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REVIEW OF *PARADJIDAUMO* BURKE (RODENTIA, EOMYIDAE) FROM THE EOCENE AND OLIGOCENE (DUCHESNEAN-WHITNEYAN) OF NORTH AMERICA

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ABSTRACT

The eomyid rodent *Paradjidaumo* Burke, 1934, is reviewed. Eight species are recognized for the genus ranging from the Duchsnean (late Eocene) to the Whitneyan (middle Oligocene). *Paradjidaumo disjunctus* new species from the Chadronian (late Eocene) of Montana is described. The Orellan (early Oligocene) species *P. hypsodus* Setoguchi, 1978, is considered a junior synonym of the type species, *P. trilophus* (Cope, 1873). Two distinct subgenera can be recognized, *Paradjidaumo (Macroadjidaumo)*, including the species *P. (M.) alberti* Russell, 1954 and *P. (M.) reynoldsi* Kelly, 1992, which is distinguished by having lower molars longer than wide with highest crown-height for the genus, and *Paradjidaumo (Paradjidaumo)*, which includes *P. (P.) nanus* Emry and Korth, 2013, *P. (P.) trilophus*, P. *(P.) spokanensis* White, 1954, *P. (P.) validus* Korth, 1980, and *P. (P.) disjunctus*, diagnosed as having lower molars wider than long and increases through time in size, relative length of p4, and crown-height (never attaining the crown-height of *Macroadjidaumo*). *Paradjidaumo (P.) hansonorum* (Russell 1972) is unique among species of the genus, although it is retained in the subgenus *Paradjidaumo*, because of its derived feature of disproportionately long premolars and retained primitive molar morphology (unattached anterior cingulid on lower molars in early stages of wear).

INTRODUCTION

Historical Review—Burke (1934) first named *Paradjidaumo*, with two referred species, one each from the Chadronian and Orellan. The first detailed review of *Paradjidaumo* was by Wood (1937) when he recognized the same two species as Burke, *P. minor* (Douglass 1901) and *P. trilophus* (Cope 1873), from the Chadronian and Orellan, respectively (also see Korth 1980:934). Later, two additional species of *Paradjidaumo* were named, *P. alberti* Russell, 1954, from the Chadronian of the Kishenehn Formation of British Columbia (originally considered Duchesnean [see discussion under *P. alberti*]) and *P. spokanensis* White ,1954, from the Orellan Canyon Ferry area of Montana.

Over two decades later, Setoguchi (1978) named *P. hypsodus* from the Orellan of central Wyoming (originally referred to Whitneyan age [see Korth, 1980, 1981, 1989a for age determination]). In that same year, Storer (1978) referred *Adjidaumo hansonorum* Russell, 1972, from the Chadronian of Saskatchewan to *Paradjidaumo*. Shortly afterward, Korth (1980) named a new species, *P. validus*, from the Orellan of Nebraska and synonymized *P. minor* and *P. trilophus*, with the latter the type species of the genus. Kelly (1992) named *P. reynoldsi* from the Duchesnean of southern California and Korth (2007, 2010) recognized specimens referable to *Paradjidaumo* from the Whitneyan of South Dakota and suggested that they represented a new species. Most recently, Emry and Korth (2013) named *P. nanus* from the middle Chadronian of Wyoming. In all, eight valid species of *Paradjidaumo* have been identified from the Duchesnean to the Whitneyan of western North America.

Here, the previously described species of *Paradjidaumo* are compared in detail and new material of the genus is described which allows for better definitions of the existing species and introduction of new taxa.

Methods.—Dental terminology used herein follows that of Wood and Wilson (1936). Upper teeth are indicated by capital letters, lower teeth by lower-case letters (e.g., M1 and m1). The index of crown-height of lower molars (H/W) is based on the height of the crown from its base to the base of the lingual valley between the metaconid and entoconid divided by the maximum width of the tooth (Table 1). Crown-height is divided into four ranges, Low (0.28-0.30); Intermediate (0.31-0.33), High (0.34-0.36) and Highest (0.37-0.39).

The occlusal morphology of the cheek teeth of *Paradjidaumo* has been described elsewhere in detail (Burke 1934; Wood 1937; Black 1965; Setoguchi 1978; Korth 1980). Dental descriptions included here

focus on the deviations from the generalized *Paradjidaumo* morphology.

Abbreviations for Institutions—AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; F:AM, Frick Collections, AMNH; LACM, Museum of Natural History, Los Angeles County; NMC, National Museum of Canada, Ottawa; ROM, Royal Ontario Museum; SDSM, Museum of Geology, South Dakota School of Mines and Technology; UMCV, University of Montana Museum of Paleontology, Vertebrate Collections; USNM, National Museum of Natural History, Smithsonian Institution.

TABLE 1. Comparative crown-height of lower molars of species of *Paradjidaumo*. Abbreviations: N, number of specimens measured; H/W, crown-height index of m1s and m2s (lingual crown-height divided by maximum width); NALMA, North American Land Mammal Age.

	N	H/W mean	H/W range	NALMA
LOW				
P. disjunctus	30	0.28	0.21-0.36	Chadronian
P. nanus	15	0.30	0.22-0.37	Chadronian
INTERMEDIATE				
P. hansonorum	48	0.33	0.22-0.39	Chadronian
P. spokanensis	8	0.33	0.29-0.37	Orellan
HIGH				
P. trilophus	85	0.35	0.20-0.49	Chadronian-Whitneyan
P. validus	2	0.35	0.32-0.38	Orellan
HIGHEST				
P. alberti	4	0.38	0.25-0.45	Chadronian
P. reynoldsi	11	0.38	0.32-0.43	Duchesnean

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1921
Family Eomyidae Winge, 1887
Genus *Paradjidaumo* Burke, 1934

Type Species—*Paradjidaumo trilophus* (Cope, 1873)

Range—Duchesnean to Whitneyan (middle Eocene to middle Oligocene) of western North America.

Emended Diagnosis—Small eomyines, larger than *Adjidaumo*; sciuromorphous zygomasseteric structure; P3 lacking; cheek teeth mesodont and lophate; omega pattern on all cheek teeth (five cross-lophs on unworn molars, three on worn molars); posterior cingulid on m1-m2 short; anterior cingulid attached to protoconid on lower molars at buccal end (buccal end free with more linguad attachment in other genera).

Subgenus *Paradjidaumo* Burke 1934

Type Species—*Paradjidaumo trilophus* (Cope, 1873)

Referred Species—*P. (P.) spokanensis* White, 1954; *P. (P.) hansonorum* (Russell, 1972); *P. (P.) validus* Korth, 1980; *P. (P.) nanus* Emry and Korth 2013; and *P. (P.) disjunctus* n.sp.

Range—Chadronian to Whitneyan (late Eocene to middle Oligocene) of western North America.

Diagnosis—Small to large species; lower molars (m1-m2) wider than long; mean crown-height index ranges from 0.29-0.36, becoming progressively higher-crowned through time; P4/p4 become progressively larger relative to M1/m1.

Paradjidaumo (Paradjidaumo) trilophus (Cope, 1873)
(Figure 1A, 2A, 3A; Tables 2, 3)

Gymnoptychus nasutus Cope, 1873 (in part)
Gymnoptychus trilopohus Cope, 1873
Adjidaumo trilophus (Cope) Hay, 1899
Adjidaumo nasutus (Cope) Hay, 1899
Eumys minor Douglass, 1901
Gymnoptychus minor (Douglass) Matthew, 1903
Gymnoptychus liophus Matthew, 1903
Adjidaumo minor (Douglass) Hay, 1930
Paradjidaumo minor (Douglass) Burke, 1934
Paradjidaumo nasutus (Cope) Burke, 1934
Paradjidaumo trilophus (Cope) Wood, 1937
Paradjidaumo hypsodus Setoguchi, 1978
Paradjidaumo sp. Korth, 2007, 2010

Type Specimen—AMNH 5401, right mandible with dp4-m2.

Additional Referred Specimens—From Canyon Ferry, Montana (Chadronian): USNM 18759, and USNM 362426, mandibles with p4-m3; USNM 19937, mandible with m1-m3. From Canyon Ferry, Montana (Orellan): USNM 18758 and USNM 544074, mandibles with p4-m2; USNM 20635 mandible with m1-m2. From Slim Buttes, South Dakota (Orellan): CM 11742, two mandibles, one with p4-m2 and one with m1-m2; CM 9759, mandible with p4-m2; CM 9758, three mandibles one with p4-m2, two with p4-m1 and partial skull with right P4-M2 and left P4-M1. From Blue Ash fauna, South Dakota (Whitneyan): SDSM 11855, left mandible with i1 and p4-m3; CM 76137, left p4; SDSM 11850, CM 84663, CM 84664, m1 or m2; CM 84667, m3; SDSM 11852, left maxilla

TABLE 2. Combined dental measurements for *Paradjidaumo (Paradjidaumo) trilophus* from Canyon Ferry, Montana (Chadronian-Orellan); Slim Buttes, South Dakota (Orellan) and Blue Ash, South Dakota (Whitneyan). Abbreviations: L, maximum anteroposterior length; W, maximum transverse width; N, number of specimens measured; M, mean; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, co-efficient of variation.

	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3L
N	12	12	15	16	12	12	6	6	7
M	1.37	1.28	1.36	1.43	1.31	1.42	1.36	1.26	5.60
Min	1.22	1.04	1.15	1.33	1.16	1.24	1.17	1.08	5.26
Max	1.52	1.44	1.53	1.58	1.48	1.58	1.55	1.40	6.26
SD	0.10	0.09	0.12	0.08	0.11	0.09	0.16	0.13	0.34
CV	7.47	7.34	8.48	5.75	8.58	6.45	11.77	10.23	6.16

	P4L	P4W	M1L	M1W	M2L	M2W
N	4	4	9	9	1	1
M	1.30	1.42	1.30	1.42	1.24	1.48
Min	1.25	1.32	1.20	1.33		
Max	1.34	1.47	1.38	1.55		
SD	0.04	0.07	0.07	0.08		
CV	3.26	4.78	5.06	5.78		

TABLE 3. Crown-height indices of *Paradjidaumo (Paradjidaumo) trilophus* from different localities. Abbreviations as in Table 1.

	N	m1-2L mean	m1-2W mean	H/W mean	H/W range	NALMA
Pipestone Springs, MT; Canyon Ferry, MT	31	1.51	1.57	0.35	0.20-0.48	Chadronian
Sioux County, NE	19	1.51	1.60	0.35	0.24-0.40	Orellan
Cedar Ridge fauna, WY (=*hypsodus*)	16	1.47	1.58	0.35	0.27-0.49	Orellan
Canyon Ferry,MT; Slim Buttes, SD	19	1.32	1.42	0.35	0.25-0.44	Orellan
Blue Ash, SD	6	1.34	1.40	0.33	0.26-0.43	Whitneyan
Mean		1.43	1.51	0.35	0.20-0.49	

with P4-M1; SDSM 11851, SDSM 11853, CM 76294, CM 76295, CM 84665, M1 or M2; CM 84666, M3. Also see Wood (1937), Wilson (1949), Galbreath (1953), Black (1965), Wahlert (1978), and Korth (1980) for additional referred specimens from other institutions.

Occurrence—Middle Chadronian (late Eocene) of Montana and Wyoming; Orellan (early Oligocene) of Nebraska, Montana, Colorado, Wyoming, and South Dakota; and Whitneyan (middle Oligocene) of South Dakota.

Emended Diagnosis—Intermediate sized (smaller than *P. (P.) validus* and *P. (P.) spokanensis*,

larger than all other species); high molar crown-height (mean = 0.35); mesolophs (-ids) long on cheek teeth, generally reaching opposite side of tooth; anterior cingulid always attached directly to protoconid on lower molars even at earliest stages of wear; P4/p4 equal to, or slightly longer than, M1/m1.

Discussion—The skull and cheek teeth of *Paradjidaumo trilophus* (=*P. minor*) have been described in detail elsewhere (Wood 1937; Wilson 1949; Wahlert 1978; Korth 1980). Nothing need be added to these previous descriptions. *Paradjidaumo (P.) trilophus* is the longest lived species, ranging from the middle Chadronian through the Whitneyan. It is also the widest ranging species geographically, being known from throughout the northern Rocky Mountains and northern Great Plains. It is distinct from all other species in its intermediate size (Wood 1937:245; Korth 1980:table 2; Table 2, this paper) and high crown-height of the lower molars (mean index = 0.35; Table 1). Unlike some earlier occurring species such as *P. hansonorum*, *P. disjunctus* (described below), and *P. reynoldsi*, the anterior cingulid on the lower molars is attached to the protoconid even on unworn specimens (separated in early wear on the latter species). P4/p4 averages slightly longer than M1/m1. This is generally true of other species, but distinct from *P. disjunctus* and *P. nanus* and the subgenus *Macroadjidaumo* (defined below), in which p4 is shorter than m1.

There is little variation in size and crown-height of the molars of *Paradjidaumo (P.) trilophus* from different horizons and localities (Table 3). Korth (2010) suggested that a small sample of *Paradjidaumo* from the Whitneyan of South Dakota might represent a distinct species due to its greater average crown-height of the lower molars. However, only two specimens were reported. With a greater number of specimens (see above "Additional Referred Specimens"), including mandibles with lower cheek teeth, it is evident that the Whitneyan material is well within the range and average crown-height of *P. (P.) trilophus*. Even though some samples have slightly smaller dimensions of the lower molars (Table 3), there is no statistical difference in all of the populations studied, all of them being with the range of variation of the large sample from the Orellan of Nebraska (Korth 1980).

Setoguchi (1978) named a new species, *Paradjidaumo hypsodus*, and differentiated it from all other species of the genus by its higher-crowned cheek teeth with higher lophs and deeper valleys. However, the measurements of crown-height do not differ in range or mean value with those of *P. trilophus* (Table 3). The entire hypodigm of *P. hypsodus* consists of isolated cheek teeth. Many of these specimens have no wear at all and appear to have been unerupted, making the lophs seem higher and thinner when compared to specimens of other species with even minimal wear. In his discussion and description of *P. hypsodus*, Setoguchi (1978) noted that the M3 was similar in size to that of *P. trilophus*, but the occlusal pattern was less reduced than in the latter. However, this difference was not listed in the diagnosis of the species. No specimens of M3 were figured by Setoguchi (1978:fig. 18). No difference can be found between the referred material of *P. hypsodus* M3s and those of *P. trilophus* upon reanalysis. M3 is one of the most variable cheek teeth of *Paradjidaumo* (Black 1965; Korth 1980), so any minor variation is to be expected and not likely a diagnostic feature. Because the greater height of the crowns of the cheek teeth of *P. hypsodus* may be the only diagnostic feature, and this cannot be verified, *P. hypsodus* is considered a junior synonym of *P. (P.) trilophus*.

Paradjidaumo (Paradjidaumo) disjunctus n. sp.
(Figures 1B, 2B, 3B, 4A-B; Table 4)

Paradjidaumo sp., cf. *P. trilophus* (Cope) Tabrum et al., 1996

Type Specimen—CM 71450, mandible with left p4-m3.

Referred Specimens—From Diamond O Ranch: CM 71455, 71458, 71459, 71460, 78885, mandibles with p4-m3; CM 71451, 71452, 71461, mandibles with p4-m2; CM 71463, 71462, 71453, partial mandibles p4-m1; UMVC 2655, 2622, partial mandibles with m1-m2; CM 71454, fragmentary mandible with p4; UMVC 2656, CM 71456, 71457, m1s; CM 73953, m3; UMVC 2654, palate with right and left P4-M2; CM rostrum of skull with incisors, left P4-M1, and right M1; CM 78878, 72541, 71448, maxillae with P4-M3; CM 71447, 71449 partial maxillae with P4-M1; CM 71464, 71465, 71466, 78880, isolated M1 or M2. From McCarty's Mountain: CM 16999, partial skull with incisors and right P4-M3 and left M1-M3; CM 296, partial skull with incisors and right P4-M2 and left M1-M2; CM 78976, mandible with p4-m3; CM 9243, mandible with p4-m2; CM 16386, partial mandibles with p4-m1; CM 84009, partial mandible with m1-m2; CM 13938, mandible fragment with m2.

Occurrence—Early Chadronian (late Eocene): Diamond O Ranch fauna, Renova Formation, Climbing Arrow Member, Beaverhead County, Montana; and McCarty's Mountain fauna, Renova Formation, Madison County, Montana (see Tabrum et al. 1996).

Diagnosis—Small species, similar in size to *P. (P.) hansonorum*, larger than *P. (P.) nanus*, smaller than all other species; lowest crowned lower molars for the genus (mean index = 0.28); buccal end of anterior cingulid on molars does not attach to the protoconid until moderate wear; mesoloph (-id) on cheek teeth

short (never reaching opposite side of tooth); P4/p4 shorter anteroposteriorly than M1/m1.

Etymology—Latin, *disjunctus*, separate.

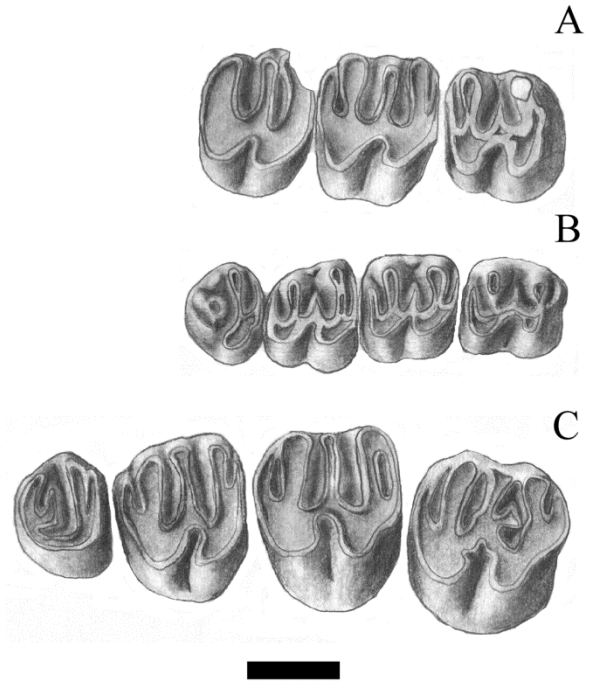

FIGURE 1. Upper cheek teeth of *Parajdaumo (Paradjidaumo)*. A, *P. (P.) trilophus*, CM 9758, right P4-M2. B, *P. (P.) disjunctus*, CM 71448, right P4-M3. C, *P. (P.) spokanensis*, F:AM 9994, right P4-M3. Anterior to right. Bar scale = 1 mm.

Description—Of the three partial skulls referred to *P. (P.) disjunctus*, two are from McCarty's Mountain (CM 16999, CM 296) and one is from Diamond O (CM 87363). All consist of the rostrum and varying amounts of the palate and orbital wall (Figure 4A, B). Their morphology does not differ from that described for *P. (P.) trilophus* (Wilson 1949; Wahlert 1978). The length of the upper diastema of *P. (P.) trilophus* was given by Wilson (1949:41) as 9.1 mm. In the three skulls of *P. (P.) disjunctus* this length averages 8.72 mm, but the greatest measurement is 9.17 mm (CM 296).

All cheek teeth are mesodont and lophate as in all species of the genus. The crown-height is the lowest of all species (mean = 0.28). The general morphology is the same as that of other species.

P4 has a variable anterior cingulum (Figure 1B). On most specimens (7 of 11) there is a short anterior cingulum at the anterobuccal corner of the tooth, just anterior to the paracone. In the other specimens it is lacking. The mesolophid is short on all upper cheek teeth except one isolated molar (CM 71464) where it extends to the buccal margin of the tooth, uniting with the distinct mesostyle. The mesostyle is absent on P4 of half of the specimens.

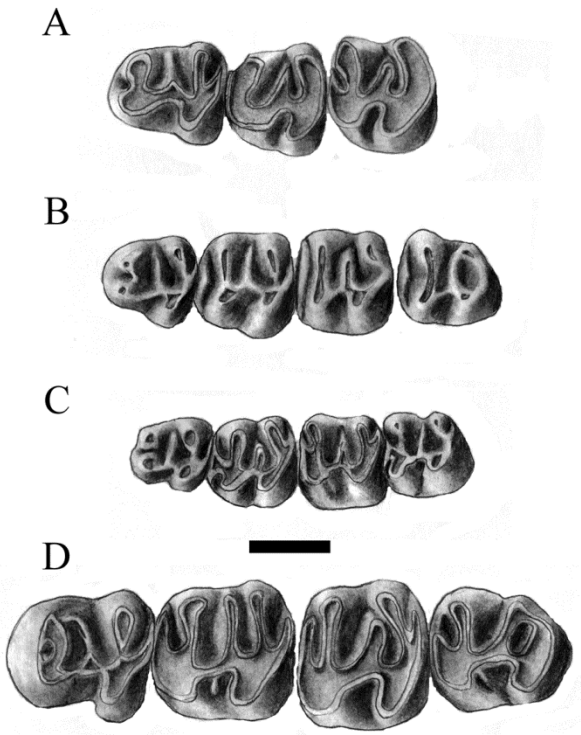

FIGURE 2. Lower cheek teeth of species of *Paradjidaumo* (*Paradjidamumo*). A, *P. (P.) trilophus*, CM 9758. Right p4-m2 (reversed). B, *P. (P.) disjunctus*, CM 71450 (holotype), left p4-m3. C, *P. (P.) nanus*, CM 84006, right p4-m3 (reversed). D. *P. (P.) spokanensis*, USNM 20505, left p4-m3. Anterior to left. Bar scale = 1 mm.

The anteroposterior length of M3 is variable (Table 4), but the morphology does not greatly differ; the shorter teeth have the same morphology as the longer M3s, but the lophs are more compressed anteroposteriorly.

The p4 is always smaller than m1 (Figure 2B, Table 4). The occlusal pattern generally follows that of other species. A minute, circular trigonid basin is always present, and closed anteriorly on 12 of 15 specmiens. The posterior cingulum is generally short but minute to absent on three specimens. The mesolophid is always short, never reaching the lingual margin of the tooth.

The molars are similar to those of other species, but the anterior cingulid does not fuse with the protoconid until at least moderate wear. The mesolophid never reaches the lingual margin of the tooth as it does in other species. The posterior cingulid

TABLE 4. Dental measurements of *Paradjidaumo (Paradjidaumo) disjunctus*. Measurements in mm. Abbreviations as in Table 2.

	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3L
N	19	19	24	24	18	18	12	12	12
M	1.24	1.25	1.29	1.35	1.29	1.37	1.27	1.16	5.28
Min	1.19	1.15	1.20	1.25	1.20	1.24	1.16	1.09	5.01
Max	1.36	1.40	1.36	1.44	1.41	1.54	1.33	1.24	5.53
SD	0.05	0.07	0.05	0.05	0.06	0.09	0.05	0.05	0.16
CV	3.64	5.30	3.79	3.46	4.98	6.36	3.80	3.95	3.09
	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
N	10	10	17	16	9	9	5	5	5
M	1.23	1.35	1.30	1.49	1.16	1.43	0.88	1.11	4.80
Min	1.13	1.24	1.23	1.40	1.06	1.22	0.80	0.95	4.48
Max	1.33	1.45	1.40	1.67	1.27	1.50	0.95	1.25	5.08
SD	0.07	0.06	0.06	0.07	0.07	0.08	0.07	0.15	0.26
CV	5.94	4.69	4.32	4.55	5.87	5.87	7.36	13.30	5.34

is minute to absent on all specimens of m2 (absent on three of 12 specmiens). The m3 is the smallest of the molars. The mesolophid is continuous with the entoconid on all specimens except CM 71458, where it ends just short of the entoconid. On most specimens, the posterior cingulid is continuous with the entoconid, forming an oval enamel lake on the posterior half of the tooth enclosed anteriorly by the mesolophid. On two specimens, the posterior cingulid ends before meeting the entoconid, forming a small, narrow valley between them.

Discussion—*Paradjidaumo (P.) disjunctus* differs from other species of the genus in the lower crown-height of the molars, incomplete connection of the anterior cingulid to the protoconid on the lower molars, short mesolophs (-ids), and having premolars shorter than the first molar (Table 5). In size, it is similar to *P. (P.) hansonourm*, larger than the Chadronian *P. nanus*, and smaller than all other species of the subgenus (Table 5).

The crown-height indices for the specimens of *Paradjiaumo (P.) disjunctus* average 0.28, making it the lowest-crowned species of the genus (Table 1). *Paradjidaumo (P.) disjunctus* is closest to *P. (P.) hansonorum* in size and crown-height, but differs from the latter in having premolars that are equal to, or shorter than, the first molars. In *P. (P.) hansonorum*, P4 and p4 are longer than the molars (Storer 1978; Emry and Korth 2013). Statistical analysis of the measurements of the premolars (Student's t-test and Mann-Whitney test) demonstrates that *P. (P.) disjunctus* is distinct at the 95% confidence level from the two populations of *P. (P.) hansonorum* in the length of the premolars. The crown-height of the molars of *P. (P.) disjunctus* is slightly less than that of *P. (P.) hansonorum* (Table 1).

Paradjidaumo (Paradjidaumo) nanus Emry and Korth, 2013
(Figure 2 C, 3C; Table 6)

Type Specimen—USNM 256759, right mandible with i1 and p4-m3.

Additional Referred Specimens—From McCarty's Mountain: CM 84006, mandible with i1 and p4-m3; CM 84007, 84008, mandible with p4-m2; and CM 84010, partial mandible with m2-m3. From Diamond O: UMVC 2621, partial mandible with p4 and m1.

Occurrence—Holotype and hypodigm from the middle Chadronian White River Formation of the Flagstaff Rim area, Wyoming (Emry and Korth 2013). CM and UMVC specimens from early Chadronian (late Eocene) McCarty's Mountain fauna, Renova

Formation, Madison County, Montana, and Diamond O Ranch fauna, Renova Formation, Climbing Arrow Member, Beaverhead County, Montana (see Tabrum et al. 1996:291).

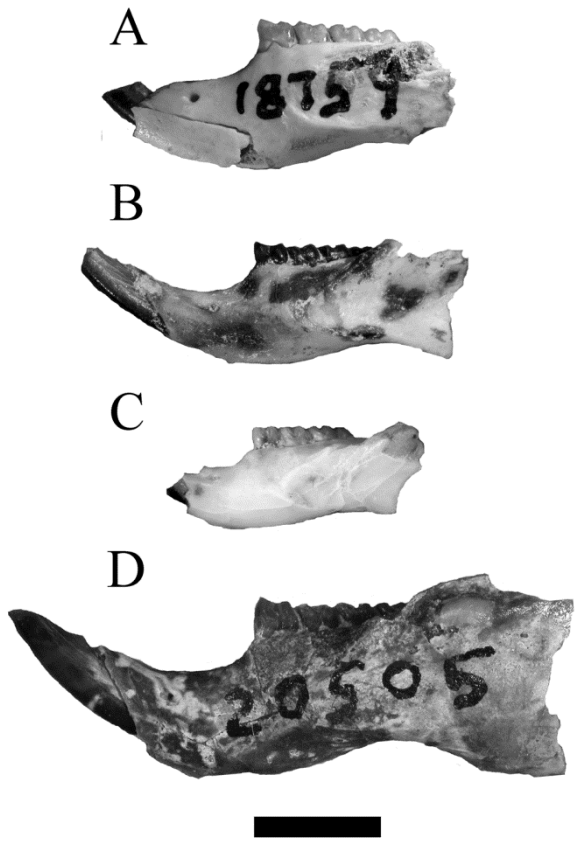

FIGURE 3. Lateral view of mandibles of species of *Paradjidaumo*. Anterior to left. A, *P. (P.) trilophus*, USNM 18759. B, *P. (P.) disjunctus*, CM . C, *P. (P.) nanus*, CM 84006, (reversed). D. *P. (P.) spokanensis*, USNM 20505. Bar scale = 5 mm.

Discussion—*Paradjidaumo (P.) nanus* was originally described by Emry and Korth (2013) from the middle Chadronian of Flagstaff Rim, Wyoming. The additional referred specimens of *P. (P.) nanus* from the early Chadronian of Montana do not alter the diagnosis of the species, but extend the range of the species back into the early Chadronian. There is only one slight variation of morphology in the referred Montana material from the original sample of *P. nanus*. The anterior cingulid on lower molars unites with the protoconid as in other species of the genus, but on the least worn specimens, there is a distinct anterostylid just anterior to the protoconid. In one specimen, CM 84006 (Figure 2C), the initial junction of the cingulid on m1 and m3 is lingual to the buccal end as in *Adjidaumo*. On m2 of this specimen and on all other specimens, the union is at the buccal end of the cingulid. It is likely that after moderate wear, a similar connection will form on m1 and m3 of CM 84006. All other morphologies of the lower cheek teeth are as in other species. In the earliest stages of wear, the anterior cingulid is attached to the protoconid and not separated as in *P. (P.) hansonorum* and *P. (P.) disjunctus*.

TABLE 5. Ratio of lengths of p4 to m1 (p4L/m1) and alveolar length of lower tooth row (p4-m3L) in species of *Paradjidaumo*. Length of p4-m3 in mm. Range of values for *P. (P.) trilophus* based on samples from different localities. *, species known only from isolated teeth or incomplete tooth rows.

	mean p4L/m1L	mean p4-m3L
P. (M.) alberti	0.93	*
P. (M.) reynoldsi	0.95	*
P. (P.) nanus	0.95	4.79
P. (P.) disjunctus	0.96	5.28
P. (P.) trilophus	1.01-1.04	5.60-5.73
P. (P.) spokanensis	1.02	6.47
P. (P.) validus	1.12	7.24
P. (P.) hansonorum	1.12	*

Paradjidaumo (Paradjidaumo) validus Korth, 1980

Type Specimen—UNSM 55811, mandible with right p4-m2.

Referred Specimen—UNSM 81067, mandible with right m2.

Occurrence—Late Orellan (early Oligocene), Orella Member, Brule Formation, Sioux County Nebraska (see Korth 1989b:43).

Amended Diagnosis—Largest sized species; long mesolophid on lower molars; accessory anteroposterior lophid between mesolophid and hypolophid on p4-m2; posterior cingulid on lower molars shorter than in type species; p4 longer relative to m1 than in other species; high crown-height (mean index = 0.35).

Discussion—No additional material of this species has been recovered since its description and last review (Korth 1980, 1989b). Measurement of the crown-height of the available specimens shows that, along with its larger size, *Paradjidaumo (P.) validus* has high-crowned molars, comparable to those of the contemporaneous type species, *P. (P.) trilophus* (Table 1).

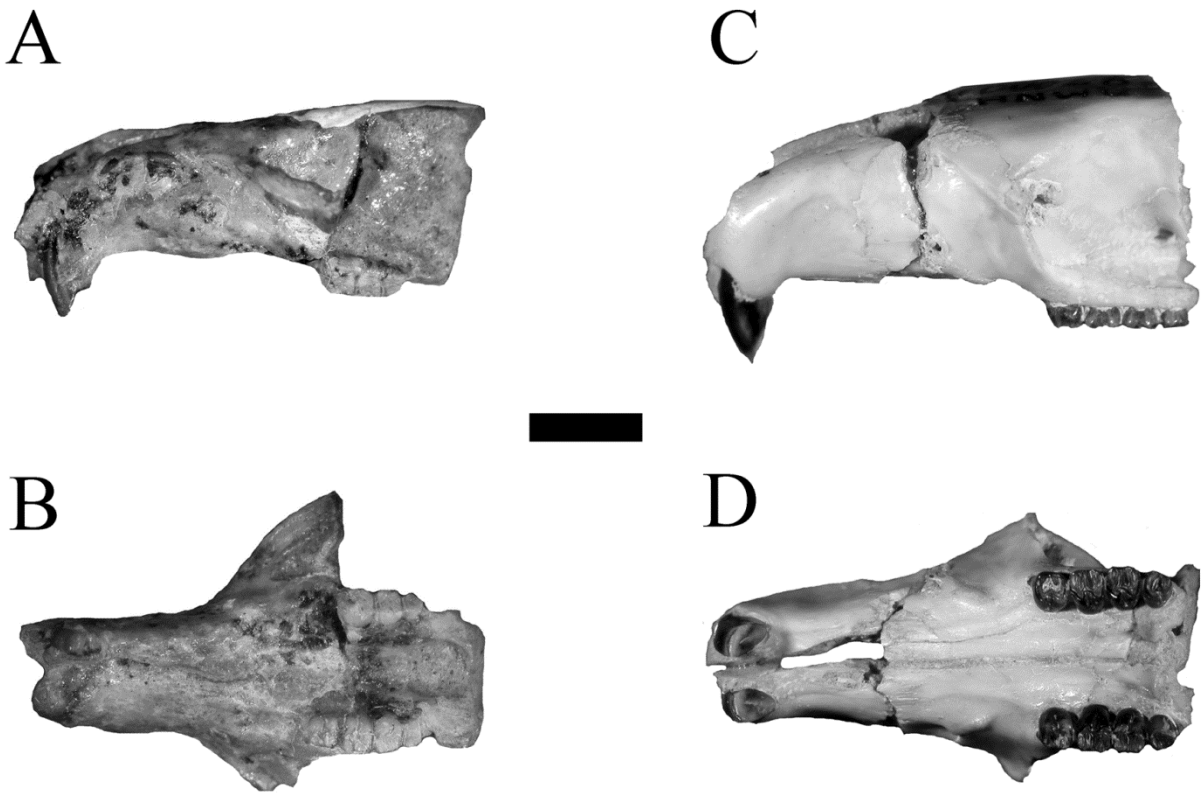

FIGURE 4. Crania of *Paradjidaumo* (*Paradjidaumo*) *disjunctus* and *P. (P.) spokanensis*. A-B, *P. (P.) disjunctus*, CM 296. A. lateral view. B, ventral view. C-D, *P. (P.) spokanensis*, AMNH 9700. C, lateral view, D, ventral view. Anterior to left. Bar scale = 5 mm.

TABLE 6. Dental measurements of *Paradjidaumo (P.) nanus* from McCarty's Mountain, Montana. Measurements in mm. Abbreviations as in Table 2.

	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3L
N	7	4	7	4	4	4	2	2	5
M	1.06	1.00	1.12	1.17	1.08	1.18	1.05	1.03	4.79
Min	0.98	0.94	1.04	1.10	1.04	1.12	1.01	0.97	4.43
Max	1.23	1.10	1.20	1.24	1.10	1.27	1.09	1.08	4.98
SD	0.10	0.07	0.06	0.06	0.03	0.07	0.06	0.08	0.22
CV	9.04	7.36	5.36	4.91	2.62	5.58	5.39	7.59	4.59

Paradjidaumo (Paradjidaumo) spokanensis White, 1954
(Figure 1C, 2D, 3D, 4C-D; Tables 7, 8)

Type Specimen—USNM 18760, crushed partial skull with left and right P4-M3 and associated right mandible with i1 and p4-m3 (Korth 1980:text-fig. 3).

Referred Specimens—From Canyon Ferry: USNM 20505, left mandible with i1 and p4-m3; from North Dakota: F:AM 94994, AMNH 9700, and AMNH 96967 anterior portions of skulls with incisors and cheek teeth, F:AM 949468, F:AM 94936, and F:AM 94971, mandibles with i1 and p4-m3.

Occurrence—Holotype and USNM 20505 from Orellan (early Oligocene) locality 24LC15, Dunbar Creek Formation, Lewis and Clark County, Montana (see White 1954). F:AM and AMNH specimens from Orellan Brule Formation, Chalky Buttes, Slope County, and Fitterer Ranch, Stark County, North Dakota (see Murphy et al. 1993).

Emended Diagnosis—Larger than all other species except *P. (P.) validus*; crown-height of molars intermediate (mean index = 0.33); P4/p4 longer than M1/m1; anterior cingulid on lower molars attached to protoconid on unworn specimens.

Description—The skull morphology does not differ from that previously described for the genus (Wilson 1949; Wahlert 1978) except in slightly larger size reported here (Table 8). Two of the specimens referred to *P. (P.) spokanensis*, AMNH 96967 and AMNH 97000, were included in the description of the skull of *Paradjidaumo* presented by Wahlert (1978:3), listed as "*P.* sp. cf. *trilophus*."

The overall occlusal pattern of the lower cheek teeth is similar to that of other species of *Paradjidaumo* (see Wood 1937; Black 1965). The upper cheek teeth also share the distinct morphology of the genus (Figure 1C). The anterior cingulum of P4 is always minute, but present. The variation in P4 is in the length and shape of the mesoloph. In one specimen, AMNH 9700, it is very short, and the central basin of the tooth is closed buccally by a loph that runs from the paracone to the metacone along the buccal margin. The most distinct morphology is on F:AM 94994, in which the mesoloph ends short of the buccal margin of the tooth but has several short branches that extend both anteriorly and posteriorly.

On M1 and M2, the mesolophs are long and extend to the buccal edge of the tooth. All other morphologies are the same as in other species. M3 is greatly reduced in size, and is oval in occlusal outline. The measurements of M3 are approximately 80% that of M2. The paracone and protocone are the only recognizable cusps; the posterior half of the tooth is greatly reduced.

On the lower cheek teeth, the greatest variability is in p4. The trigonid basin can either be open or closed anteriorly by a short metalophulid I, enclosing a minute basin. The posterior cingulid on p4 is not as variable as in other species, extending for approximately the lingual third of the tooth. The mesolophids are long on all the lower cheek teeth, generally reaching the opposite edge of the tooth (Figure 2D). On p4 and m3 of USNM 20505, the lingual end of the mesolophid fuses with one of the lingual cusps; the entoconid on m3 and the metaconid on p4. The p4 is slightly longer than m1 on average (Tables 5, 8).

Discussion—The holotype of *Paradjidaumo (P.) spokanensis* has been described and figured elsewhere (White 1954; Korth 1980:fig. 3). The cheek teeth of the holotype are heavily worn so few details of the occlusal morphology are evident. Since the original description, one additional specimen referable to this species has been discovered from the holotype locality, USNM 20505, a mandible with complete dentition and only moderately worn cheek teeth. In addition, numerous specimens referable to *P. (P.) spokanensis* have been recovered from the Orellan of North Dakota, which has allowed for a more detailed understanding of the morphology of the species. *Paradjidaumo (P.) spokanensis* is distinct from other species in its larger size (only *P. (P.) validus* is larger). *P. (P.) spokanensis* differs from *P. validus* in also having slightly lower-crowned molars (Table 1), having shorter p4 relative to m1 (Table 5), and lacking the accessory lophid on the lower cheek teeth of *P. (P.) validus* (see Korth 1980).

Paradjidaumo (Paradjidaumo) hansonorum (Russell, 1972)

Adjidaumo hansonorum Russell, 1972
Paradjidaumo hansonorum (Russell) Storer, 1978

Occurrence—Middle Chadronian Cypress Hills Formation, Saskatchewan, and early to middle Chadronian White River Formation, Flagstaff Rim Area, Wyoming.

Discussion—*Paradjidaumo hansonorum* was originally described from the Chadronian of Saskatchewan (Russell 1972; Storer 1978). Recently, Emry and Korth (2013) described a large sample of isolated cheek teeth of *Paradjidaumo* from Wyoming that was referable to this species. *Paradjidaumo (P.) hansonorum* is distinguished by its intermediate crown-height (Table 1), the union of the anterior cingulid on the lower molars occuring only after moderate wear, and the P4/p4 are relatively larger compared to the first molar than in other species (Table 5). In size and morphology, *P. (P.) hansonorum* is closest to *P. (P.) disjunctus* but differs from the latter in having larger premolars and slightly higher-crowned cheek teeth.

TABLE 7. Cranial measurements of *Paradjidaumo (Paradjidaumo) spokanensis* compared to those of *P. (P.) trilophus*. Measurements in mm. * *P. (P.) trilophus* measurements form Wilson (1946).

	*P. trilophus**	*P. spokanensis*			
Specimen #		F:AM 9700	F:AM 96967	F:AM 94994	mean
Rostrum depth	6.4	8.56		7.20	7.88
Rostrum width	5.8	8.90		7.77	8.34
Postorbital constriction	4.8	5.54		6.60	6.07
Palate width at M3	3.6	4.91		4.48	4.70
palate width at P4	2.6	4.10	3.77	3.95	3.94
Incisive foramen (in) length			2.88	2.65	2.77
Diastema length	9.1	11.71	10.38	12.21	11.43
in/diastema index	0.24-0.31		0.28	0.22	0.25

TABLE 8. Dental measurements of *Paradjidaumo (P.) spokanensis*. Measurements in mm. Abbreviations as in Table 2.

	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3L
N	5	5	5	5	5	5	2	2	5
M	1.61	1.50	1.57	1.59	1.53	1.64	1.55	1.40	6.47
Min	1.52	1.41	1.50	1.57	1.47	1.51	1.50	1.39	6.18
Max	1.70	1.56	1.70	1.60	1.60	1.71	1.59	1.40	6.76
SD	0.07	0.06	0.08	0.01	0.05	0.08			0.25
CV	4.39	3.86	4.87	0.85	3.14	5.15			3.87

	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
N	7	7	7	7	6	6	5	5	5
M	1.62	1.69	1.52	1.76	1.44	1.76	1.12	1.48	6.21
Min	1.43	1.60	1.43	1.55	1.36	1.55	1.00	1.36	6.00
Max	1.92	1.79	1.58	1.90	1.50	1.90	1.20	1.70	6.43
SD	0.18	0.08	0.05	0.11	0.06	0.12	0.10	0.14	0.17
CV	11.14	4.48	3.30	6.00	4.00	6.88	8.52	9.33	2.66

Subgenus *Macroadjidaumo* n. subgen.

Type Species—*Parajadjidaumo alberti* Russell, 1954.

Referred Species—*P. (M.) reynoldsi* Kelly, 1992.

Range—Duchesnean (middle Eocene) of southern California and Chadronian (late Eocene) of Saskatchewan.

Diagnosis—Small species; lower molars (m1-m2) longer than wide; mean crown-height index of lower molars greater than 0.37; p4 always smaller than m1.

Etymology—Greek, *makros*, long; and *Adjidaumo*, commonly used root for eomyid rodents from North America.

Paradjidaumo (*Macroadjidaumo*) *alberti* Russell, 1954
(Figure 5A, Table 9)

Type Specimen—NMC 8915, mandible with p4-m2.

Referred Specimen—CM 19933, partial mandible with m1-m2.

Occurrence—Chadronian (late Eocene), Kishenehn Formation (locality E4 of Russell [1954] and NFF-2 of Pierce and Constenius [2001]), British Columbia.

Emended Diagnosis—Larger than *P. reynoldsi*; anterior cingulid on lower molars attached to protoconid on all specimens; ectolophid not complete on p4.

Discussion—*Paradjidaumo (M.) alberti* is distinguishable from other species by its small size, higher crown-height (mean index = 0.38), and proportions of m1 and m2. This is also true for *P. (M.) reynoldsi*, but in the latter, the difference between the length and width is slight, whereas in *P. (M.) alberti* the length is 6 to 7% greater than the width. As in *P. (M.) reynoldsi*, despite its early occurrence, the molars of *P. (M.) alberti* are higher-crowned than other species (Table 1). These latter unique features (proportions of lower molars and high crown-height) unite these two species into the subgenus *Macroadjidaumo*.

Previously, *Paradjidaumo (M.) alberti* has been entirely based on the type specimen (NMC 8915), a mandible with p4-m2 (Russell 1954). Since the original description only one additional specimen has been discovered from the type area, CM 19933, a partial mandible with m1-m2. The size and crown-height of the referred specimen are nearly identical to that of the holotype (Table 9).

In the original description of *Paradjidaumo (M.) alberti*, Russell (1954) suggested a Duchesnean age for the fauna. More recently, Pierce and Constenius (2001) made a detailed study of the geology of the Kishenehn Formation and referred all of the specimens from Russell's fauna to the Chadronian.

Paradjidaumo (Macroadjidaumo) reynoldsi Kelly, 1992
(Figure 5B-G; Table 9)

Type Specimen—LACM 131042, right p4.

Referred Specimens—Over 100 isolated cheek teeth (see Kelly [1992:106]; Kelly [2010:55]).

Emended Diagnosis—Small species (smaller than *P. (M.) alberti*); anterior cingulid separated from protoconid on little-worn specimens; ectolophid complete on p4.

Occurrence—Late Duchesnean (late middle Eocene), Simi Valley Landfill local fauna, Middle Member, Sespe Formation, Los Angeles County, California.

Discussion—*Paradjidaumo (M.) reynoldsi* is fully described and figured elsewhere (Kelly 1992, 2010). It is the earliest occurring species of the genus (Duchesnean). Its record is limited to isolated teeth. It can be distinguished from other species of *Paradjidaumo* by its small size and having m1 and m2 slightly longer than wide. In all other species except *P. (M.) alberti*, these teeth are wider than long. The anterior cingulid attaches to the protoconid on the lower molars only after moderate wear, as in *P. (P.) hansonorum* and *P. (P.) disjunctus*. *P. (M.) reynoldsi* is also one of the higher-crowned species (Table 1).

In the original diagnosis of *P. (M.) reynoldsi*, Kelly (1992) noted that p4 was relatively larger compared to the molars than in *P. (M.) alberti*. However, with additional specimens of *P. (M.) reynoldsi*, the relative measurements of p4 and the molars is nearly identical in the two species (Kelly 2010:table 4; Table 5, this paper). Besides its slightly smaller size, *P. (M.) reynoldsi* can be distinguished from *P. (M.) alberti* by the ectolophid being continuous to the hypoconid on p4 (interrupted in *P. (M.) alberti*), the lower molars being more nearly square in occlusal outline (not quite as elongated as in *P. alberti*; both features cited in the original diagnosis of *P. (M.) reynoldsi* [Kelly 1992]), and the anterior cingulid not being attached to the protoconid in early stages of wear (always connected in *P. (M.) alberti*).

Due to the similarity in size minor morphological differences (ectolpohid of p4) of the two species referred to the subgenus *Macroadjidaumo*, it is possible that they are synonymous even though they differ in age of occurrence. Before a synonymy can be proposed, direct comparison must be made of the available material. This comparison was not done as part of this study, so such a synonymy will not be proposed here.

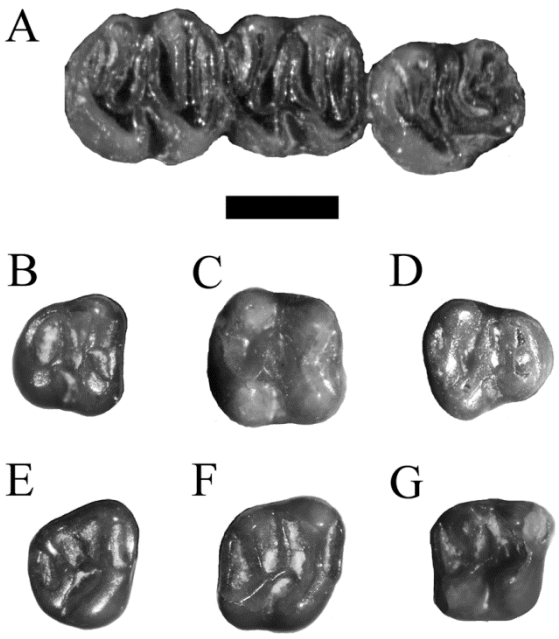

FIGURE 5. Cheek teeth of *Paradjidaumo* (*Macroadjidaumo*). A, *P.* (*M.*) *alberti*, NMC 9815 (holotype), right m1-m3. B-G, *P.* (*M.*) *reynoldsi*. B, LACM 153858, left m3 (reversed). C. LAMC 153826, right m1f or m2. D, LACM 153791, right p4. E, LACM 153848, right M3. F, LACM 153804, right M1 or M2. G, LACM 153772, right P4. Anterior to right. Bar scale = 1 mm.

CONCLUSIONS

Occurrence—In a chart of occurrence of eomyids from North America Flynn (2008:fig. 25.3) showed the range of *Parajidaumo* as occurring from the end of the Bridgerian (middle Eocene) into the Hemingfordian (early Miocene). The only Arikareean occurrence was from the Blue Ash fauna (=Harris Ranch) of South Dakota that has been shown to be Whitneyan in age (Korth 2010). The Hemingfordian occurrence is based on a questionable reference of four isolated teeth from Saskatchewan identified as ?*Paradjidaumo* (Skwara 1988). Although four teeth of the latter were cited, only a single M1 or M2 was described and figured (Skwara 1988:pl. 14, fig. 1). As noted by Skwara (1988), these specimens may possibly be referable to another mesodont eomyid such as *Metadjidaumo* (Setoguchi 1978; Korth 1981). Thus, the latest definite occurrence of *Paradjidaumo* is from the Whitneyan.

The earliest occurrence of *Paradjidaumo* according to Flynn (2008) is from the late Uintan. This was based on specimens from southern California cited by Walsh (1996). However, it was later determined that these specimens were referable to an unnamed eomyid genus and not *Paradjidaumo* (Kelly et al. 2012). Thus, the range of *Paradjidaumo* extends from the Duchesnean (late middle Eocene) through the Whitneyan (middle Oligocene).

TABLE 9. Dental measurements of *Paradjidaumo (Macroadjidaumo)*. Measurements in mm. Abbreviations as in Table 2. Mean measurements of *P. (M.) reynoldsi* from Kelly (2010:table 4). *, indicates m1 or m2 (based only on isolated teeth).

	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
P. alberti								
NMC 8915 (type)	1.16	1.13	1.25	1.24	1.32	1.23		
CM 19933			1.32	1.23	1.35	1.26		
Mean	1.16	1.13	1.29	1.23	1.34	1.25		
P. reynoldsi								
Mean	1.15	1.11	1.21*	1.18*			1.00	0.99

Evolution within Paradjidaumo—Few morphological changes within the species of *Paradjidaumo* can be traced from its earliest occurrence through its latest. The only morphology that appears in the earliest species that is later modified is the attachment of the anterior cingulid on the lower molars. In the early species of both subgenera (Duchesnean and Chadronian), *P. (Macroadjidaumo) reynoldsi*, *P. (Paradjidaumo) disjunctus*, and *P. (P.) hansonorum*, the anterior cingulid is unattached until at least moderate levels of wear on the teeth. In all other Chadronian and later species this connection is complete on even unworn teeth.

Paradjidaumo reynoldsi and *P. alberti* are unique among species of the genus because of the proportions of m1 and m2 (length greater than width) and the crown-height is among the highest of all species (Table 1). Because of these morphologies they have been referred to the subgenus *Macroadjidaumo*. Within *P. (Macroadjidaumo)* the Duchesnean species, *P. (M.) reynoldsi*, lacks the attachment of the anterior cingulid on the lower molars and the Chadronian species does not. *P. (M.) reynoldsi* has lower molars that are slightly longer than wide, and in *P. (M.) alberti*, the length is

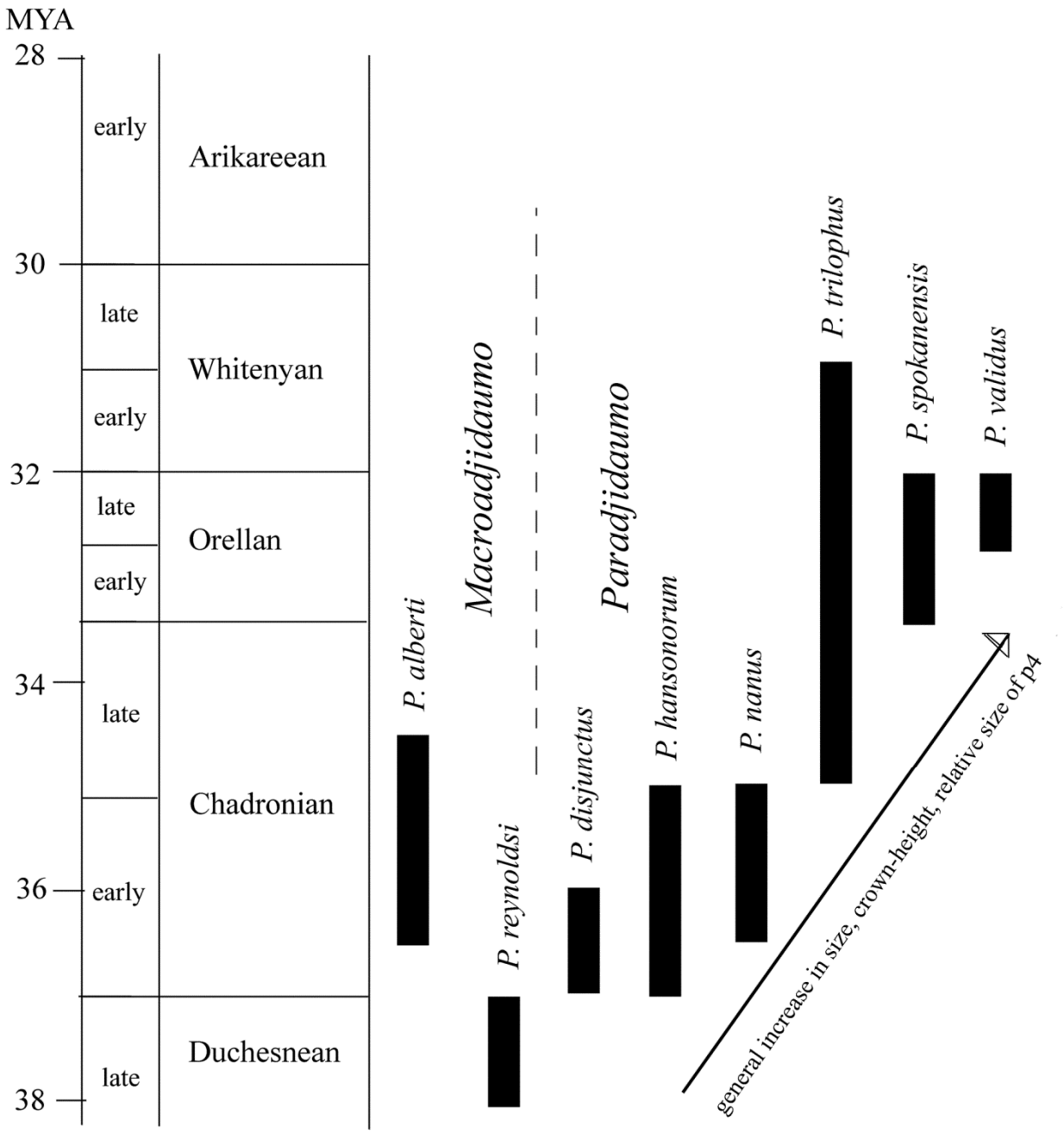

FIGURE 6. Occurrence of species of *Paradjidaumo* from North America.

distinctly greater, demonstrating an increased length through time.

Within the subgenus *Parajidaumo (Paradjidaumo)* a group of species appears to show an increase in size, relative length of p4, and crown-height through time (Figure 6); *P. (P.) nanus*, *P. (P.) trilophus*, *P. (P.) spokanensis*, and *P. (P.) validus*). Within this group, the Chadronian *P. (P.) nanus* is the smallest, with the shortest p4 relative to m1 (Table 5) and lowest crowned lower molars (Table 1). The remainder, *P. (P.) trilophus*, *P. (P.) spokanensis* and *P. (P.) validus* show increase in size and relative size of the lower premolar (Table 5). In crown-height, the only species in this sequence that does not follow the trend is *P. spokanensis* which has slightly lower-crowned molars than *P. (P.) validus* and *P. (P.) trilophus*. The latter two species have molars of equal crown-height (Table 1). In terms of occurrence, *P. (P.)*

trilophus is known from the middle Chadronian through the Whitneyan whereas the other two species are limited to the Orellan. However, if the first occurrence is considered, *P. (P.) trilophus* first appears in the middle Chadronian, *P. (P.) spokanensis* in the Orellan, and *P. (P.) validus* in the late Orellan. The increase in size and relative length of the premolar follows this sequence.

Paradjidaumo (P.) disjunctus may be associated with the *P. nanus-trilophus-spokanensis-validus* group. It has a lower crown-height index than this entire group (Table 1), has a small p4 relative to m1 (equivalent to that of *P. (P.) nanus* (Table 5); and maintains the primitive condition of the anterior cingulid on the lower molars. Its occurrence also fits with this group in that it is limited to the early Chadronian or early-middle Chadronian boundary, earlier than all of the other species. The feature of *P. (P.) disjunctus* that makes its inclusion in this group questionable is its size. It is slightly larger than *P. (P.) nanus*. Other than size, *P. (P.) disjunctus* would fit into the morphological sequence of this group.

Paradjidaumo (P.) hansonorum has an intermediate crown-height of the molars and retains the primitive condition of the lack of attachment of the anterior cingulid on the lower molars. *P. (P.) hansonorum* is unique in that the premolars are of a much greater length relative to M1/m1 than all other species except the most derived and later occurring *P. (P.) validus* (Table 5). *P. (P.) hansonorum* cannot be easily grouped with any other species of the subgenus but is retained in it due to its shared morphology of the proportions and crown-height of the lower molars.

Systematic Relationships—Burke (1934), in first naming *Paradjidaumo*, recognized two groups of rodents within the family "Adjidaumidae": the more primitive *Protadjidaumo-Adjidaumo* group, and the more derived *Paradjidaumo*. Fahlbusch (1979:fig. 1) recognized *Paradjidaumo* as part of the North American radiation of the family, but viewed it as isolated from both earlier and later genera. Korth (1980) noted that the unique attachment of the anterior cingulid on the lower molars of *Paradjidaumo* was elsewhere only known in the Chadronian *Centimanomys* Galbreath, 1955, and Orellan *Metadjidaumo* (Setoguchi, 1978; Korth, 1981). However, only the latter of these shares the mesodonty of the cheek teeth with *Paradjidaumo*. A third mesodont eomyid, *Orelladjidaumo* was diagnosed as having mesodont, lophate cheek teeth as in *Paradjidaumo* and a close relationship between *Orelladjidaumo*, *Metadjidaumo*, and *Paradjidaumo* was suggested (Korth, 1989b). More recently, in his review of North American Eomyidae, Flynn (2008:fig. 25.2) presented a phylogeny where *Paradjidaumo*, *Orelladjidaumo*, and *Metadjidaumo* were grouped in a single clade. Korth (2008) named a new genus, *Neoadjidaumo* from the Arikareean, and noted the similarity in crown-height and occlusal morphology (particularly the reduced posterior cingulid on the lower cheek teeth) with *Metadjidaumo*.

It appears that the crown-height (mesodonty), reduction of the posterior cingulids and buccal attachment of the anterior cingulid of the lower molars, unite *Paradjidaumo*, *Metadjidaumo*, and *Neoadjiadumo*. Within this group there is a continued reduction of the posterior cingulids on the lower molars and closer position of the anterior cingulids with the metalophids as well (shallower valley between metalophid and anterior cingulid) that is progressive through the aforementioned sequence of genera. The only mesodont and lophate eomyid previously considered closely related to *Paradjidaumo* that cannot be definitely included in this group is *Orelladjidaumo*. The latter differs from the other genera in the presence of unilateral hyposonty on the upper molars and having upper cheek teeth longer relative to width. Unfortunately, the lower dentition is not known for *Orelladjidaumo*. At present *Orelladjidaumo* cannot be placed in the *Paradjidaumo-Metadjidaumo-Neoadjidaumo* clade with confidence.

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