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Small Oligocene Amphicyonids from North America (*Paradaphoenus*, Mammalia, Carnivora)

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ABSTRACT

North American amphicyonid carnivorans are important members of the mid-Cenozoic terrestrial carnivore community during the late Eocene to late Miocene (Duchesnean to Clarendonian). Species range in size from < 5 kg to > 200 kg. Among the smallest and rarest amphicyonids are Oligocene species of *Paradaphoenus* Wortman and Matthew, found at a few localities in the Great Plains and the Pacific Northwest. *Paradaphoenus* is known from only 10 individuals placed in 3 species (*P. minimus*; *P. tooheyi*, n. sp.; *P. cuspigerus*), representing a single lineage ranging from the Orellan to Arikareean. The existence of three skulls, one with associated mandibles, allows the identification of diagnostic basicranial and dental traits that place the genus in the Amphicyonidae. Basicranial anatomy, including a rudimentary ectotympanic auditory bulla, distinguishes the genus from more abundant small contemporary canids, such as *Hesperocyon*. The species of *Paradaphoenus* most likely adopted ecological roles similar to the smaller living foxes.

INTRODUCTION

Amphicyonid carnivores are a geographically widespread family of mid-Cenozoic arctoid carnivorans ranging in size from < 5 kg to > 200 kg. Although known from Eurasia, North America, and Africa, most fossils have come from western Europe and the United States. The oldest North American amphicyonids from the late Eocene and early Oligocene were relatively small (< 20 kg) carnivores, but by the early to mid-Miocene a number of lineages exceeded 100 kg and had become the dominant predators of the Holarctic continents (Hunt, 1996, 1998).

The earliest North American amphicyonids are Duchesnean (late Eocene) fossils referable to *Daphoenus lambei*, a small (2–4 kg) carnivore occurring from southern Canada to Texas (Hunt, 1996). *Daphoenus* rang-

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es from the Duchesnean to the early Arikareean and is the most common North American Paleogene amphicyonid. The Duchesnean *D. lambei* is the smallest species of this lineage and is a likely ancestor to all later *Daphoenus*. After the appearance of *Daphoenus* in the early Duchesnean, *Daphoenictis* and *Brachyrhynchocyon* first occur in the late Duchesnean and early Chadronian, respectively, coexisting with *Daphoenus* throughout the Chadronian: all of these genera are small, fox-sized carnivores (~4–10 kg). *Daphoenictis* and *Brachyrhynchocyon* become extinct at the end of the Chadronian, but *Daphoenus* persists into the Orellan (early Oligocene), and progressively increases in size during the Whitneyan. By the early Arikareean (late Oligocene), *Daphoenus* approaches the size (~20–30 kg) of a small wolf (Hunt, 1996).

Much less familiar to paleontologists is another lineage of very small amphicyonids, *Paradaphoenus* Wortman and Matthew, 1899, entirely restricted to North America. The genus first appears in Orellan sediments of the Great Plains, continues through the Whitneyan, and terminates in the early or mid-Arikareean. Members of this lineage increase only slightly in size over ~6 million years, never exceeding 3–4 kg, and are the smallest New World amphicyonids. Their remains were often placed in disparate taxa or went unrecognized in collections.

The North American hypodigm of *Paradaphoenus* includes the remains of just 10 individuals (fig. 1), allocated to 3 species, *P. minimus* (Hough, 1948a) and *P. tooheyi*, n. sp., from White River and lower Arikaree sediments of Nebraska and South Dakota, and a terminal species, *P. cuspigerus* (Cope, 1878), from the John Day beds of Oregon. Fortunately, the genus is represented by three skulls with well-preserved teeth and basicrania. *Paradaphoenus cuspigerus* is based on two skulls from the John Day beds, one of which (the holotype, fig. 2) includes both mandibles of the same individual, demonstrating a critical association between lower and upper teeth. The Orellan species, *Paradaphoenus minimus*, is oldest and is represented by a skull, several isolated mandibles, and the only known postcranial material attributable to the lineage; it has dentally plesiomorphic molars that resemble those of European *Cynodictis* from Quercy in France. The previously undescribed Whitneyan and early Arikareean *Paradaphoenus* fossils, represented by only two mandibles and an unassociated maxilla from Nebraska and South Dakota, warrant the naming of a new species, *P. tooheyi*.

A functional interpretation of the teeth, skull, and postcranial skeleton suggests that *Paradaphoenus* was a small terrestrial omnivore lacking cursorial specializations, and probably able to climb when necessary. These characteristics would be compatible with a wooded habitat, whether savanna or riverine gallery forest. Its basicranial anatomy establishes it as a member of the Amphicyonidae (Hunt, 1998).

ABBREVIATIONS

Anatomical

A	alisphenoid
ac	alisphenoid canal
BO	basioccipital
BS	basisphenoid
ca	pit for anterior crus of ectotympanic
E	caudal entotympanic
F	facet on petrosal promontorium for ectotympanic
gf	postglenoid foramen
h	hypoglossal (condyloid) foramen
L	middle lacerate foramen
m	mastoid
me	mastoid-exoccipital suture
P	petrosal promontorium
plf	posterior lacerate foramen
pp	paroccipital process
ps	basioccipital embayment for inferior petrosal venous sinus
SQ	squamosal
T	ectotympanic
x	partial M3 alveolus

Institutional

AMNH	American Museum of Natural History, New York, NY
LACM	Los Angeles County Museum of Natural History, Los Angeles, CA
UNSM	University of Nebraska State Museum, Lincoln, NE
NMB	Naturhistorisches Museum, Basel, Switzerland
SDSM	South Dakota School of Mines and Technology, Rapid City, SD

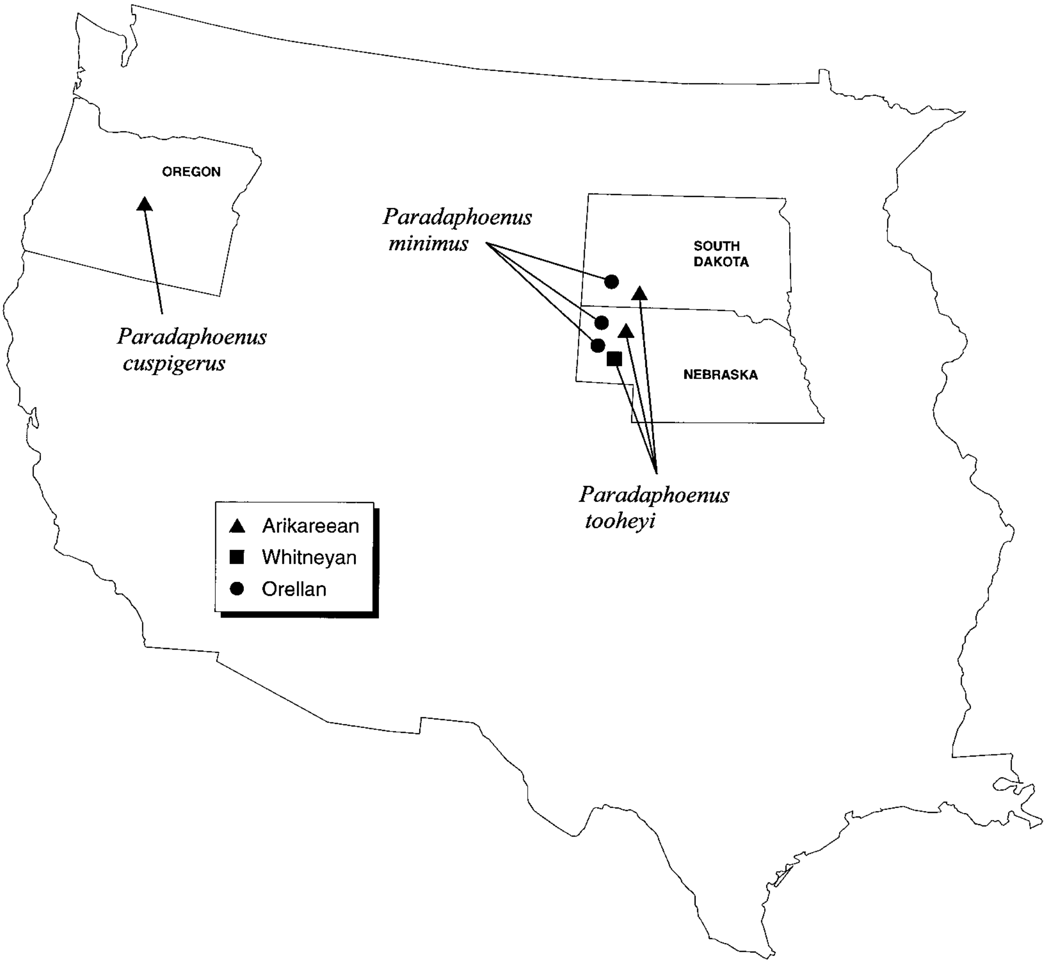

Fig. 1. Geographic distribution of *Paradaphoenus* in North America: all fossils are from Oligocene sediments of the central Great Plains (White River and Arikaree Groups, *P. minimus*, *P. tooheyi*) and Oregon (John Day Formation, *P. cuspigerus*).

SYSTEMATICS

ORDER CARNIVORA BOWDICH, 1821

DIVISION ARCTOIDEA FLOWER, 1869

FAMILY AMPHICYONIDAE TROUESSART, 1885

Paradaphoenus Wortman and Matthew, 1899

TYPE SPECIES: *Paradaphoenus cuspigerus* (Cope, 1878).

INCLUDED SPECIES: *Paradaphoenus cuspigerus*, *Paradaphoenus minimus* (Hough, 1948a), *Paradaphoenus tooheyi*, new species.

KNOWN DISTRIBUTION: Orellan, Whitneyan, and early Arikareean of western Nebraska; Orellan and early Arikareean of southwestern South Dakota; early or mid-Arikareean of central Oregon.

DIAGNOSIS: Smallest (< 3–4 kg) North American amphicyonid carnivorans with m1 lengths of 8.3–9.4 mm; rudimentary auditory bulla formed by a slightly inflated ossified ectotympanic that does not fully enclose the middle ear; dental formula 3-1-4-3/3-1-4-3; P4 length short relative to combined lengths of M1-2 (P4L/M1-2L: Orellan, 80.8%; early Arikareean, Great Plains, 77.6%; early or mid-Arikareean, Oregon, 67.7–73.2%); P4 with abbreviated protocone relative to *Da-*

Fig. 2. **(A)** Cranium and mandibles of the genoholotype of *Paradaphoenus* (*P. cuspigerus,* AMNH 6852) from the John Day Formation, Oregon (in lateral view); **(B)** stereophotographs of the same individual, initially figured by Cope (1884, P1. 68, figs. 1–4) as *Amphicyon cuspigerus*. Scale bar in this and all subsequent figures is 1 cm in length unless otherwise noted.

phoenus, *Hesperocyon*, and *Cynodictis*; M1 with well-developed meta- and paraconules as in *Cynodictis*; M2 prominent and the central member of an upper molar row that gradually diminishes in size from M1-3; m1 with basined talonid, m1 paraconid blade not anteriorly extended (it is extended in *Hesperocyon*); prominent rectangular m2 with basined talonid and anterolabial swelling of the cingulum (m1-2 talonids are markedly enlarged with prominent basins in Whitneyan and Arikareean species, less so in Orellan); postorbital/preorbital length ratio ~2:1 (table 1). Lower molars become wider in younger species; upper molars are correspondingly enlarged (table 2).

DISCUSSION: The fossils of *Paradaphoenus* fall into four samples of decreasing geologic age: (1) an Orellan sample, comprising the holotype cranium of ‘‘Daphoenus’’ *minimus* Hough 1948a (fig. 3, AMNH 39099) from near Scenic, South Dakota, and four isolated mandibles from western Nebraska (fig. 4, UNSM 25030, 25305, 26139; UNSM 25148 not illustrated), all from White River sediments; (2) an isolated Whitneyan mandible from White River sediments of western Nebraska (fig. 4, UNSM 26130, *P. tooheyi*, n. sp.), with its molar dentition evolved beyond that of the Orellan specimens, but not to the degree observed in the early Arikareean fossils; (3) a mandible from lower Arikaree sed-

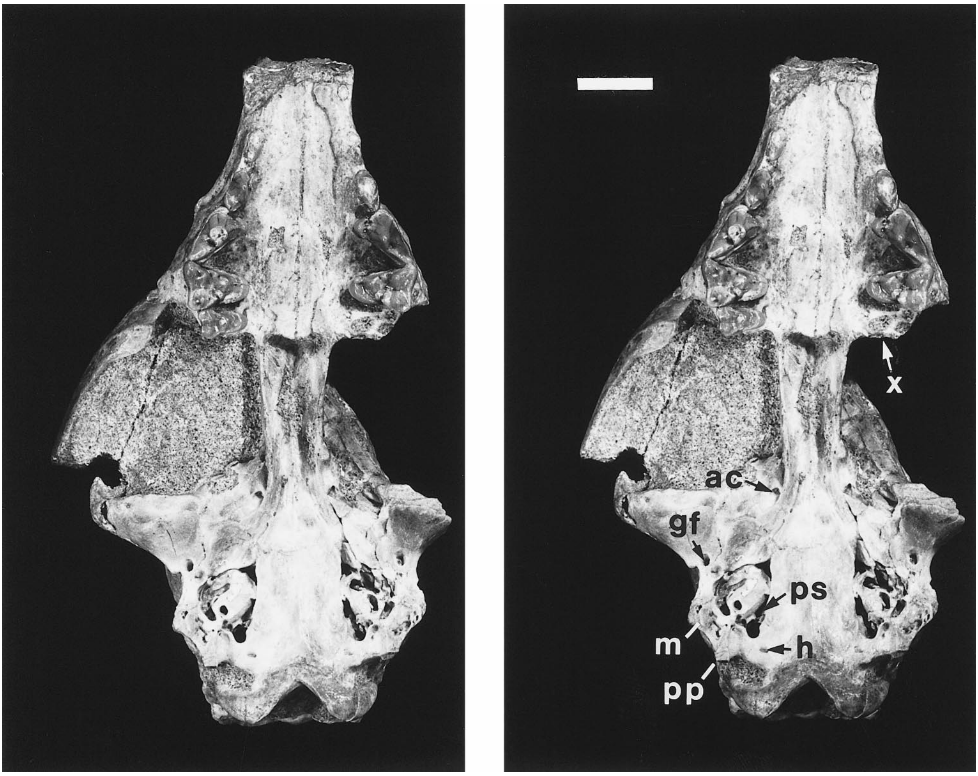

Fig. 3. Stereophotographs of the holotype cranium (in ventral view) of *Paradaphoenus minimus* (AMNH 39099), Orellan, White River Group, South Dakota. For abbreviations in this and subsequent figures, see p. 2.

iments, Wagner Quarry, Dawes Co., Nebraska (UNSM 6002-92, holotype of *P. tooheyi*, n. sp.), and a maxilla of the same species from the Sharps Formation of South Dakota (LACM 21649, *P. tooheyi*, n. sp.), both of early Arikareean age (fig. 5); (4) the cranium and associated mandibles (fig. 2, AMNH 6852, genoholotype) of *Paradaphoenus cuspigerus* (Cope, 1878), and a referred cranium of the same species (AMNH 6853, holotype of ''Amphicyon'' *entoptychi* Cope, 1879) from the John Day beds, central Oregon, both fossils unfortunately lacking exact stratigraphic data, but probably of late early to mid-Arikareean age. Geographic and stratigraphic information for these fossils is presented in appendix 1.

The Orellan cranium and mandibles are the geologically oldest remains of the genus and retain the most plesiomorphic dentition. These mandibles show no transverse broadening of m1-2 (in particular, no widening of the basined molar talonids), a character found in the younger species of the genus. This broadening of the molars is first observed in the only Whitneyan specimen of *Paradaphoenus*, a mandible with p2-m1 (UNSM 26130), and becomes most pronounced in the lower molars of the Arikareean mandibles (fig. 6). The Orellan fossils include the smallest individuals of the *Paradaphoenus* lineage, based on dental measurements and the size of the only known Orellan cranium (AMNH 39099, table 1, basilar length ∼8.8 cm). The plesiomorphic features of the molars warrant retention of Hough's (1948a) species *minimus* for the Orellan hypodigm.

The early Arikareean fossils from South Dakota and Nebraska include a maxilla with M1-2 (alveoli or broken roots of P3-4, M3) from the Sharps Formation of southwestern South Dakota, and an isolated mandible with p4-m2 (alveoli of p1-3, canine root) from a

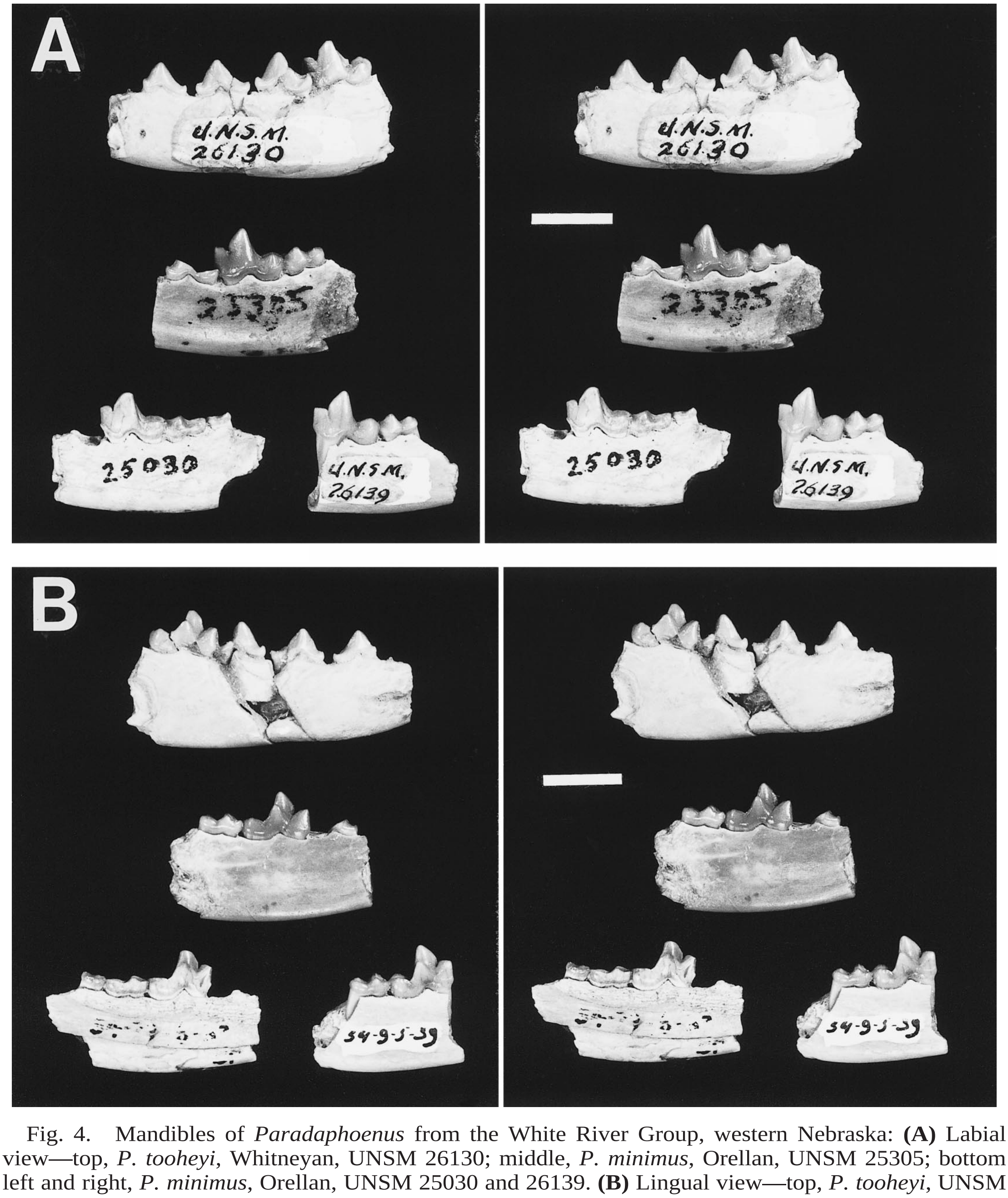

Fig. 4. Mandibles of *Paradaphoenus* from the White River Group, western Nebraska: **(A)** Labial view—top, *P. tooheyi*, Whitneyan, UNSM 26130; middle, *P. minimus*, Orellan, UNSM 25305; bottom left and right, *P. minimus*, Orellan, UNSM 25030 and 26139. **(B)** Lingual view—top, *P. tooheyi*, UNSM 26130; middle, *P. minimus*, UNSM 25305; bottom left and right, *P. minimus*, UNSM 25030 and 26139 (stereophotographs).

lower Arikaree channel fill (Wagner Quarry) in northwestern Nebraska (fig. 5). The Sharps maxilla was discovered in the collection of the Los Angeles County Museum, and is from LACM Wounded Knee Loc. 1981 (reported by J. R. Macdonald [1970] to be equivalent to SDSM Loc. V5359, near the middle of the Sharps Formation). The Wagner Quarry mandible was found in 1992 during a UNSM excavation of a basal Arikaree

TABLE 1

Preorbital, Postorbital, and Basilar Lengths of *Paradaphoenus* Crania (in mm)[a]

Taxon	Museum no.	Preorbital	Postorbital	Ratio	Basilar
Paradaphoenus cuspigerus[b]	AMNH 6852	36.4	70.2	1.93	94.8
Paradaphoenus cuspigerus	AMNH 6853	~38	68.3	1.80	~100
Paradaphoenus minimus[b]	AMNH 39099	~30	66.2	2.20	~88

[a] Preorbital length is measured from the tip of the premaxilla to the anterior border of the orbit; postorbital length is measured from the anterior border of the orbit to the occipital condyle.

[b] Holotype.

fluvial channel fill cut into sediments of the White River Group near Chadron, Nebraska; associated mammals included anthracothere, entelodont, rhinoceros, nimravid, and several rodents.

Whitneyan and early Arikareean *Paradaphoenus* fossils from Nebraska and South Dakota, although differing in age, are morphologically similar, and are placed in a new species, *Paradaphoenus tooheyi* (appendix 2), intermediate in the form of m1-2 between *P. minimus* and *P. cuspigerus*. The new species is named for Dr. Loren Toohey of Midland, Texas, who has contributed for over 60 years to UNSM field excavations in Nebraska, and participated in the 1992 Wagner Quarry excavation that discovered the holotype.

Fortunately, the Great Plains fossils of *Paradaphoenus* can be placed in established stratigraphic sequences that either are within, or can be directly correlated with, the type areas of the Orellan, Whitneyan, and Arikareean land mammal ages. The recent discovery and identification of the Whitneyan and early Arikareean fossils from Nebraska and South Dakota allowed a more accurate age estimate for the John Day specimens, which previously were difficult to date. These new fossils also document successive evolutionary stages in the *Paradaphoenus* dentition during the Orellan to Arikareean interval that support the placement of the three known species in a single lineage.

This scenario is based on an observed progressive alteration in the form of m1-m2. For example, the recently discovered Wagner Quarry mandible of *P. tooheyi* has an m2 morphology likely to have been derived from the plesiomorphic m2 of the Orellan *P. minimus*. In the Wagner Quarry m2, the trigonid is reduced and crowded to the front of the

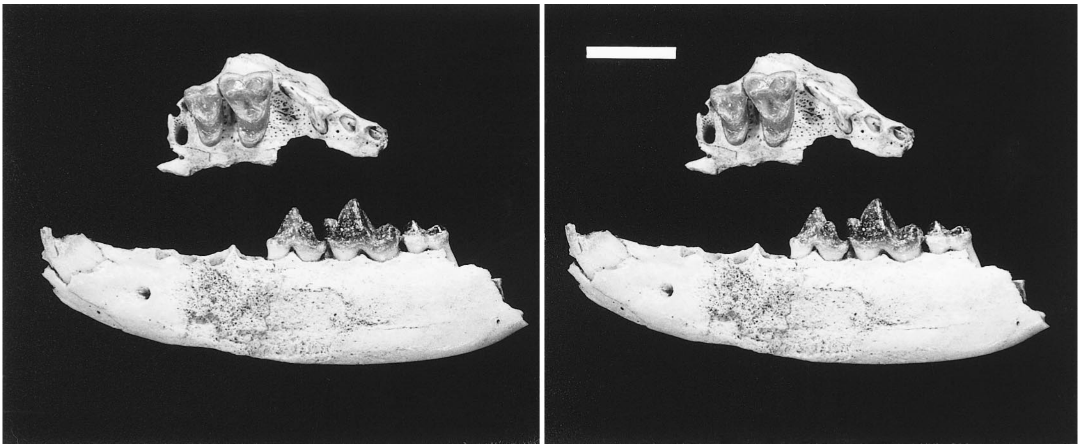

Fig. 5. Stereophotographs of the maxilla (LACM 21649, Sharps Formation, South Dakota) and holotype mandible (UNSM 6002-92, lower Arikaree Group, Nebraska) of early Arikareean *P. tooheyi*, n. sp., known only from the central Great Plains. Note alveoli for well-developed M3 in maxilla.

Fig. 6. Stereophotographs of the lower dentition of holotypes of *Paradaphoenus tooheyi* (left, UNSM 6002-92) and *P. cuspigerus* (right, AMNH 6852) in occlusal view. Note wider molars and more anteriorly placed m2 trigonid in AMNH 6852.

tooth, and the talonid is widened and more prominently basined, relative to the *P. minimus* m2, in which the unreduced trigonid occupies the anterior half of m2 and the talonid is not expanded. In the holotype mandible of the John Day *P. cuspigerus*, the widening of the molars observed in the Wagner Quarry mandible is even more pronounced (fig. 6): the m2 trigonid of the John Day species remains crowded to the anterior end of the tooth as in the Wagner Quarry mandible, but the m2 talonid is even more expanded. The lower carnassial also is broadened, particularly the basined talonid. The upper molars of the two John Day crania (AMNH 6852, 6853) also demonstrate this trend (fig. 7), for they are enlarged and broadened relative to the upper molars in the maxilla from the Sharps Formation of South Dakota (fig. 5).

The John Day crania, then, are unlikely to be of earliest Arikareean age, because their molars are more derived than those in the Wagner Quarry mandible and Sharps Formation maxilla. The John Day *P. cuspigerus* is apparently somewhat younger, possibly of late early to mid-Arikareean age, based on the observation that the amount of change in the molar teeth between *P. tooheyi* from Wagner Quarry and *P. cuspigerus* is rather modest. Lower Arikaree sediments at Wagner Quarry are probably time equivalent to lower Arikaree fluvial rocks of the Gering Formation at Wildcat Ridge in the southern Nebraska panhandle, dated at ~28.1–28.3 Ma (Tedford et al., 1996; MacFadden and Hunt, 1998). John Day *P. cuspigerus* would necessarily postdate this interval, but the amount of time involved is uncertain. Gray tuffaceous siltstone adhering to the skulls could have been derived from a number of tuffaceous units within the upper John Day Formation, but the exact horizon is indeterminate. A speculative upper age limit for the *Paradaphoenus* lineage, based on the sum of present evidence, is estimated at ~25–23 Ma.

DENTITION

Incisors: No specimens of the Orellan or Whitneyan species of *Paradaphoenus* preserve either upper or lower incisors. The anterior rostrum of the only known Orellan skull (AMNH 39099) is missing, and none of the mandibles retains the anterior part with incisor alveoli.

The early Arikareean Wagner Quarry specimen preserves the anterior part of the left mandible: although no incisors remain, there is a large i3 alveolus, but the part of the dentary with the i1-2 alveoli was lost.

In the *P. cuspigerus* holotype mandible, a partial, poorly defined i3 alveolus lies internal to the canine root. However, the upper incisor row in the premaxillae preserves an intact acuminate I3, slightly recurved and without accessory cusps. I1-2 progressively decrease in size internal to I3, but are broken off at their roots.

Canines: No canines are preserved in the Orellan or Whitneyan fossils. The Wagner Quarry Arikareean mandible retains a robust, slightly laterally compressed canine root (5.3 × 3.2 mm). The mandible of the *P. cuspigerus* holotype also contains a robust, somewhat laterally compressed canine root (5.5 × 2.8 mm), but the crown was lost. The delicate upper canine of the holotype (AMNH

6852) is laterally compressed (4.5 × 3.3 mm), and although incomplete, shows the posterior and anterointernal longitudinal enamel ridges typical of amphicyonids.

Premolars: Only one Orellan mandible (UNSM 25305, fig. 4) retains any part of a premolar; all other mandibles are broken anterior to m1. UNSM 25305 retains the base of p4 (for dental measurements, see table 2), which suggests that the premolars in the Orellan *Paradaphoenus minimus* were similar to the laterally compressed premolars in the younger species of the genus. The only mandible of Whitneyan age (*P. tooheyi*, UNSM 26130, fig. 4) retains p2-4 and a single-rooted p1 alveolus. Here p2-4 are elongate, laterally compressed teeth separated by very short diastemata; each premolar has a relatively low central cusp, an extended posterior heel with a small posterior cingulum cusp, and a slightly extended anterior cingulum; there is a small anterior cingulum cusp on p2-4.

Although the Wagner Quarry mandible (UNSM 6002-92, fig. 5) retains only p4, this tooth is somewhat taller and less elongate relative to the Whitneyan p4 of UNSM 26130. Also, the dimensions of the p2-3 alveoli in the Wagner Quarry mandible indicate that these premolars were not as elongate as in the Whitneyan specimen. In fact, the Wagner Quarry mandible and the holotype mandible of the John Day *P. cuspigerus* (AMNH 6852, figs. 2, 6) share shorter premolars without evident diastemata, relative to the Whitneyan mandible. The John Day *P. cuspigerus* mandible preserves p2-4: each premolar has a principal cusp placed slightly forward of center descending to a posterior heel that increases in size from p2 to p4; a prominent, somewhat laterally placed posterior accessory cusp occurs on p4 but is absent on p2-3. A fine enamel ridge descends the anterior face of each premolar: it is deflected to the anterointernal margin of p2, less so on p3, and continues directly forward to the anterior border of p4.

Only P3-P4 are adequately preserved in the Orellan skull (AMNH 39099, fig. 7A). In lateral view, P3 is triangular, with a small heel, but lacking a posterior accessory or cingulum cusp. P2 is separated from P1 by a diastema 4.3 mm in length in AMNH 39099, whereas diastemata between the other premolars are negligible. There is a progressive decrease in size from P3 to P1; this is also seen in the Arikareean *Paradaphoenus* skulls from the John Day beds (figs. 7B, 7C).

P4 in all *Paradaphoenus* skulls (AMNH 39099, 6852, 6853) is a short, robust carnassial, surrounded by a pronounced cingulum. P4 has a prominent but abbreviate protocone that in occlusal view is nearly confluent with the medial face of the carnassial; the protocone is not strongly extended toward the midline as in, for example, *Hesperocyon* and *Daphoenus*.

P2-4 in the John Day skulls (AMNH 6852, 6853, fig. 7) are very similar to these teeth in the Orellan skull (AMNH 39099). AMNH 6852, the *P. cuspigerus* holotype, preserves P1-4, the only complete upper premolar row known in the genus. P1 is a small, laterally compressed tooth with an anteriorly placed main cusp. P4 retains the diagnostic shape seen in all other specimens; however, the encircling cingulum is even more pronounced.

Molars: Upper molars are present in the Orellan and Arikareean skulls of *Paradaphoenus* (fig. 7), and also in the Arikareean maxilla from the Sharps Formation (fig. 5). In these specimens the molars are largely unworn, with a well-defined cusp pattern; AMNH 6853 is an exception, with somewhat worn molars. Both John Day skulls and the Sharps Formation maxilla have three upper molars. M3 is actually present in AMNH 6853, and this tooth is represented by alveoli in the Sharps maxilla and in AMNH 6852. In the Orellan AMNH 39099 an indentation in the posterior border of the left maxilla suggests M3 was initially present (fig. 3, x). Thus, *Paradaphoenus* retained three upper molars throughout its known range, and Wortman and Matthew (1899:129) included the presence of M3 in their definition of the genus.

In all the skulls and in the maxilla, the molars diminish in size from M1 to M3. However, there is a proportional size increase in M2 relative to M1 between the Orellan and Arikareean species. This is particularly evident in the John Day species, *P. cuspigerus*, in which the M2 is conspicuously enlarged (fig. 7).

The distinguishing features of M1-2 are:

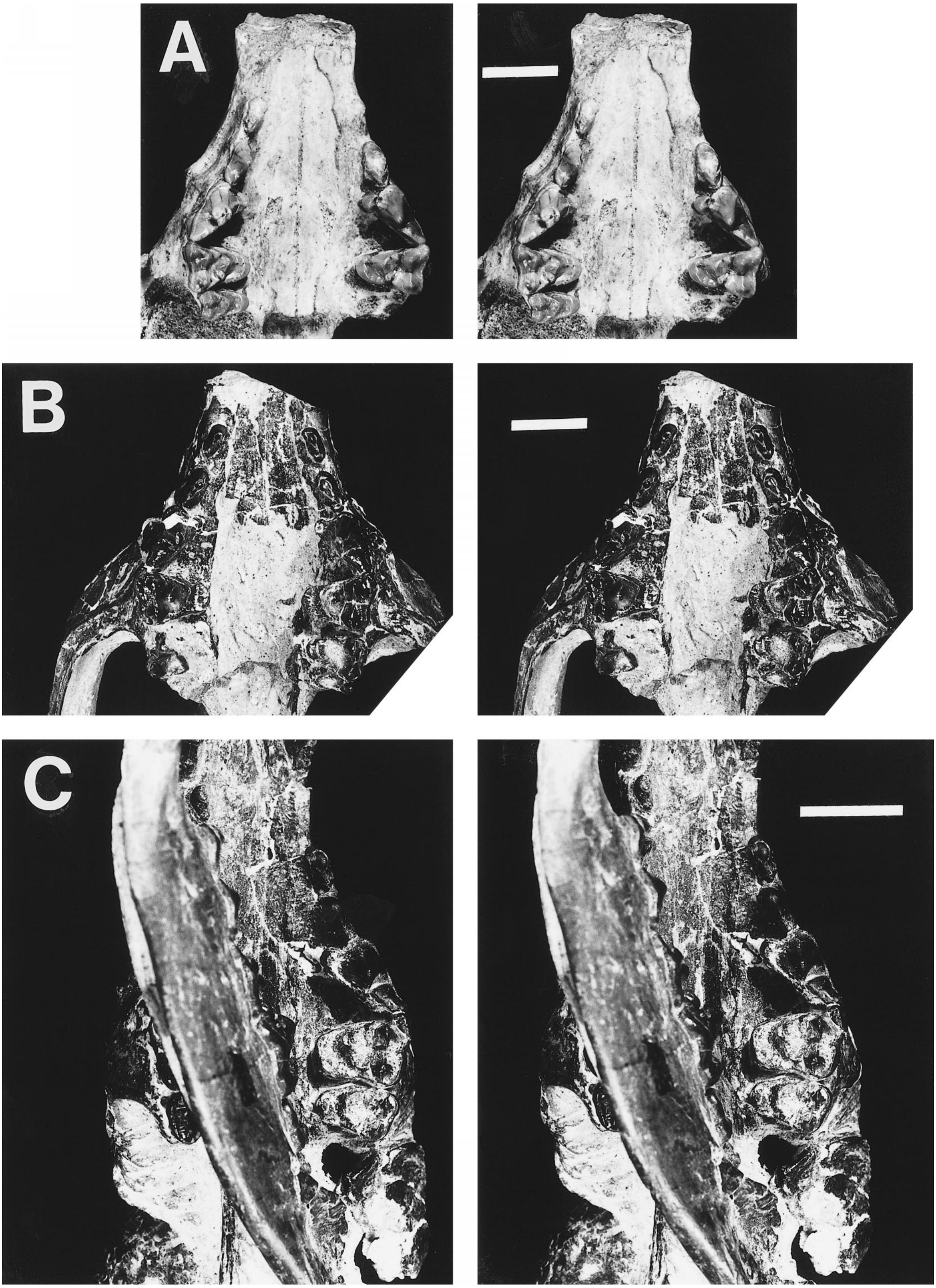

Fig. 7. Stereophotographs of the upper dentition (palatal view) of **(A)** *Paradaphoenus minimus* (AMNH 39099, holotype) from the Brule Formation, South Dakota, and **(B, C)** *Paradaphoenus cuspi*-

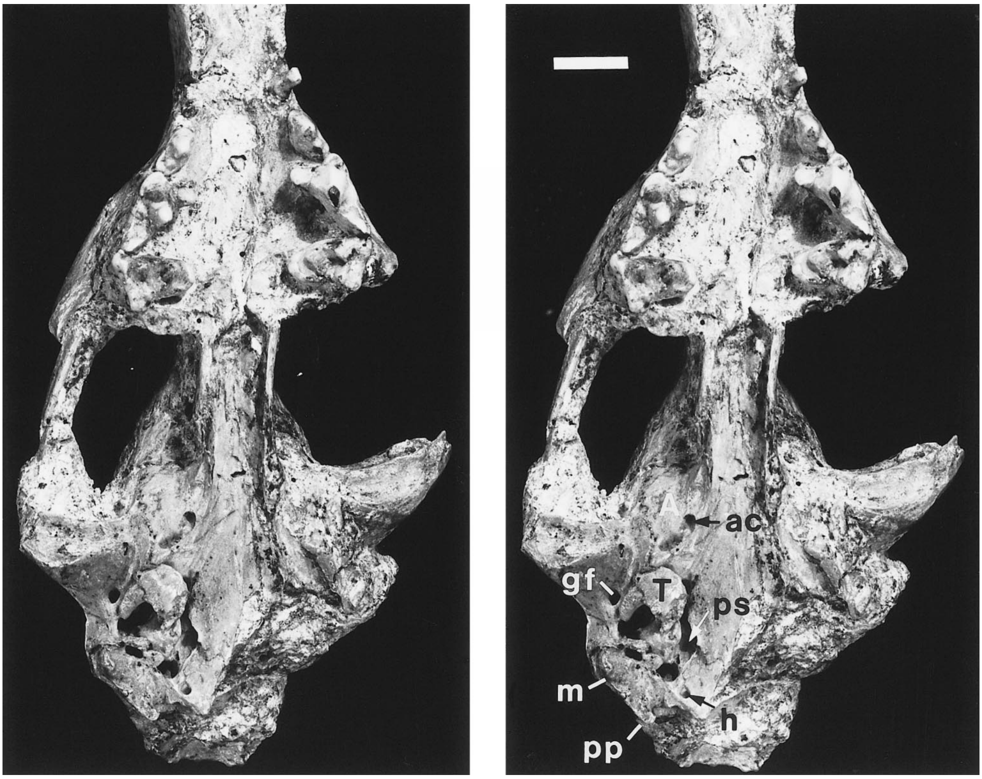

Fig. 8. Stereophotographs of the cranium (in ventral view) of the amphicyonid *Cynodictis* cf. *longirostris*, Quercy district, France (NMB Q.V. 412); M3 is absent in this individual. The basicranium preserves the anterior half of the ectotympanic bulla and the deep embayment in the lateral margin of the basioccipital, presumably for an expanded inferior petrosal venous sinus.

(a) the presence of prominent para- and metaconules, particularly on M1—in addition, there is often an accessory cusp on the postprotocrista lingual to the metaconule (also present in *Cynodictis*); (b) a parastylar cusp with a narrow stylar region and cingulum on M1, and a more reduced stylar region on M2, evidenced by the strong labial placement of the M2 paracone and metacone (the stylar region and parastyle are less reduced in *Cynodictis*); (c) M1-2 transversely extended by development of a thick lingual cingulum and shelf; and (d) the lingual margin of M2 does not extend as far medially as does the lingual margin of M1.

The M1 of *Paradaphoenus* is very similar in cusp pattern to the M1 of *Cynodictis* (fig. 8), yet M2 in the latter is much more reduced and M3 is often absent, although Teilhard (1915) reported the presence of M3 in some individuals of European *Cynodictis*.

There are three lower molars in *Paradaphoenus*. Only an Orellan mandible (UNSM 25030, fig. 4) and the holotype mandible of *P. cuspigerus* retain m3. These two specimens represent the oldest and youngest species of the *Paradaphoenus* lineage, and the transformation of m3 over this interval is related to the broadening of m2-3 that characterizes the genus. In the Orellan species,

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gerus from the John Day Formation, Oregon: **(B)** AMNH 6853, referred; **(C)** AMNH 6852, holotype. Note the enlarged M2 in both skulls of *P. cuspigerus* and the presence of M3 in AMNH 6853. A partial M3 alveolus exists in AMNH 39099 (see fig. 3).

TABLE 2

Measurements (L × W in mm)[a] of the Dentition of North American *Paradaphoenus*

Museum no.	p1	p2	p3	p4	m1	m2	m3	p1-4L
Orellan								
UNSM 25305	—	—	—	6.6 × 3.2	8.7 × 4.3	5.8 × 3.6	—	—
UNSM 25030	—	—	—	(6.3 × 2.5)[b]	(8.4) × 4.2	5.2 × 3.8	3.1 × 2.4	—
UNSM 26139	—	—	—	—	8.3 × 4.2	5.1 × 3.9	—	—
UNSM 25148	—	—	—	—	9.4 × 4.2	5.2 × 3.7	—	—
Whitneyan								
UNSM 26130	(2 × 1.3)	5.6 × 2.1	6.8 × 2.6	7.3 × (3)	9.0 × 4.4	—	—	24.6
Arikareean								
UNSM 6002-92	(2.7 × 1.5)	(5.3 × 2)	(6.7 × 2.8)	6.7 × 3.2	8.7 × 4.5	5.7 × 4.3	—	24.1
AMNH 6852	(3.3 × 1.5)	5.1 × 2.1	6.3 × 2.7	7.4 × 3.6	9.3 × 5.2	5.7 × 4.4	4.2 × 3.2	22.8
	P1	P2	P3	P4	M1	M2	M3	P1-4L
Orellan								
AMNH 39099	—	4.6 × 2.2	6.2 × 2.9	8.8 × 5.6	6.8 × 9.7	4.1 × 6.8	alv[c]	27.6
Arikareean								
LACM 21649	—	—	(5.6 × 2.5)	(8.3 × 4.0)	6.2 × 9.3	4.5 × 7.5	(3.4 × 5.5)	—
AMNH 6852	3.3 × 1.8	4.7 × 2.1	5.8 × 3.0	9.3 × 5.6	7.4 × 10.3	5.3 × 8.1	alv	25.2
AMNH 6853	—	4.5 × 2.1	6.2 × 3.2	8.8 × 5.7	7.5 × 10.5	5.5 × 8.6	(2.7) × 5.0	25.6

[a] L × W = length × width.

[b] () = estimated measurement.

[c] alv = alveolus(i) present.

the m3 trigonid with normally proportioned cusps occupies the anterior half of the tooth; the trigonid is wider than the smaller talonid. However, in AMNH 6852 the m3 trigonid is displaced to the anterior end, the entire tooth is broadened, and the talonid is deeply basined and wider than the trigonid.

The m2 reflects the same transformation as m3, but this is even more pronounced. The transition from a normally proportioned m2 to the widened m2 with trigonid crowded to the front is demonstrated by three mandibles: UNSM 25305 (*P. minimus*, fig. 4), UNSM 6002-92 (*P. tooheyi*, fig. 5), and AMNH 6852 (*P. cuspigerus*, fig. 6). In the Orellan *P. minimus* (UNSM 25305), the m2 trigonid occupies slightly more than 50% of the occlusal surface; the three trigonid cusps are placed at the corners of an equilateral triangle, and the trigonid is noticeably wider than the talonid. The narrow basin of the talonid is bordered by hypoconid and entoconid ridges. The anterointernal corner of m2 protrudes as a low shoulder, and the three trigonid cusps diminish in size from the large protoconid to a smaller metaconid to a small yet distinct paraconid.

The proportions of m2 in the early Arikareean Wagner Quarry mandible (*P. tooheyi*, UNSM 6002-92) are much different from the Orellan m2. The trigonid occupies only ~40% of the occlusal surface and is confined to the anterior part of m2. The protoconid and metaconid are accentuated, whereas the paraconid is diminished in height relative to the Orellan species. The anterolabial corner of m2 protrudes even more than in the Orellan mandible. Because the talonid is broadened, with a larger basin, m2 has a more rectangular occlusal outline than in the Orellan m2.

AMNH 6852 (*P. cuspigerus*) represents the end member in this trend to broaden and enlarge m2-3 in the *Paradaphoenus* lineage (fig. 6). Its m2 trigonid is strongly crowded to the front of the tooth, more toward the anterolingual corner; an expansion of the anterolabial shoulder completes the rectangular form of m2. A cingulum surrounds m2, particularly prominent labially, where it also contributes to the squaring of the tooth. The talonid is very broad and strongly basined, with developed entoconid and hypoconid ridges. In *P. cuspigerus*, m2-3 have become small crushing platforms accompanying the expanded M2-3 in the maxilla.

The characteristic form of the *Paradaphoenus* m1 is altered only by a progressive broadening of the tooth over time. Throughout the range of the genus, the form of the trigonid and the placement of its cusps changes very little. The paraconid is not advanced anteriorly as it is in canids, hence the trigonid cusps remain in the same relative positional relationship. However, in the Whitneyan mandible (UNSM 26130) the m1 talonid is broadened and develops a prominent basin, and the trigonid is slightly diminished in height relative to the Orellan sample. In the early Arikareean, the m1 talonid of the Wagner Quarry mandible (UNSM 6002-92) is slightly widened relative to the Whitneyan m1, but otherwise m1 proportions are similar. In the John Day m1 (AMNH 6852) the entire carnassial is wider, but here the talonid is conspicuously broadened and the talonid basin attains its maximum development.

Thus, the trend observed in the dentitions of *Paradaphoenus* from the Orellan into the Arikareean involved a slight increase in size, accompanied by progressive broadening of the molars, particularly evident in the altered form of M2/m2. In addition, the short, robust carnassials retain a distinctive form in which the abbreviated protocone of P4 is not medially extended, and the paraconid blade of m1 maintains its plesiomorphic orientation and has not migrated anteriorly—*Paradaphoenus* differs from small contemporary canids such as *Hesperocyon* in these carnassial traits.

It is particularly interesting that the teeth of some living foxes have converged on the dental pattern seen in the younger species of *Paradaphoenus*. For example, the second molars of the North American Gray Fox, *Urocyon cinereoargenteus*, are enlarged relative to M1/m1; the P4 is short with abbreviate protocone, and the premolars and canines are similar in form to these teeth in John Day *P. cuspigerus* (Hough, 1948b). However, despite the dental similarities, basicranial anatomy demonstrates that these small amphicyonids and small canids are only distantly related.

BASICRANIUM

The three known skulls of *Paradaphoenus* (AMNH 39099, AMNH 6852, 6853) have well-preserved basicrania, including the auditory regions. An Orellan skull of *P. minimus* (fig. 3), originally described by Hough (1948a) as *Daphoenus minimus*, is slightly crushed dorsoventrally, but is otherwise intact except for the anterior rostrum and the auditory bullae, which have been lost. The Arikareean skull of the John Day *P. cuspigerus* holotype (fig. 2, AMNH 6852) is uncrushed, includes both mandibles, and preserves not only the auditory region but also the right auditory bulla in life position (fig. 9). The second *P. cuspigerus* skull from the John Day (AMNH 6853) also includes the right bulla in life position, but was dorsoventrally crushed and is lacking much of the dorsal surface of the rostrum, orbital region, and braincase. Its basicranium is one of the best preserved parts of this skull (fig. 10).

These skulls demonstrate the small size of *Paradaphoenus*. Basilar lengths of the three known crania are: 94.8 mm, AMNH 6852 (holotype); ~100 mm, AMNH 6853; ~88 mm, AMNH 39099 (table 1). This range is similar to skulls of European *Cynodictis* (fig. 8, NMB Q.V. 412, ~109 mm; also Teilhard, 1915, P1. II, ~100 mm; Petter, 1966).

Basilar lengths for *Paradaphoenus* (~88–100 mm) are smaller than those of the larger living foxes and jackals:—*Vulpes vulpes* (basilar length of 125–137.5 mm, N = 12), *Urocyon cinereoargenteus* (110.4–119.1, N = 7), *Canis mesomelas* (137–141 mm, N = 2), and *Alopex lagopus* (119.2, N = 1). *Paradaphoenus* more closely approaches the smaller foxes, *Vulpes velox* (105–106 mm, N = 2) and *Fennecus zerda* (78.6–83.5 mm, N = 3). The skulls of late Eocene and Oligocene *Hesperocyon* from the White River beds of North America are often somewhat smaller, ranging between 80 and 90 mm.

Fennec foxes of north Africa are the smallest living canids, with body weights of 1–2 kg. The Swift Fox (*Vulpes velox*) is somewhat larger at 1.8–3 kg (Nowak, 1991). Although the species of *Paradaphoenus* are not as large-brained as these small living canids, body size relative to basilar length of skull is probably comparable, hence the range of body weights for Orellan to Arikareean *Paradaphoenus* is estimated at ~1–3 kg.

Because two of the three *Paradaphoenus* skulls are crushed, details of cranial anatomy, such as suture pattern, are difficult to interpret. However, general anatomical proportions and structures are evident. In life, these small carnivores were narrow-snouted and dolichocephalic. The postorbital length is nearly two times the preorbital (table 1), indicating cranial proportions like those of many primitive arctoid, cynoid, and aeluroid carnivorans. Although the volume of the braincase is somewhat greater in Arikareean *P. cuspigerus* relative to Orellan *P. minimus*, the cerebrum has not overgrown the cerebellum to the extent seen in living canids of similar body size, such as the smaller foxes. The form of the cranium is not significantly different from that of an early canid such as *Hesperocyon*.

The auditory bulla and its relationship to surrounding basicranial elements distinguishes *Paradaphoenus* from small contemporary canids such as *Hesperocyon*. The osseous bulla more completely encloses the auditory region in *Hesperocyon* relative to *Paradaphoenus*. Even in very young juveniles of *Hesperocyon*, the auditory bulla is fully ossified and completely encompasses the auditory region, including the petrosal promontorium. This enclosure is accomplished by the application of an ossified caudal entotympanic element to the inner edge of the ectotympanic, and the extension of this caudal entotympanic to the margins of the posterior auditory region. Caudal entotympanic expansion (resulting from posterior inflation of the bulla) during ontogeny in *Hesperocyon* is indicated by the lesser degree of caudal entotympanic inflation in the juvenile (UNSM 25700) than in the adults (UNSM 25402, 25704). However, in both juvenile and adult *Hesperocyon*, the posterior auditory region is always completely enclosed by the bulla. The caudal entotympanic is closely applied against mastoid and occipital bones, and as a result, the only openings exiting the posterior auditory region are the posterior lacerate and stylomastoid foramina. In *Paradaphoenus* the posterior auditory region is not completely enclosed by the ossified bulla; the posteromedial corner of the petrosal

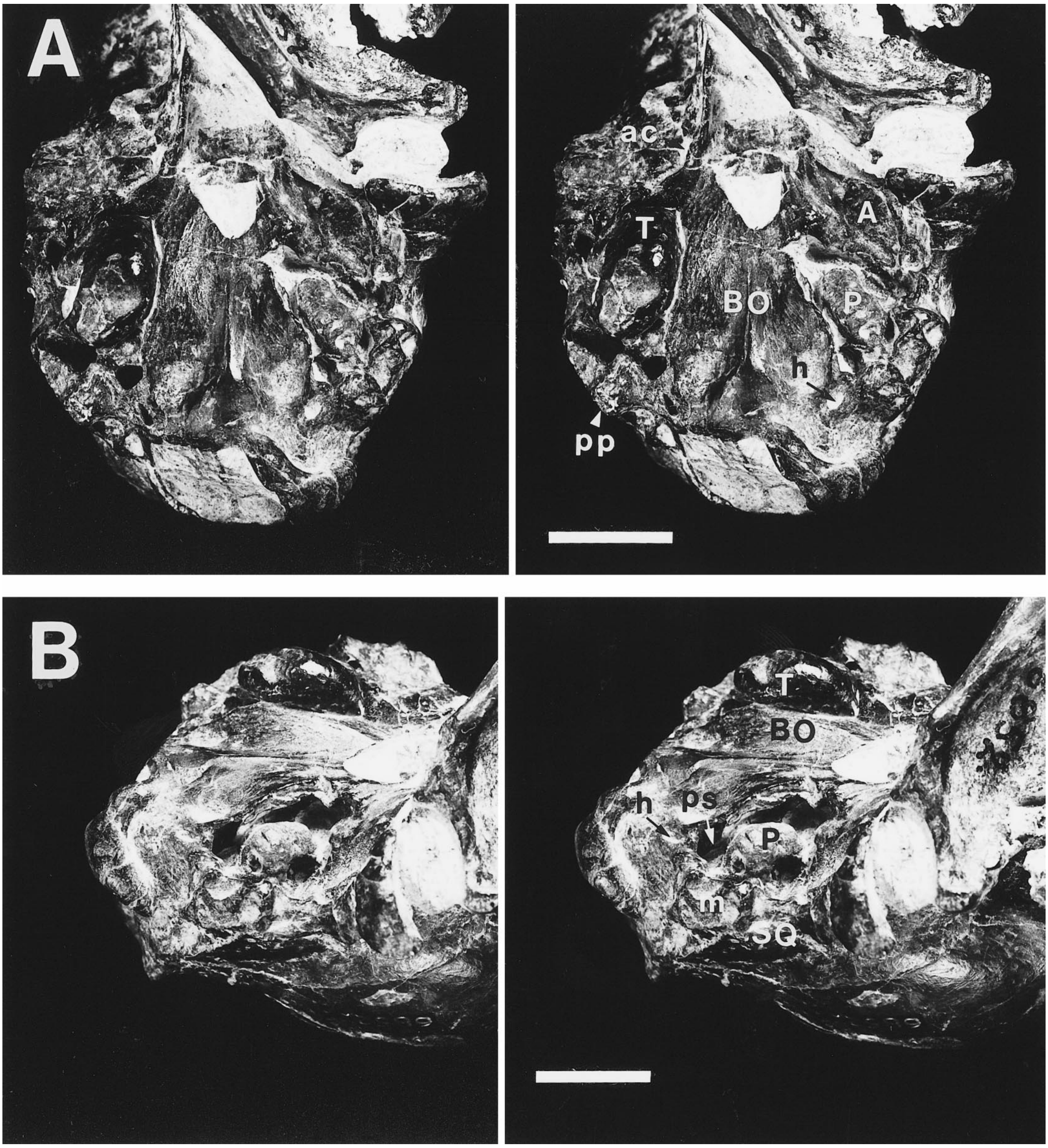

Fig. 9. Stereophotographs of the basicranium of *Paradaphoenus cuspigerus* (AMNH 6852, holotype), John Day Formation, Oregon: **(A)** ventral view; **(B)** lateral view.

is exposed, and the ossified bulla extends at most 1–2 mm behind the point of attachment of the tympanohyal.

The ossified bulla of *Paradaphoenus* appears to be formed by the ectotympanic alone, whereas in *Hesperocyon*, an ossified caudal entotympanic is added to the ectotympanic (fig. 11). The ectotympanic of *Paradaphoenus* is slightly wider and more inflated, relative to the ectotympanic of contemporary *Daphoenus*, suggesting that a small amount of ectotympanic growth has occurred in *Paradaphoenus* in an attempt to more fully enclose the auditory region. Because the presence of an ossified caudal entotympanic is certain in *Hesperocyon*, where it can be observed in older juveniles (UNSM 25700), it probably does not occur in *Paradaphoen*-

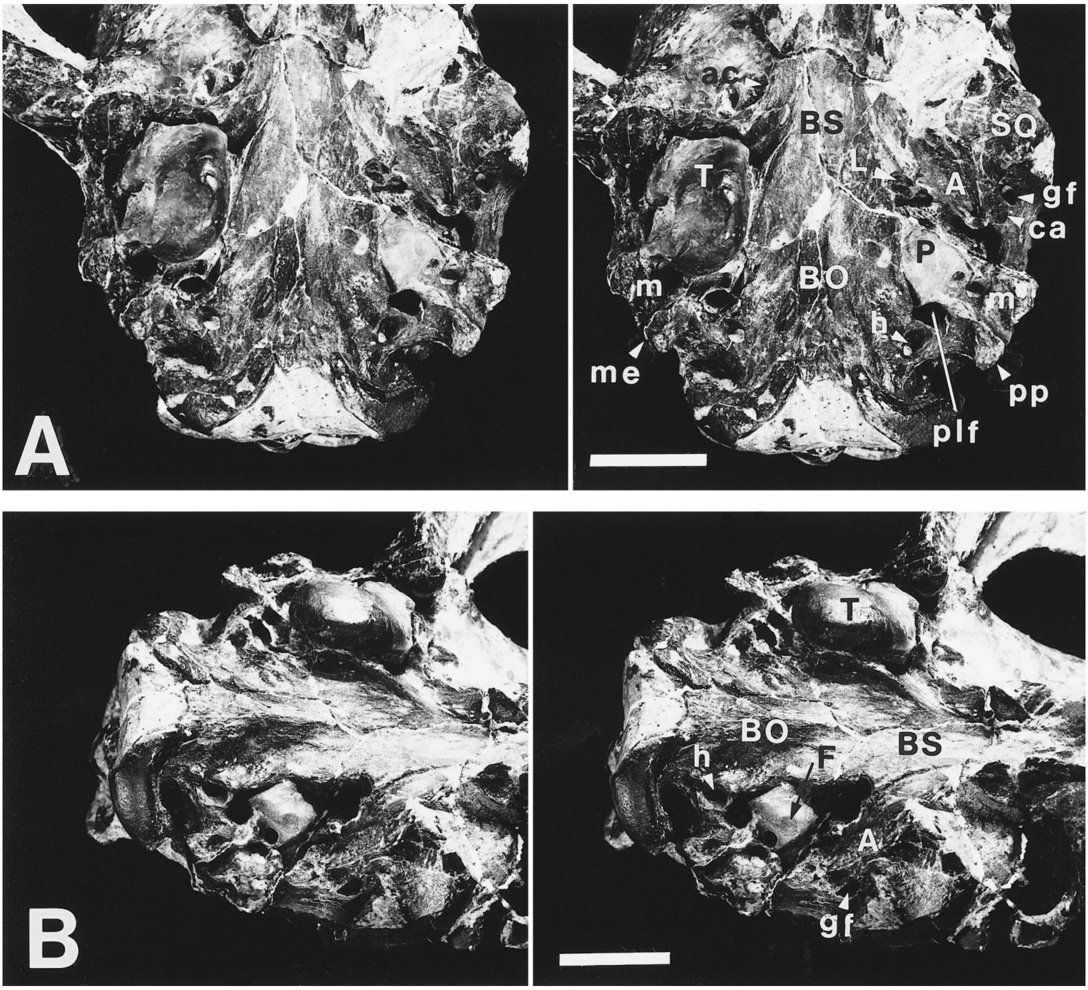

Fig. 10. Stereophotographs of the basicranium of *Paradaphoenus cuspigerus* (AMNH 6853, referred), John Day Formation, Oregon: **(A)** ventral view; **(B)** lateral view.

us, although the possible presence of a small, narrow, laminar caudal entotympanic attached to the medial rim of the ectotympanic (as in *Ursus americanus*, Hunt 1974, figs. 13, 14) cannot be entirely ruled out in *Paradaphoenus*. Nevertheless, in comparing the bullae of Arikareean *Paradaphoenus* (AMNH 6852, 6853) to juvenile *Hesperocyon* bullae (in which the ectotympanic and caudal entotympanic can be certainly identified) and to the bullae of adult carnivorans (*Daphoenus*, *Nandinia*), in which an ossified ectotympanic is present as a separate element, it seems most probable that the bulla of *Paradaphoenus* is formed exclusively by a widened and only slightly posteriorly inflated ectotympanic bone.

The petrosal and surrounding middle ear region can be observed in all three *Paradaphoenus* skulls. In the two John Day skulls, the bulla has been lost from the left auditory region, providing a clear view of the middle ear (this area is slightly crushed and displaced in AMNH 6853). The auditory regions of the John Day skulls and the Orellan *Paradaphoenus* skull are extremely similar, although the Orellan species was smaller in body size. In addition, the form of the petrosal and the detailed anatomy of the auditory region of the Orellan *P. minimus* are also

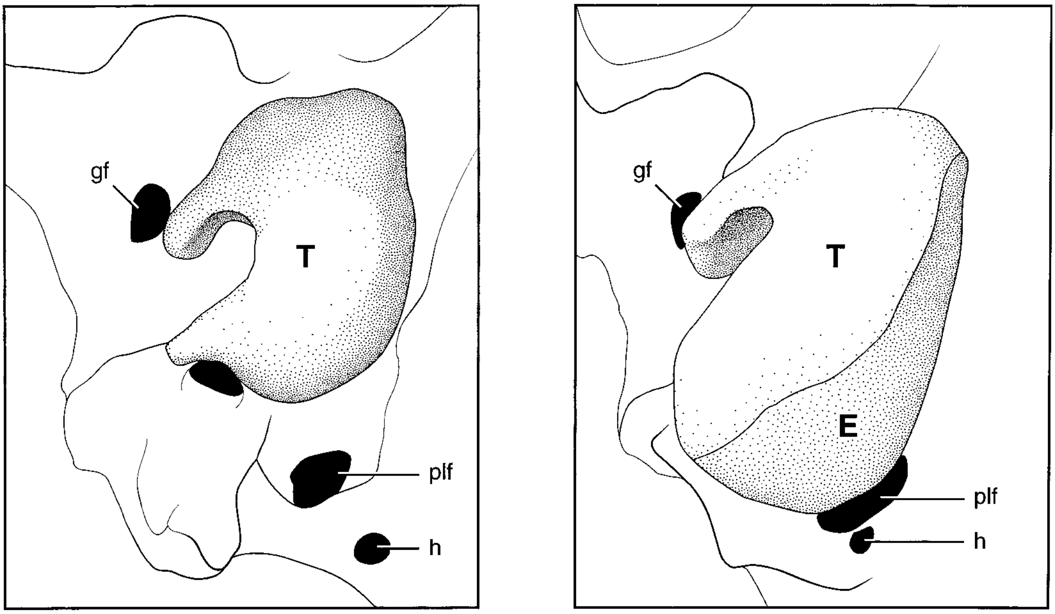

Fig. 11. Comparison of ontogenetic elements contributing to the auditory bulla of the small amphicyonid *Paradaphoenus* (left) and the canid *Hesperocyon* (right). T, ectotympanic; E, caudal entotympanic.

comparable to the larger Orellan amphicyonids *Daphoenus vetus* and *D. hartshornianus*. Thus, a common basicranial structure is shared by the Oligocene North American *Daphoenus* and *Paradaphoenus* that places them within the Amphicyonidae.

The form of the petrosal promontorium is similar in these amphicyonids. All are of the arctoid type, in which the posterior promontorium is slightly elevated, its surface gradually sloping dorsad anteriorly. There is no ventral process of the promontorium as seen in aeluroid carnivorans (Hunt, 1989). By comparing damaged and undamaged petrosals of *Paradaphoenus* and *Daphoenus*, it is evident that the medial part of the promontorium in these genera is a rather fragile cancellous extension of the bone directly enclosing the cochlea. In some individuals this medial part is broken open to reveal internal cancellae.

In the skulls of *Paradaphoenus*, the medial margin of the petrosal contacts the edge of the basioccipital, but there is no suturing of petrosal to basioccipital as occurs in canids. The margin of the basioccipital is deeply excavated for the inferior petrosal venous sinus (Hunt, 1977; Hunt and Barnes, 1994). The basioccipital is wide relative to the narrow basioccipital of Oligocene canids in which the expanding bulla restricts the width of the basicranial axis. The plesiomorphic state of the *Paradaphoenus* auditory region is indicated by the broad basioccipital, the rudimentary auditory bulla, and by the lack of any extension of the middle ear cavity behind the promontorium and mastoid process (in many living aeluroids the middle ear cavity is extended posteriorly by inflation of the caudal entotympanic).

The widened ectotympanic of the *P. cuspigerus* holotype (AMNH 6852) indents the tympanic wing of the alisphenoid, creating a moderately deep depression on its surface. Lateral to this depression is the postglenoid foramen for the external jugular vein and posterior to it, a prominent pit for the anterior crus of ectotympanic. The indentation for the alisphenoid and the depth of the pit for the anterior crus are much more developed in AMNH 6852 relative to AMNH 39099, the Orellan species, indicating that the ectotympanic was not as broadened and inflated in the Orellan *P. minimus*.

Because the ectotympanic is in life position in the John Day *Paradaphoenus* skulls, its relationship to the petrosal promontorium and to adjacent basicranial bones can be determined. In both skulls, the inner margin of the ectotympanic broadly contacts the basioccipital, resting against it, and in AMNH 6853 the basioccipital margin is deflected ventrad to support the ectotympanic. Furthermore, the posterointernal margin of the ectotympanic in AMNH 6853 rests against the promontorium just anteromedial to the round window where it produces a flat facet; on the left promontorium of AMNH 6853, this facet is conspicuous (fig. 10). In AMNH 6852 the ectotympanic closely approaches the promontorium and the edge of the ectotympanic is configured to fit against its surface, but contact is not made, because tuffaceous silt intervenes to prevent the seating of the ectotympanic against the promontorium. Because of a damaged promontorium in AMNH 39099, the presence of a similarly placed facet in the Orellan species is uncertain.

It is interesting that the form of the posteromedial face of the ectotympanic that contacts the promontorium is somewhat differently shaped in AMNH 6852 and 6853; in addition, the basicranium of AMNH 6853 is slightly larger in size and more robust than that of AMNH 6852. Whether this is the result of intraspecific or sexual variation, and/or due to a temporal difference, is unknown because of the lack of detailed stratigraphic information for these two skulls. Nevertheless, the form of the ectotympanic, its relationship to the promontorium, the embayed lateral margin of the basioccipital, and the plesiomorphic state of the auditory region separates *Paradaphoenus* from contemporary canids, and allies the genus with the Amphicyonidae.

SUMMARY AND CONCLUSIONS

This report summarizes all known fossil material of the genus *Paradaphoenus* from North America. These fossils appear to belong to a single lineage of very small amphicyonids (~1–3 kg) that ranged from the Pacific Northwest eastward to the central Great Plains. The lineage includes three species: the Orellan *P. minimus*; the Whitneyan to early Arikareean *P. tooheyi*, n. sp.; and the late early or possibly mid-Arikareean *P. cuspigerus*. Teeth of the oldest species, *P. minimus*, are little modified and unspecialized. Molars of *P. tooheyi* are the first to show the broadening that typifies the descendant species of *Paradaphoenus*. The broadened molars of the youngest species, John Day *P. cuspigerus*, are more derived than the molars of either *P. minimus* or *P. tooheyi* from the Great Plains.

The recent discovery of *P. tooheyi* from Whitneyan and early Arikareean sediments fills both a temporal and morphological gap between *P. minimus* and *P. cuspigerus*. The temporal range of the genus is estimated to be from ~34 Ma to possibly as young as ~23–25 Ma, but the upper range limit is uncertain because of the absence of detailed stratigraphic data for the John Day fossils.

Three skulls of *Paradaphoenus* are known (an Orellan skull of *P. minimus* and two John Day skulls of *P. cuspigerus*), and they adequately preserve skull form, dentition, and basicranium. The two John Day skulls also retain the auditory bulla. Basicranial anatomy reflects the amphicyonid pattern and is similar to that of the early amphicyonids, *Daphoenus* and *Cynodictis*.

Despite similarities in skull form, body size, and dentition, basicranial anatomy distinguishes small amphicyonids such as *Paradaphoenus* (North America) and *Cynodictis* (Europe) from contemporary small hesperocyonine canids in North America. From their earliest appearance, canids fully enclose the auditory region with an ossified auditory bulla formed by an ectotympanic and a caudal entotympanic. An ossified caudal entotympanic exists as a discrete element applied to the inner edge of the ectotympanic in juvenile *Hesperocyon*; the subsequent growth and inflation of this caudal entotympanic, completely enclosing the auditory region, is the hallmark of the Canidae. In *Paradaphoenus* and other contemporary North American Oligocene amphicyonids, only the ectotympanic is ossified, and in *Paradaphoenus* it appears to be the only bulla component, at most only slightly broadened and inflated, leaving the posterior promontorium exposed. Based on the capsular form of the *Paradaphoenus* ectotympanic, the existence of additional fibrous or cartilaginous contributions from the tympanic membrane are considered unlikely, and the auditory bulla appears to be formed entirely by an ossified ectotympanic element.

Using extant small foxes (e.g., *Vulpes velox*, *Fennecus zerda*) as analogs, the species of *Paradaphoenus* are interpreted as small, foxlike carnivores that preyed upon small vertebrates, but also relied on insects, eggs, fruits, and seeds in season. Their interaction and possible competition with the small contemporary hesperocyonine canids remains speculative, but if the relative representation of fossils of small canids and *Paradaphoenus* in the North American record is an accurate reflection of their abundance in Oligocene environments, the canids must have far outnumbered these small amphicyonids. Wang (1994) lists 5 Orellan, 8 Whitneyan, and at least 14 early Arikareean hesperocyonine canids in North America. Even if the actual number of hesperocyonine species is to some degree exaggerated, the canids are clearly more diverse. After the Arikareean land mammal age, small, fox-sized amphicyonids are extinct in North America, yet a variety of small canids (< 20 kg) thrive in the early, medial, and late Miocene, most species failing to attain large body size (80–100 kg). In the early and medial Miocene, as well as the early part of the late Miocene (Clarendonian), these smaller canids are accompanied by large amphicyonids and hemicyonine ursids, which at that time dominate the niche for large predatory carnivorans in North America.

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APPENDIX 1 (Stratigraphic and Locality Data)

Orellan

1) AMNH 39099, Lower Oreodon beds, Brule Fm., southwest of Sheep Mountain, near Scenic, South Dakota, collected by J. Bird, 25 July 1940.

2) UNSM 25305, Orella ''A'', Brule Fm., UNSM Loc. Sx-25, northwest of Crawford, Nebraska.

3) UNSM 25030, Orella ''A'', Brule Fm., UNSM Loc. Sx-26, northwest of Crawford, Nebraska.

4) UNSM 25148, Orella Member, Brule Fm., UNSM Loc. Sx-14, northwest of Crawford, Nebraska.

5) UNSM 26139, Brule Fm., White River Group, Scottsbluff Co., Nebraska.

Whitneyan

6) UNSM 26130, Brule Fm., 30 feet below Brule-Gering contact, E1/2, section 36, T.20N., R.56W., Banner Co., Nebraska.

Arikareean

7) UNSM 6002-92, Wagner Quarry, excavated in a lower Arikaree Group fluvial channel fill incised in White River Group sediments, southwest of Chadron, Nebraska.

8) LACM 21649, Sharps Fm., LACM Loc. 1981, Wounded Knee area, South Dakota, collected by J. R. Macdonald, 23 July 1962.

9) AMNH 6852, John Day Fm., John Day valley, Oregon.

10) AMNH 6853, John Day Fm., John Day valley, Oregon.

APPENDIX 2

Differential diagnosis of *Paradaphoenus tooheyi*, n. sp.:

P4 length/ M1-2 length, 77-78% relative to 80-81% for *P. minimus* and 67-74% for *P. cuspigerus*; m1-2 talonids transversely broadened with prominent basins relative to *P. minimus* which lacks broadly basined talonids; m2 trigonid reduced and crowded to the front of the tooth relative to *P. minimus* in which crowding does not occur; m2 proto- and metaconids accentuated, and paraconid diminished, relative to *P. minimus*; m2 width 4.3 mm relative to 3.6–3.9 mm in *P. minimus*; m1-2 talonids not as expanded as in *P. cuspigerus*; m1 width 4.4–4.5 mm relative to 5.2 mm in *P. cuspigerus*; M1-2 not as enlarged and transversely broadened as M1-2 of *P. cuspigerus* (table 2).