I<sup>3</sup> is somewhat larger than the other incisors and is about 1.13 mm long and 1.04 mm wide. The I<sup>3</sup> has been lost from the left side of the premaxilla as the result of breakage and distortion in this part of the specimen. Part

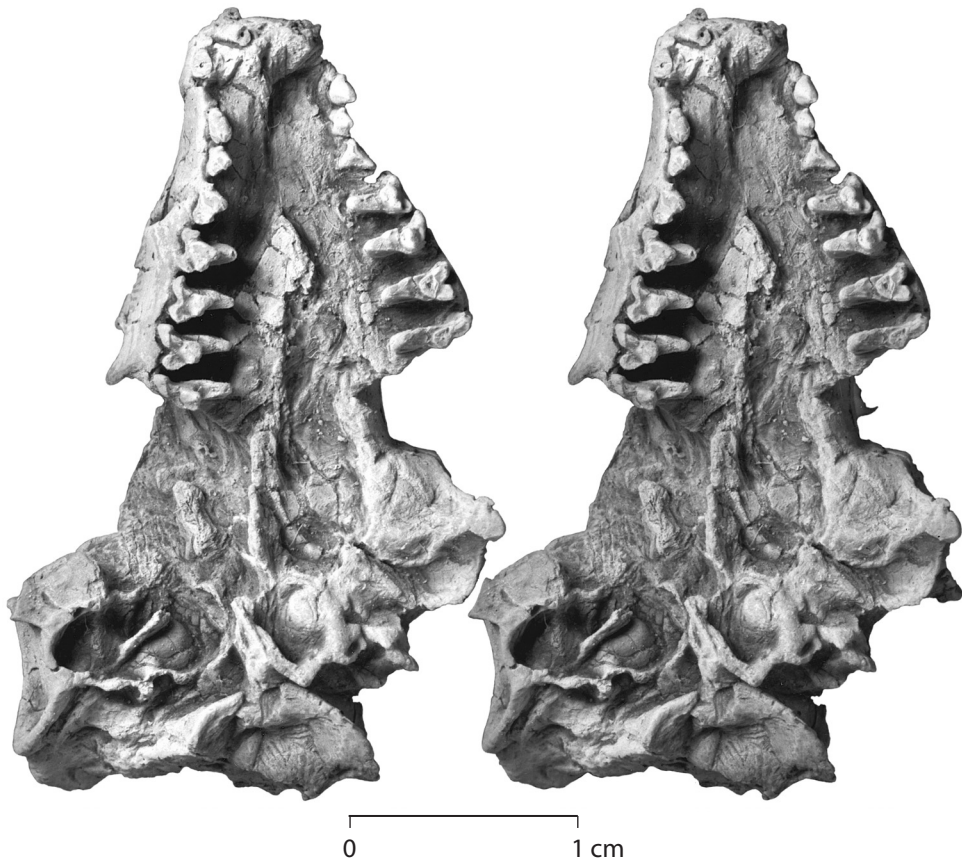


FIG. 10 — Stereophotograph of the palate and basicranium of *Ottoryctes winkleri* (UM 72624; holotype) from locality GR-7 (Wa-5; middle Wasatchian) in the Bighorn Basin. Roots of I<sup>2-3</sup> and crowns of C<sup>1-M3</sup> are preserved on the right side; roots of I<sup>1-2</sup>, part of the alveolus for I<sup>3</sup>, and crowns of C<sup>1-M3</sup> are preserved on the left side.

of what we interpret as the alveolus for the left I<sup>3</sup> is visible in lateral view. While the crown of I<sup>3</sup> has not been preserved, the tooth appears to have had a simple, peg-like morphology with an oval cross-section.

C<sup>1</sup> is complete on both the right and left sides of the holotype. The C<sup>1</sup> is large with two roots which are parallel and closely appressed. The C<sup>1</sup> measures 1.4 mm in length and 0.9 mm in width on the right side, and 1.5 mm in length and 0.8 mm in width on the left side.

P<sup>2</sup> is complete on both the right and left sides of the holotype. P<sup>2</sup> is similar in morphology to C<sup>1</sup>, although it is somewhat shorter. The P<sup>2</sup> is double-rooted with distinct anterior and posterior accessory cuspules.

Right P<sup>3</sup> is complete but the left P<sup>3</sup> is damaged, with the buccal side sheared and missing. The crown of P<sup>3</sup> is very similar to that described for *Eoryctes melanus*. It has no protocone but does have a lingual bulge at the base of the crown that covers the lingual root. The paracone is rounded anteriorly and has a sharp edge posteriorly, a small parastyle, a small posterior cuspule, and a cingulum that is present only on the posterolabial side. *Ottoryctes winkleri* has a large metacone closely appressed to a somewhat larger paracone and a small anterior cuspule preserved on the P<sup>3</sup>. This morphology cannot be compared to *E. melanus* because of damage to the holotype.

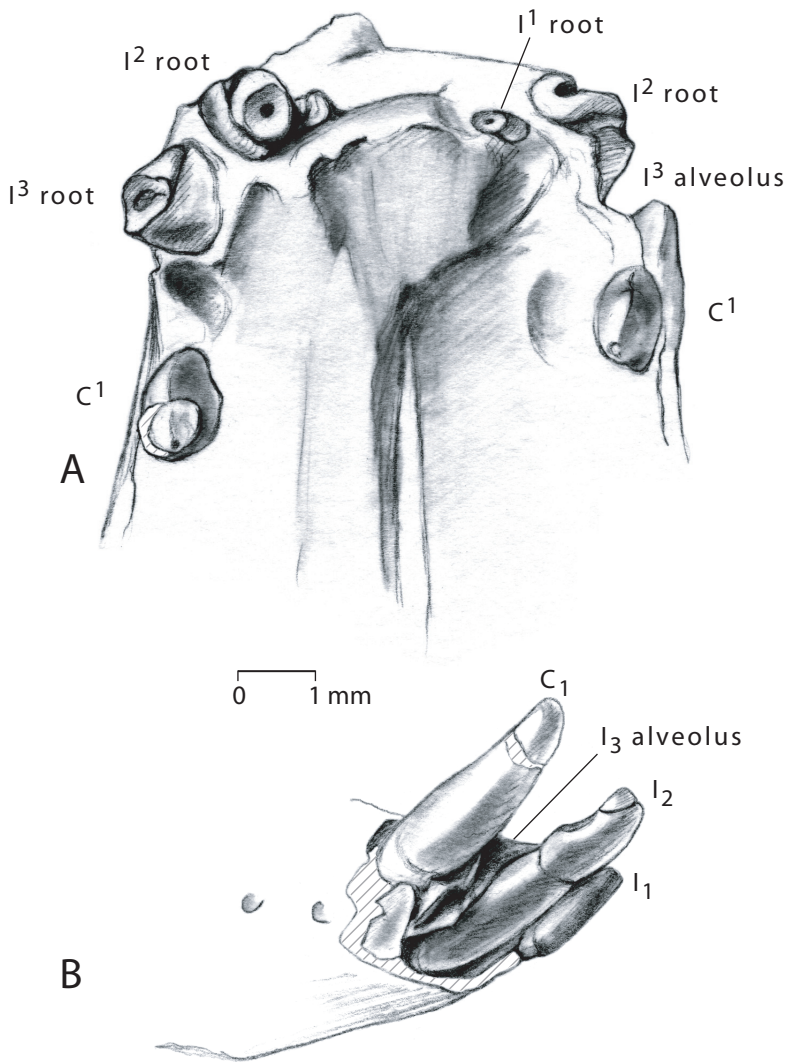


FIG. 11 — Palatal view of the anterior part of the skull (A) and buccal view of the anterior part of the right mandible (B) of *Ottoryctes winkleri* (UM 72624; holotype) from locality GR-7 (Wa-5; middle Wasatchian) in the Bighorn Basin.

Right P<sup>4</sup> in the holotype is slightly damaged, with a fragment missing from the lingual face of the protocone. The left P<sup>4</sup> is complete, with the paracone and metacone moderately worn. The P<sup>4</sup> is very molariform and has a large metacone closely appressed to the paracone. It lacks conules and a stylocone, has a strong protocone which is lower than the paracone, lacks lingual cingula, has a strong parastyle, is transversely wide, has a strong metastyle, and is not inflated. In lateral view the P<sup>4</sup> is equal in height to M<sup>1</sup> and slightly taller than P<sup>3</sup>. The ectoflexus is strong and P<sup>4</sup> has a narrow profossa.

The parastyle of the right M<sup>1</sup> in the holotype is slightly damaged and the metastyle is damaged on the left M<sup>1</sup>. The paracone and metacone are moderately worn on the left M<sup>1</sup>. The M<sup>1</sup> has a very deep ectoflexus, a wide styler shelf at the labial corner that virtually disappears in the middle, a parastylar area that forms a large hook and has a prominent parastyle and a weak stylocone, and a large and rounded metastylar lobe with no mesostyle or metastyle. The paracone is large and high, situated centrally on the labial half of M<sup>1</sup>. The metacone is subequal and closely appressed to the

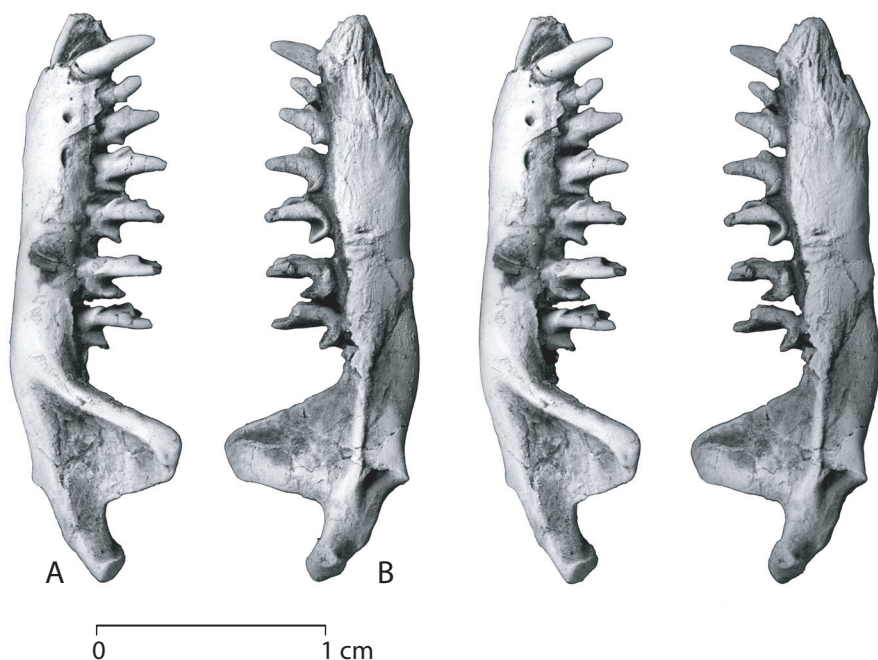


FIG. 12 — Stereophotographs showing buccal (A), and lingual (B) views of the left dentary of *Ottoryctes winkleri* (UM 72624; holotype) from locality GR-7 (Wa-5; middle Wasatchian) in the Bighorn Basin. Left dentary includes the root of I<sub>2</sub>, and the crowns of C<sub>1</sub>-P<sub>3</sub>, P<sub>4</sub>-M<sub>3</sub>. I<sub>1</sub> and I<sub>3</sub> are missing, but the alveolus for I<sub>3</sub> is preserved.

paracone. The M<sup>1</sup> has a very high protocone, a narrow profossa, a weak postparaconular crista with a remnant paraconule, no metaconule, a postprotocrista that is lower than the preprotocrista, a faint precingulum, and a moderate postcingulum.

The parastyle of the right M<sup>2</sup> is damaged, but the left M<sup>2</sup> is complete. The paracone and metacone are moderately worn on the right M<sup>2</sup> and heavily worn on the left M<sup>2</sup>. The morphology of M<sup>2</sup> is very similar to that of M<sup>1</sup>, although it has a deeper ectoflexus.

Both the right and left M<sup>3</sup> are complete. The paracone and metacone are heavily worn on the left M<sup>3</sup>. The morphology of M<sup>3</sup> differs from that of M<sup>1-2</sup> only in lacking a metastylar area. The protocone of M<sup>3</sup> is high and the metacone is very reduced. M<sup>3</sup> is similar in size to M<sup>1</sup>.

The mandibular symphysis of the dentary (Figs. 12-14) reaches as far posteriorly as P<sub>3</sub>, and mental foramina are situated below P<sub>4</sub>, P<sub>3</sub>, and the P<sub>2</sub>-C<sub>1</sub> junction. The root of I<sub>2</sub>, C<sub>1</sub>-P<sub>3</sub>, P<sub>4</sub>-M<sub>3</sub> are preserved in the left mandible. The trigonid of P<sub>4</sub> was lost sometime after its original illustration. The I<sub>1</sub> and I<sub>3</sub> are missing, but the alveolus for I<sub>3</sub> is preserved. The root of I<sub>1</sub>, crown of I<sub>2</sub>, alveolus for I<sub>3</sub>, and crowns of C<sub>1</sub>-M<sub>3</sub> are preserved in the right mandible (Fig. 13).

I<sub>1</sub> is a very small tooth preserved on the most anterior part of the right dentary. The I<sub>1</sub> measures about 0.49 mm in length and 0.41 mm in width on the right side of the holotype.

The crown of I<sub>2</sub> is broken on the left side and complete on the right side. The I<sub>2</sub> is larger than I<sub>1</sub> and I<sub>3</sub>, and is semi-procumbent. The I<sub>2</sub> is pointed at the tip and has a central anteroposteriorly directed rib that is bordered medially and laterally by smaller crests. The crown terminates posteriorly with a small basal cuspule. The I<sub>2</sub> measures 1.07 mm in length and 0.74 mm in width on the left side, and 1.03 mm and 0.70 mm in width on the right side.

I<sub>3</sub> is missing in both the left and right mandibles of the holotype, but the alveoli are present in both mandibles. The I<sub>3</sub> was smaller than I<sub>2</sub> and larger than I<sub>1</sub>, based on the relative sizes of alveoli.



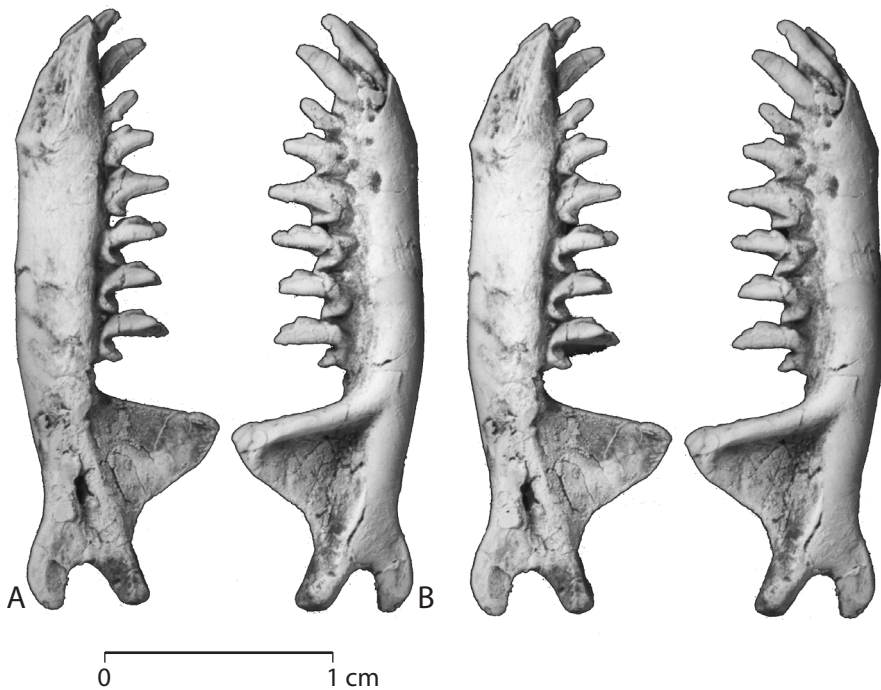


FIG. 13 — Stereophotographs showing lingual (A), and buccal (B) views of the right dentary of *Ottoryctes winkleri* (UM 72624; holotype) from locality GR-7 (Wa-5; middle Wasatchian) in the Bighorn Basin. Right dentary includes the root of I<sub>1</sub>, the crown of I<sub>2</sub>, an alveolus for I<sub>3</sub>, and the crowns of C<sub>1</sub>-P<sub>3</sub>, P<sub>4</sub>-M<sub>3</sub>.

C<sub>1</sub> is complete in both the left and right mandibles of the holotype. The C<sub>1</sub> is single-rooted, semiprocumbent, and larger than P<sub>2</sub>. C<sub>1</sub> measures 1.16 mm in length and 1.09 mm in width on the left side, and 1.23 mm in length and 1.00 mm in width on the right side.

P<sub>2</sub> is complete in both the left and right mandibles of the holotype. The P<sub>2</sub> is high crowned with a low flat talonid heel that has an incipient, centrally oriented cusplule, and is single-rooted with no anterior cusplule.

P<sub>3</sub> is complete in both the left and right mandibles of the holotype. It is smaller than C<sub>1</sub>, has a high protoconid, has an anterior cusp about half way down the anterior flank of the protoconid, and has a distinct posterior cusp that forms an unbasined talonid blade. The P<sub>3</sub> is moderately compressed and double-rooted.

P<sub>4</sub> in the left mandible was broken sometime after its original illustration and the trigonid was lost. The P<sub>4</sub> in the right mandible is complete. The P<sub>4</sub> is higher than the P<sub>3</sub> and has a tall and narrow protoconid. The talonid is blade-like and unbasined. On the trigonid a low anterior bulge or incipient cusplule is present on the anterior face of the protoconid.

M<sub>1-3</sub> are complete in both dentaries. As is typical for Palaeoryctinae, the lower molars have very tall trigonids with acute cusps. They have a high protoconid connected to the metaconid by a notched protolophid. The cristid obliqua is moderate on M<sub>1</sub> and weak on M<sub>2-3</sub>. The M<sub>1-3</sub> have expanded talonids with weak talonid cusps.

*Comparisons.*— The most important differences between *Ottoryctes winkleri* and other palaeoryctines are given in the diagnosis. Further more subtle differences that may also be of importance are listed here.

*Ottoryctes winkleri* differs from *Eoryctes melanus* in having: (1) M<sup>1</sup> with a stylocone and faint pre- and postcingula (rather than no pre- or postcingula); (2) P<sub>4</sub> with a weaker anterior cusplule situated much lower on the anterior face of the protoconid; and (3) M<sub>1-3</sub> with less distinct cusps.

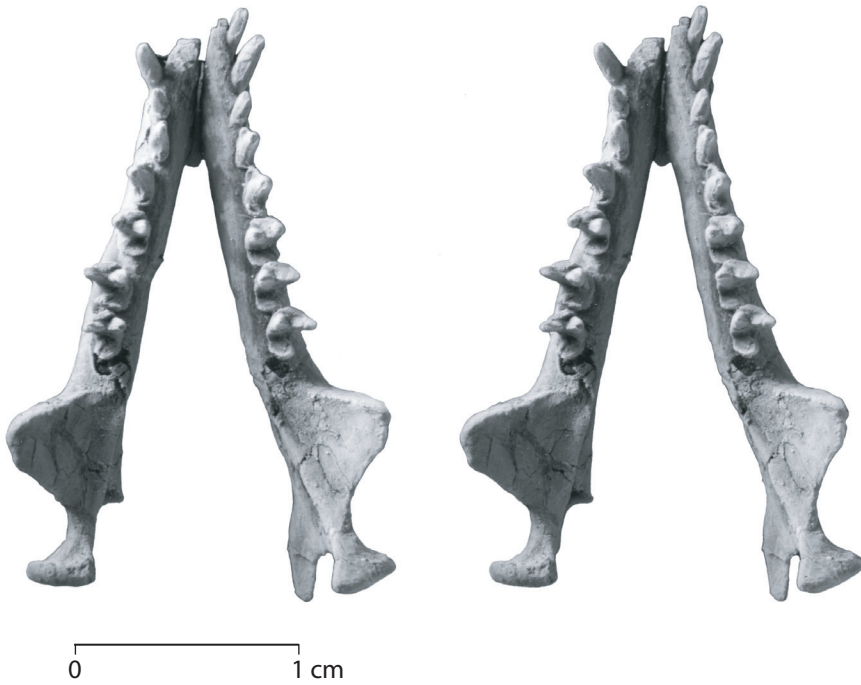


FIG. 14 — Stereophotograph showing occlusal view of the left and right dentaries of *Ottoryctes winkleri* (UM 72624; holotype) from locality GR-7 (Wa-5; middle Wasatchian) in the Bighorn Basin. The root of I<sub>2</sub>, and the crowns of C<sub>1</sub>-P<sub>3</sub>, P<sub>4</sub>-M<sub>3</sub> are preserved on the left dentary. I<sub>1</sub> and I<sub>3</sub> are missing, but the alveolus for I<sub>3</sub> is preserved. The root of I<sub>1</sub>, crown of I<sub>2</sub>, alveolus for I<sub>3</sub>, and crowns of C<sub>1</sub>-M<sub>3</sub> are preserved on the right dentary.

*Ottoryctes winkleri* differs from *Palaeoryctes puercensis* in having: (1) a P<sup>2</sup> with distinct anterior and posterior accessory cusps; (2) P<sup>3</sup> with an anterior cusps and a small metacone and associated posterolingual cingulum; (3) P<sup>4</sup> with a stronger parastyle and a strong ectoflexus; (4) M<sup>1</sup> with a deeper ectoflexus, weaker stylocone, large and rounded metastylar lobe (rather than a more blade-like metastylar area), larger metacone, weaker paraconule, and faint pre- and postcingula (rather than no pre- or postcingula); (5) P<sup>2</sup> with a low, flat, talonid heel that has an incipient centrally oriented cusps (rather than a small trenchant talonid heel); and (6) P<sup>3</sup> with a distinct anterior cusps about half-way down the flank of the protoconid (rather than just an anterior bulge).

*Ottoryctes winkleri* differs from *Palaeoryctes punctatus* in having an M<sup>1</sup> with: (1) a much deeper ectoflexus; (2) a weaker stylocone; (3) a large and rounded metastylar lobe; (4) a larger metacone; (5) a weaker paraconule; (6) a lower postprotocrista relative to the preprotocrista; and (7) faint pre- and a postcingula (rather than no pre- and postcingula).

*Ottoryctes winkleri* differs from *Palaeoryctes cruoris* in having: (1) P<sup>4</sup> equal in height to M<sup>1</sup> and slightly taller than P<sup>3</sup> (rather than higher than M<sup>1</sup> and P<sup>3</sup>) in lateral view; (2) M<sup>1</sup> with a much deeper ectoflexus, a narrower stylocone, a weaker stylocone, a large and rounded metastylar lobe, no metaconule, a lower postprotocrista relative to the preprotocrista, and faint pre- and postcingula; and (3) P<sup>4</sup> with a higher crown than P<sup>3</sup> (rather than of similar height), a much weaker anterior cusps, and a blade-like unbasined talonid.

*Ottoryctes winkleri* differs from *Aptoryctes ivyi* in having: (1) P<sup>2</sup> with distinct anterior and posterior accessory cusps; (2) P<sup>4</sup> with a stronger parastyle, a much less inflated crown, a crown

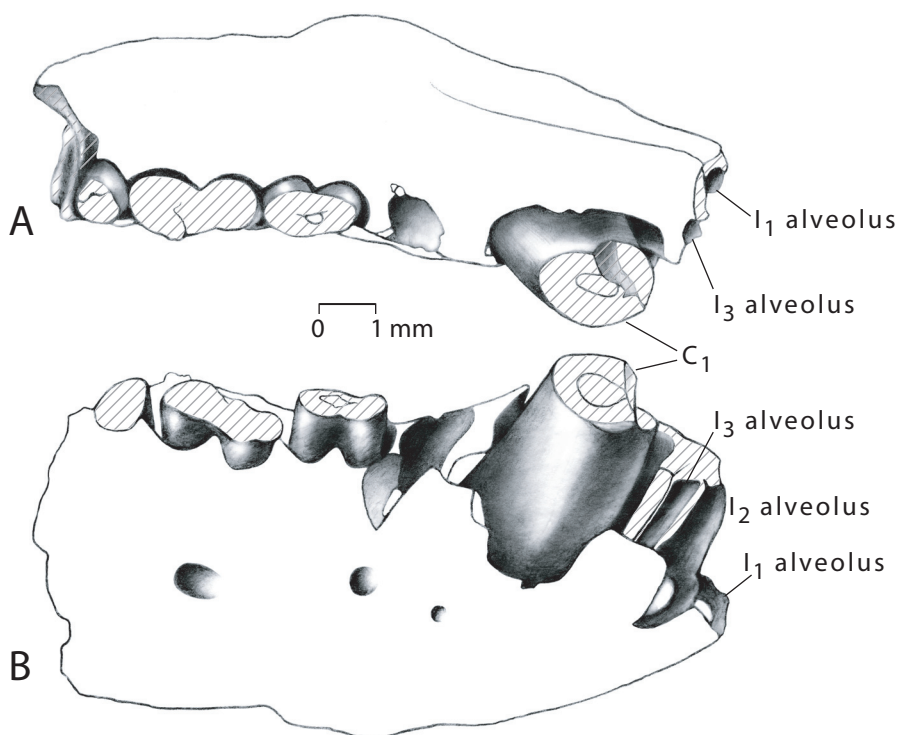


FIG. 15 — Partial dentary of *Eoryctes melanus* (UM 82162) from SC-213 (Wa-3a) in occlusal (A) and right lateral (B) views. Includes alveoli for  $I_{1-3}$ , root of  $C_1$ , alveolus for  $P_2$ , roots of  $P_{3-4}$ , and anterior root of  $M_1$ . Note the robust canine compared to that of *Ottoryctes* (Fig. 7) and the presence of a mental foramen below  $P_3$  (absent in *Ottoryctes*; Fig. 7). Specimen described but not illustrated in Thewissen and Gingerich (1989).

equal in height to that of  $M^1$  and slightly taller than that of  $P^3$  (rather than higher than that of  $M^1$  and  $P^3$ ) in lateral view, a stronger ectoflexus, and a narrower protofossa; (3)  $M^1$  with a weaker ectoflexus, a wider styler shelf, a weaker stylocone, no metaconule, a lower postprotocrista relative to the preprotocrista, and a postcingulum; (4) crown of  $P_3$  smaller relative to that of  $C_1$ , with an anterior cuspule present, a distinct posterior cusp forming an unbasined talonid blade (rather than an indistinct posterior basal cusp with no talonid blade); and (5)  $P_4$  higher than  $P_3$  (rather than of similar height), with an anterior cuspule and a blade-like unbasined talonid (rather than no anterior cuspule and a basined talonid with distinct hypoconid and entoconid cusps).

*Discussion.*— The type specimen of *Ottoryctes winkleri* (UM 72624) preserves the first known  $I^1$  for Palaeoryctinae. Matthew (1913, fig. 2) illustrated the skull and mandible of *Palaeoryctes puercensis*, for which upper incisors were unknown, and reconstructed the  $I^1$  as a large caniniform tooth. While Matthew's prediction that *Palaeoryctes* had three upper incisors is supported by the discovery of  $I^1$  in *O. winkleri*, the  $I^1$  is small and peg-like, not large and caniniform, and the largest incisor was  $I^2$ . The size of  $I^1$  in *P. puercensis* is still unknown.

We included new cranial data from *Ottoryctes* in a phylogenetic analysis of fossil zalambdodont placentals (including *Eoryctes* and *Pararyctes*), following that published by Asher et al. (2002). However, these new data did not change the Asher et al. results, so we have not included the extended analysis here.

## PALAEORYCTINE PHYLOGENY

**Previous hypotheses**

Very little has been published regarding interrelationships of taxa within Palaeoryctinae. Descriptions and discussions of *Palaeoryctes puercensis* (Van Valen, 1966), *Palaeoryctes punctatus* (Van Valen, 1966; Rose, 1981), *Aptoryctes ivyi* (Gingerich, 1982), *Eoryctes melanus* (Thewissen and Gingerich, 1989), and *Palaeoryctes cruoris* (Gunnell, 1994), largely lack interpretation of how these species might be related. Inclusion of three of the taxa in the genus *Palaeoryctes* is a testable hypothesis of relationships; that is, that these species are more closely related to each other than to any species in other genera. Furthermore, the stratigraphic distribution of taxa might also suggest a certain set of relationships. The earlier occurring *P. puercensis* could be ancestral to later Paleocene *P. jepseni*, *P. cruoris*, and *Aptoryctes ivyi*. Finally, one or more of these taxa might have given rise in turn to *P. punctatus* in the late Paleocene, and to *Eoryctes melanus* and *Ottoryctes winkleri* in the early Eocene.

**Stratophenetic analysis**

A stratophenetic approach to phylogeny follows from recognition of *time* as the independent variable in evolution, with *form* (morphology, etc.) being conceptually dependent. Form changes through time, not the reverse. Recovery of phylogeny, the pattern of evolution of a group through time, requires evidence from past times (fossils), organization of this evidence relative to time (in terms of phenetic grouping of contemporary specimens into species, and in terms of the relative ages of intervals yielding these), and finally linking of the evidence through time based on overall similarity in form, time, and space (geography; Gingerich, 1976, 1979). Resulting hypotheses of diversification and genealogical relationships are then tested by new evidence as this accumulates and the record becomes denser.

The temporal and tooth size evidence bearing on evolutionary relationships of North American palaeoryctines is summarized in Figure 16. Palaeoryctine specimens from the Clarks Fork Basin are represented by solid symbols, and those correlated from elsewhere (Bighorn, Green River, and San Juan basins) are shown with open symbols. Time is shown on the ordinate here (rather than the abscissa conventionally used for independent variables) because time is vertical in stratigraphy: time is nevertheless the independent variable. Morphological characteristics other than size, like those involved in diagnosing successive species, could be plotted against time as well, but the general pattern of change through time is possibly most clearly shown by size.

There is a single species described from the Torrejonian land-mammal age. This is *Palaeoryctes puercensis* Matthew (1913) from the San Juan Basin of New Mexico. Two species are known from the middle Tiffanian land-mammal age. These are *Palaeoryctes* sp. and *P. cruoris* described by Gunnell (1994) from Chappo Type Locality in the Green River Basin of Wyoming. The two clearly differ from each other in size but there are other morphological differences as well (see Appendix).

The Clarks Fork Basin and Bighorn Basin records of Palaeoryctinae start in the middle Tiffanian with *Palaeoryctes* sp. from Cedar Point Quarry (cf. *Palaeoryctes* sp. of Rose, 1981: 152; also UM 83228). The next interval yielding palaeoryctines, in the middle-to-late Tiffanian, is that yielding *Palaeoryctes jepseni* described here and *Aptoryctes ivyi* described by Gingerich (1982). These differ in size, but in addition *Aptoryctes* is conspicuously different from *Palaeoryctes* in having enlarged crushing premolar teeth. The only palaeoryctine known from the Clarkforkian land-mammal age is *Palaeoryctes punctatus* Van Valen, 1966. Two palaeoryctine species are known from the Wasatchian land-mammal age: *Eoryctes melanus* Thewissen and Gingerich, 1989, from the early Wasatchian, and *Ottoryctes winkleri* described here from the middle Wasatchian.

## STRATOPHENETIC DISTRIBUTION OF NORTH AMERICAN PALAEORYCTINAE

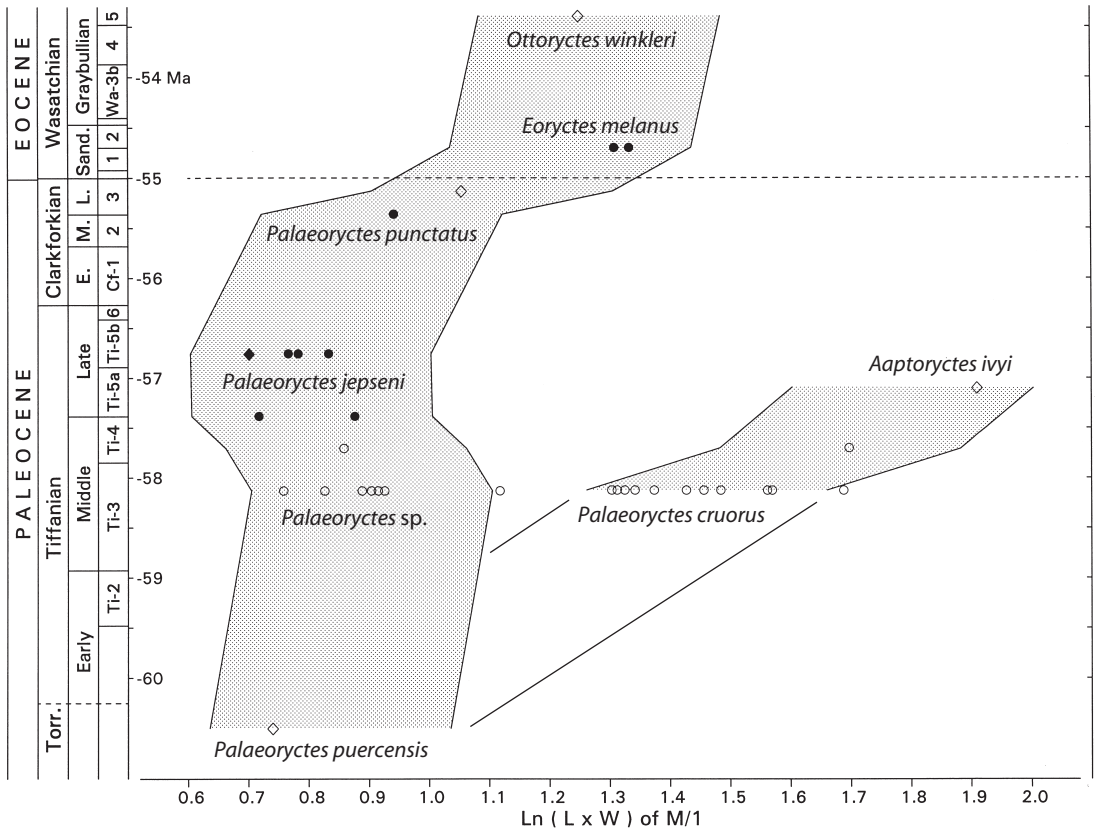


FIG. 16 — Stratophenogram showing stratigraphic distribution of  $M_1$  sizes for representative Paleocene and early Eocene palaoryctines from western North America. Abscissa is natural logarithm of  $M_1$  crown area. Ordinate is time in millions of years before present (calibration in Gingerich, 2003). Solid circles and diamonds (type specimens) represent specimens of known meter level in the Polecat Bench-Sand Coulee stratigraphic section. Open circles and diamonds (type specimens) represent specimens from localities elsewhere for which an approximate level can be estimated biostratigraphically. A minimum of two evolutionary lineages, one leading from *Palaeoryctes* to *Eoryctes* and *Ottoryctes*, and the other leading from *Palaeoryctes* to *Aptoryctes*, are required to explain the observed distribution of specimens. By this interpretation *Palaeoryctes* itself is a paraphyletic stem genus.

Van Valen (1966) suggested that *Palaeoryctes puercensis* was ancestral to *P. punctatus*, and the evidence in Figure 16 supports this, albeit with newly described *Palaeoryctes jepseni* as an intermediate form in this lineage. Figure 16 suggests that *Palaeoryctes cruoris* may have been ancestral to *Aptoryctes ivyi*, which is also supported by our stratocladistic analysis (see below). The *Palaeoryctes cruoris*-*Aptoryctes ivyi* lineage appears to be the sister group to a separate ancestor-descendant lineage that is composed of the ordered sequence *P. jepseni*, *P. punctatus*, *Eoryctes melanus*, and *Ottoryctes winkleri*, but interpretation of the latter as a single lineage may be an oversimplification. The ancestral status of *Eoryctes melanus* relative to *Ottoryctes winkleri* is equivocal in our stratocladistic analysis (see below), with the stratigraphic advantage of placing *E. melanus* in an ancestral position offset by the cost to parsimony of reversing a morphological transition that would otherwise be interpreted as an autapomorphy.

### Cladistic analysis

In order to provide at least an initial framework for future investigations of relationships within Palaeoryctinae, we first performed a cladistic analysis using 32 morphologic characters for the seven known North American species and *Asioryctes nemegetensis*, our outgroup taxon (Appendices 1 and 2). The analysis was rooted with *Asioryctes nemegetensis*, from the Cretaceous, because it is a geologically-old eutherian, it is well known from upper and lower dentitions, and it may have been close to the ancestry of all later placental mammals (Kielan-Jaworowska, 1981, 1984). The position of *Pararyctes* relative to other Palaeoryctidae is uncertain (e.g., Kellner and McKenna, 1996; McKenna and Bell, 1997) and potentially influenced by interpretations, particularly regarding dental homology and cranial anatomy of unpublished material. For this reason, *Pararyctes* is not included in our analysis, although it will likely be relevant to future analyses once the material has been described.

All characters in this analysis were treated as unordered. Morphologic data were assessed by studying the holotypes and referred material when possible of *Aptoryctes ivyi* Gingerich 1982 (UM 77291), *Eoryctes melanus* Thewissen and Gingerich 1989 (UM 68074), and *Palaeoryctes cruoris* Gunnell 1994 (UM 80621). Casts of the holotypes of *Palaeoryctes puercensis* Matthew 1913 (AMNH 15923) and *Palaeoryctes punctatus* Van Valen 1966 (AMNH 15850) were also studied. Additional comparisons were made using published descriptions of *Palaeoryctes puercensis* (also McDowell, 1958; Van Valen, 1966), *Asioryctes nemegetensis* (Kielan-Jaworowska, 1975-ZPAL MgM-I/56; also Crompton and Kielan-Jaworowska, 1978; Kielan-Jaworowska, 1981). Several of these specimens preserve details of the cranial anatomy (e.g., Matthew, 1913; Thewissen and Gingerich, 1989), but most include only teeth. For this reason, all of the morphologic data are dental. Characters that were variable within a species (characters 22 and 25) were coded as polymorphic.

Cladistic analysis was done using PAUP version 4.0b10 for Macintosh (see Swofford, 1993). An exhaustive search using 32 morphologic characters yielded four equally most-parsimonious cladograms, each with a tree length of 49 steps (51 including autapomorphies), a consistency index of 0.74, and a retention index of 0.55. A strict consensus of the four equally most-parsimonious cladograms (Fig. 17A) indicates a paraphyletic *Palaeoryctes*, with a close relationship between *P. cruoris* and *Aptoryctes*, and a sister relationship between *Eoryctes* and *Ottoryctes*. Otherwise, relationships are fairly unresolved by this analysis, suggesting substantial homoplasy in the evolution of teeth in this group.

### Stratocladistic analysis

To better resolve relationships within Palaeoryctinae we followed our cladistic analysis with a more inclusive stratocladistic analysis using the same 32 morphological characteristics and, in addition, an ordered stratigraphic character (Appendix tables 1-2), following methods outlined by Fisher (1991, 1992, 1994). We started with the cladistic analysis discussed above and imported the four equally most-parsimonious cladograms found there into MacClade version 4.0 (Maddison and Maddison, 1992), where the stratigraphic character was added. Tree lengths were then recalculated by determining overall parsimony, including morphologic and stratigraphic debt. The result was that two of the equally most-parsimonious cladograms generated by PAUP had an overall tree length of 60 (51 morphologic steps and 9 stratigraphic steps) and the remaining two had an overall tree length one step longer (51 morphologic steps and 10 stratigraphic steps). To determine whether this subset of cladograms (and the associated phylogenetic trees) includes the most parsimonious stratocladistic tree, two additional investigations were required. The first uses the "make ancestor" tool in MacClade, for all of the original equally most-parsimonious cladograms. By experimenting with combinations of ancestors for each of the four topologies, we found a single shortest tree with 51 morphologic steps and 6 stratigraphic steps (57 steps overall).

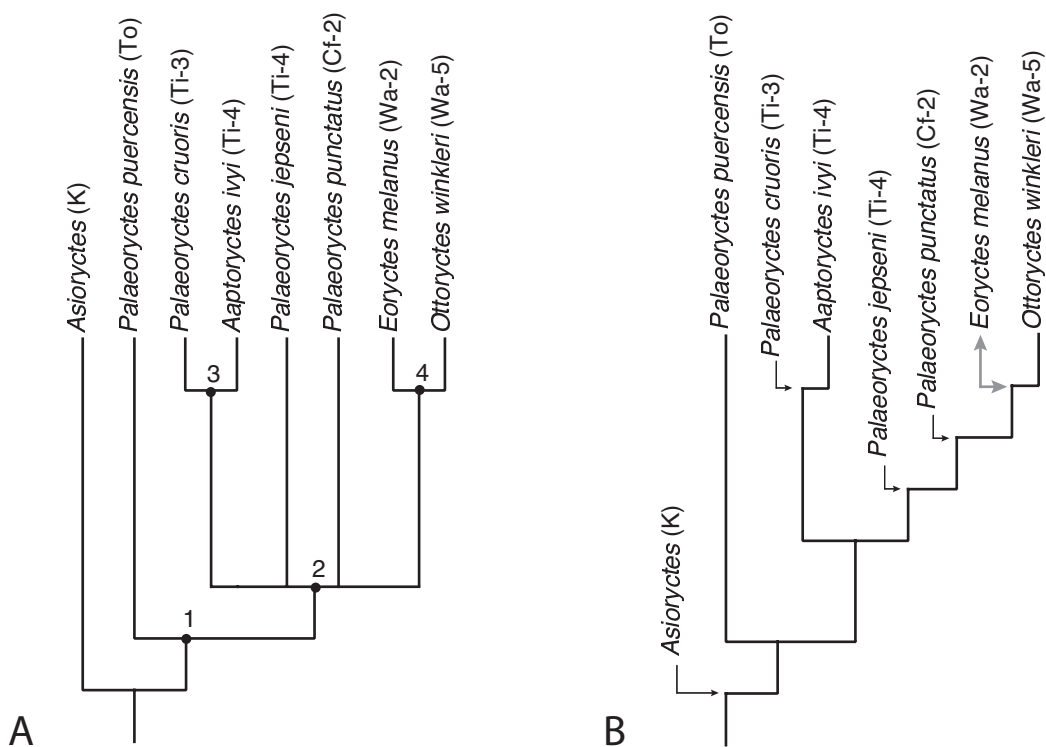


FIG. 17 — Two hypotheses of phylogenetic relationships among North American palaeoryctines, based on dental characteristics analyzed here (Appendices 1 and 2). Cladistic analysis (A) yielded four equally most-parsimonious cladograms, summarized here as a strict consensus, generated by an exhaustive search algorithm (Swofford, 1993) and rooted with outgroup *Asioryctes* (tree length = 49, consistency index = 0.74, retention index = 0.55). Unambiguous synapomorphies supporting each node are as follows (change is from 0 to 1 for binary characters; state indicated for multistate characters)— Node 1 (Palaeoryctinae): 2, 3, 4, 5, 15(1), 17, 18, 30, 32; Node 2: 1, 9(2), 13, 24, 25, 26, 27; Node 3: 6, 9(1), 10, 11, 12; Node 4: 15 (2), 16. Stratocladistic analysis (B) yielded two overall most-parsimonious trees associated with a single topology that was not included in the four equally most-parsimonious cladograms generated by PAUP. Lines with a single arrow indicate taxa that are in the ancestral position and the line with a double arrow indicates that *Eoryctes melanus* may or may not be ancestral to *Ottoryctes*.

The second investigation considered whether or not alternative topologies of relationship might allow further reduction of overall tree length. We ran the PAUP analysis again to save cladograms longer than the minimum morphologic tree length and found 12 cladograms at 50 steps, 32 at 51 steps, 85 at 52 steps, 127 at 53 steps, 249 at 54 steps, 391 at 55 steps, 495 at 56 steps, and 713 at 57 steps. As the number of cladograms under the “debt ceiling” (see Fisher, 1992; Bloch et al., 2001) became prohibitively high (2, 108) we decided to abandon this approach and instead use the more heuristic approach of manual branch swapping and reducing ancestors to search for alternative topologies with associated shorter phylogenetic trees. The result was that we found a single topology (morphologic tree length = 53), not originally selected by PAUP, with two equally most-parsimonious trees compatible with it. The final stratocladistic result comprised two trees, one with 52 morphologic steps and 3 stratigraphic steps, and the other with 53 morphologic steps and 2 stratigraphic steps (Fig. 17B; Overall Tree Length = 55 in both). The results of the stratocladistic analysis are plotted against geological time as a phylogenetic tree in Figure 18.

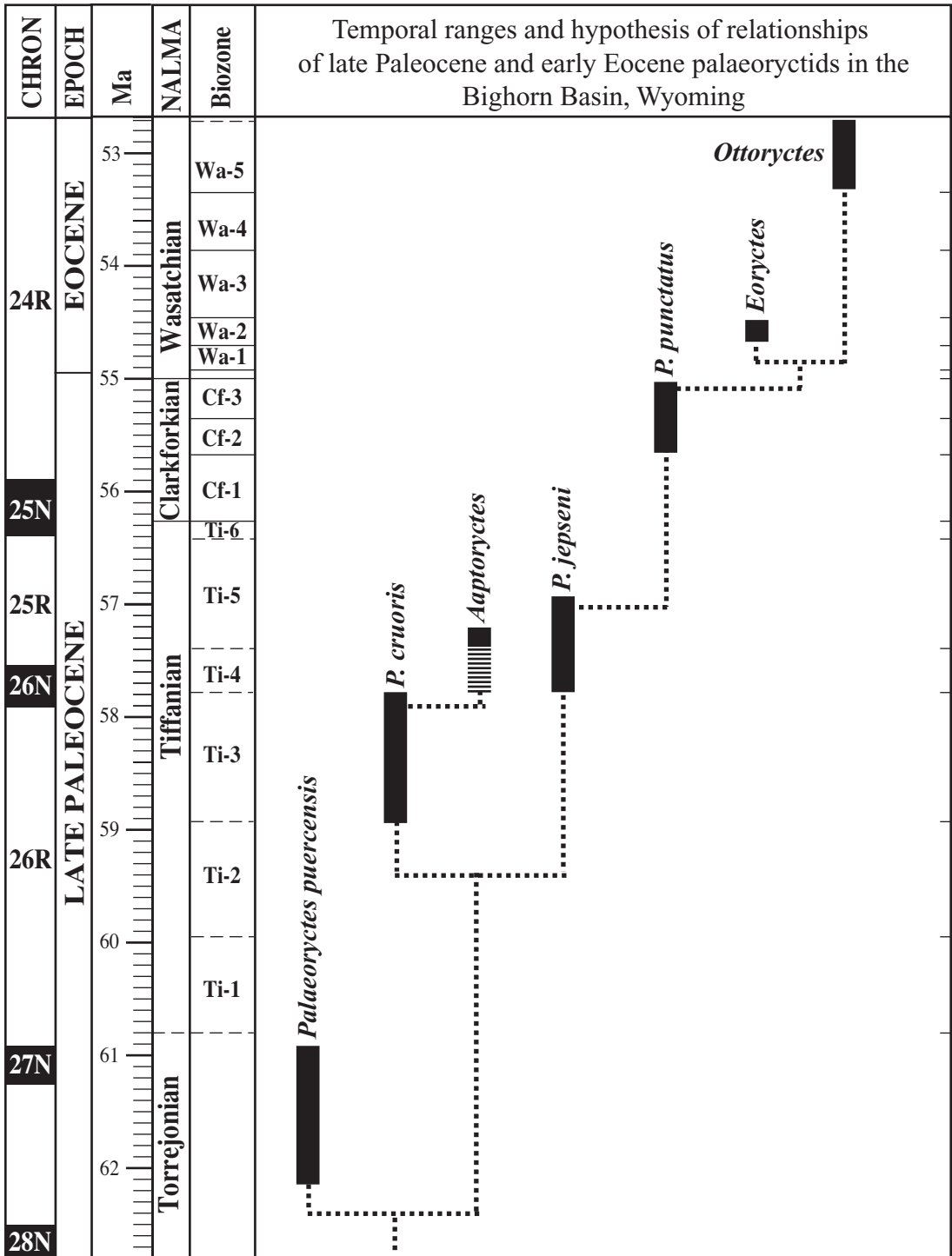


FIG. 18 — One of the phylogenetic trees (with equivocal ancestors as sisters only) resulting from the stratocladistic analysis (Fig. 17B). Divergences of sister taxa are shown schematically; no knowledge of the exact timing of cladogenesis is implied.



## DISCUSSION

Discovery of new specimens of *Palaeoryctes punctatus* that include aspects of the dental and mandibular morphology not known from previous specimens, allows for a re-assessment of the composition of the genus *Palaeoryctes*. We recognize a new species, *P. jepseni*, from the late Tiffanian, and suggest that it was ancestral to the younger *P. punctatus*.

Comparison of the skull and mandible of a new genus and species of palaeoryctid, *Ottoryctes winkleri*, to the older *Eoryctes* suggests that these taxa share a close phylogenetic relationship. *Ottoryctes* is a sister taxon of *Eoryctes*, and could also be its descendant. *Ottoryctes winkleri* is similar to *E. melanus* in most features of the cranium, including having ossified tubes marking the course of the stapedia and promontory branches of the internal carotid artery through the middle ear (previously part of the diagnosis of *E. melanus*).

Cladistic analysis of 32 dental characters yielded a poorly resolved hypothesis of relationships among North American Palaeoryctinae. Clearly, dental characters by themselves, in the absence of any other phylogenetic information, are not an ideal source of evidence for phylogenetic analysis in Insectivora (Gould, 2001), and temporal order of appearance in the fossil record provides important additional information (Clyde and Fisher, 1997; Fox et al., 1999).

Stratocladistic analysis of the North American palaeoryctine data generated a relatively highly resolved hypothesis of relationships. Not surprisingly, this was better resolved than hypotheses produced by cladistic analysis alone. Even though the fossil record of palaeoryctines is somewhat sparse, results of our stratocladistic analysis were similar to those generated by the more traditional stratophenetic approach. It has previously been stated that the two methods often converge on the same result when sampling a dense and continuous fossil record (Fisher, 1991; Bloch et al., 2001). This congruence almost certainly stems from the fact that both stratocladistics and stratophenetics allow for hypotheses of ancestry, operating at the level of phylogenetic trees, not just cladograms. As ancestor-descendant pairs are expected in the fossil record (Foote, 1996), and conventional cladistics excludes them a priori, it is not surprising that these two methods yielded hypotheses with better resolution.

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## APPENDIX

APPENDIX TABLE 1 — Description of characteristics used in cladistic and stratocladistic analyses. *Asioryctes* was used to root the preferred cladograms. All characters were unordered except character 33 (stratigraphic character, not used in cladistic analysis). Those characteristics that were variable within a species (characters 22 and 25) were coded as polymorphic. Autapomorphic characters (characters 14 and 21) were included in the stratocladistic analysis, as they can affect hypotheses of ancestry; cladistic results are reported both with and without them.

- 
- 
1. Number of lower incisors: four (0), or three or two (1)
  2. Lower incisors of similar size: (0),  $I_2$  substantially larger than other incisors (1)
  3. Lower canine: double-rooted (0), or single-rooted (1)
  4. Number of lower premolars: four (0), or three (1)
  5.  $P_2$  roots: double-rooted (0), or single-rooted (1)
  6. The central cusp of  $P_4$ : compressed buccolingually (0), or moderately to extremely inflated (1)
  7.  $P_3$  anterior basal cusp: present (0), or absent (1)
  8.  $P_4$  anterior basal cusp: present as a cuspule (0), expanded into a paraconid (1), or absent (2)
  9.  $P_4$  talonid: a posterior basal cusp, unbasin (0), expanded buccolingually, small basin developed on the lingual portion (1), or basin expressed as narrow groove on the lingual portion (2)
  10. Molar trigonids: strongly compressed anteroposteriorly (0), or longer, with the paraconid positioned more anteriorly relative to the metaconid (1)
  11. Molar trigonids: more than twice the height of the talonid (0), or less than twice the height of the talonid (1)
  12. Talonid of  $M_{1,2}$ : narrow (the distance between the lingual margin and the point at which the cristid obliqua contacts the postvallid is less than half the width of the trigonid) (0), or somewhat inflated (the distance between the lingual margin and the point at which the cristid obliqua contacts the postvallid is about half the width of the trigonid) (1)
  13.  $M_3$ : smaller than  $M_1$  and  $M_2$  (0), or equal to or larger than  $M_1$  and  $M_2$  (1)
  14.  $M_3$  talonid: hypoconulid very high even on worn specimens (0), or the hypoconulid is reduced (1)
  15. Anterior mental foramen: below  $C_1$  (0), below the junction of  $P_2$  and  $C_1$  (1), below the junction of  $P_3$  and  $P_2$  (2)
  16. Symphysis extends: back as far as  $P_2$  (0), or as far as  $P_3$  (1)
  17. Number of upper incisors: five (0), or three or two (1)
  18. Number of upper premolars: four (0), or three (1)
  19.  $P^2$  roots: double-rooted (0), or single-rooted (1)
  20.  $P^2$ : little or no anterior basal cusp (0), or distinct anterior basal cusps (1)
  21.  $P^3$  roots: three roots (0), or two roots (1)
  22.  $P^3$  metacone: absent to incipient (0), or distinctly present (1)
  23.  $P^3$  anterior cusp: distinct (0), or absent (1)
  24.  $P^3$  protocone: well developed (0), or poorly developed to absent (1)
  25.  $P^4$  metacone: absent (0), incipiently present (1), or distinctively present (2)
  26.  $P^4$  cusp height in lateral view: lower than  $P^3$  and  $M^1$  (0), or equal to or greater than  $P^3$  and  $M^1$  (1)
  27.  $P^4$  styler shelf: wide laterally and very narrow in the middle because of a strong ectoflexus (0), or ectoflexus weak with little or no styler shelf (1)
  28.  $P^4$  width: not as wide transversally as  $M^1$  (0), or as wide as or wider transversally than  $M^1$  (1)
  29.  $P^4$  protocone: not connate, having pre- and postprotocristae gradually descending buccally (0), or connate, having pre- and postprotocristae steeply descending buccally (1)
  30.  $M^1$  ectoflexus: deep with the styler shelf wide at the corners and almost disappearing in the middle (0), or shallower (1)
  31.  $M^2$  ectoflexus: deep with the styler shelf wide at the corners and almost disappearing in the middle (0), or moderately deep (1)
  32.  $M^{1-2}$  metacone: subequal to paracone (0), or smaller than paracone (1)
  33. Stratigraphic level: late Cretaceous (0), Torrejonian (1), middle Tiffanian (Ti-3; 2), late Tiffanian (Ti-4 or Ti-5; 3), Clarkforkian (4), early to middle Wasatchian (Wa-2 or Wa-3; 5), or middle Wasatchian (Wa-5; 6)
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APPENDIX TABLE 2—Character matrix used for phylogenetic analysis. Characteristics that are not known for a particular taxon, due to incomplete fossil material, are treated as missing (“?”). Letter codes: a, 0 and 1; b, 1 and 2.

Taxon	00000	00001	11111	11112	22222	22223	333
	12345	67890	12345	67890	12345	67890	123
<i>Asioryctes nemegetensis</i>	00000	00000	00000	00000	00000	00000	000
<i>Aptoryctes ivyi</i>	11111	11211	11001	1?111	00111	11111	003
<i>Eoryctes melanus</i>	11111	01120	00??2	1????	01012	11001	015
<i>Ottoryctes winkleri</i>	11111	00020	00112	11101	01012	11000	006
<i>Palaeoryctes puercensis</i>	?1111	00220	00001	01110	11100	11011	011
<i>Palaeoryctes punctatus</i>	11111	00??0	00??1	0????	????2	11??1	114
<i>Palaeoryctes cruoris</i>	????1	10011	1110?	??101	00012	11111	112
<i>Palaeoryctes jepseni</i>	?1111	00120	00101	0????	0a01b	11101	113