Chapter 6

New Procyonines from the Hemingfordian and Barstovian of the Gulf Coast and Nevada, Including the First Fossil Record of the Potosini

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ABSTRACT

Four new procyonids (Mammalia: Carnivora) are described in this paper. They include *Bassaricyonoides stewartae*, new genus and species, from the late Hemingfordian of Nevada, *Bassaricyonoides phyllismillerae*, new species, ?*Edaphocyon palmeri*, new species, both from the early Hemingfordian of Florida, and *Parapotos tedfordi*, new genus and species, from the Barstovian of Texas. *Bassaricyonoides* and *Parapotos* are the first known fossils of potosin procyonids. They support the monophyly of the Tribe Potosini, which includes the extant *Bassaricyon* and *Potos*, and indicate that the Potosini had diverged from the Procyonini by the early Miocene in North America. By the late Miocene, the Procyoninae had replaced the phlaocyonin and cynarctin canids as the dominant North American, small hypocarnivorans.

INTRODUCTION

Although they have a limited fossil record, fossil Procyonidae (Mammalia: Carnivora) are morphologically and taxonomically more diverse than their recent relatives (Baskin, 1998). Fossil procyonids include taxa that are clearly linked to the extant *Bassariscus*, *Procyon*, and *Nasua*, as well as taxa whose placement is more controversial (e.g., Kraglievich and Olazábal, 1959; Baskin, 1982, 1989, 1998; Wolsan, 1993). Among extant taxa, there is continuing debate concerning the affinities of the Old World red panda *Ailurus* to other arctoids and of *Potos* and *Bassaricyon* to other New World procyonids. For the present paper, the family Procyonidae is recognized to contain three subfamilies: Ailurinae, the extinct Simocyoninae, and Procyoninae (McKenna and Bell, 1997; Baskin, 1998). Wolsan (1993) presents an alternative interpretation of the phylogenetic relationships of the Old World genera (that Baskin [1998] includes in the Procyonidae), classifying them as primitive musteloids. Based on molecular evidence, Pecon Slattery and

O'Brien (1995) place *Ailurus* as an early offshoot within the Procyonidae. Bininda-Emonds et al. (1999) place *Ailurus* as the sister taxon to the Mustelidae and Procyonidae, although they note placement in the composite tree is ''exceptionally weak.'' Wang (1997), using cranial evidence, and Baskin (1998), using dental evidence, place the Ailurinae and Simocyoninae as sister taxa of the Procyoninae within the Procyonidae. Ginsburg et al. (1997) present additional evidence supporting the monophyly of these three subfamilies.

The Procyoninae include *Broiliana*, from the early Miocene of Europe, and the New World procyonines (Tribes Potosini and Procyonini). The extant Procyoninae are usually recognized as a monophyletic group, although the relationship of *Bassaricyon* and, especially, *Potos* to other procyonines is controversial. Decker and Wozencraft (1991) provide a character analysis and phylogeny of the Recent New World genera (their Procyonidae), which they divide into two monophyletic subfamilies: Potosinae (*Bassaricyon*

and *Potos*) and Procyoninae (*Bassariscus*, *Nasua*, *Nasuella*, and *Procyon*). Molecular evidence of this relationship is equivocal (e.g., Vrana et al., 1994; Pecon Slattery and O'Brien, 1995). New taxa described below support Decker and Wozencraft's hypothesis. In the present paper, the two subfamilies of Decker and Wozencraft are ranked as tribes. Procyonini are represented in the fossil record, but fossil Potosini were unknown until recently. Here I present new taxa that indicate an early Miocene divergence of the potosin and procyonin lineages.

INSTITUTIONAL ABBREVIATIONS

AMNH   Division of Paleontology, American Museum of Natural History, New York
F:AM   Frick Collection, American Museum of Natural History, New York
KUVP   Division of Vertebrate Paleontology, Museum of Natural History, Kansas University, Lawrence
UCR   University of California at Riverside

LOCALITIES

The Massacre Lake Local Fauna (RV 7043), Washoe County, Nevada, is late Hemingfordian (late early Miocene) in age (Morea, 1981; Woodburne and Swisher, 1995). Carnivorans and ungulates from Massacre Lake are listed in Janis et al. (1998). This locality is noteworthy for perhaps the earliest occurrence of proboscideans in North America (Morea, 1981; Woodburne and Swisher, 1995).

The Miller Local Fauna was collected by Mr. Harry Miller of Ocalla, Florida, from the Suwannee River in Dixie County, Florida. To date, the only taxa identified from this locality are the borophagine canid *Orthotomarctus matthewi* (Wang et al., 1999) and the hesperocyonine canid *Osbornodon scitulus* (Wang, chap. 8, this volume), which also occur in the early Hemingfordian Runningwater Formation of Nebraska. Undescribed mustelids from the Miller Local Fauna also support an early Hemingfordian age assignment.

Stephen Prairie is adjacent to the Trinity River in San Jacinto County, Texas, 3 to 5 km downstream from the old US 190 bridge east of Pointblank (M. Skinner, locality map on file at the AMNH). A procyonid jaw and a gomphothere palate were collected there in 1964 by N.Z. Ward and party in deposits assigned to the middle Miocene Flemming Formation. However, the Geologic Atlas of Texas (Beaumont Sheet) indicates latest Pleistocene terrace deposits at Stephen Prairie, and shows that the late Pleistocene Beaumont Formation and early Pleistocene Willis Formation, as well as the Flemming Formation crop out nearby. Reworked fossils can occur in abundance in terrace deposits of Texas rivers (Baskin, 1991). Notwithstanding, the Geologic Atlas also shows that the Trinity River Pit 1 quarry (Patton and Taylor, 1971), which has produced an early Barstovian (medial Miocene) fauna, is in the Beaumont Formation, indicating that the geologic map contains errors. Stephen Prairie (elevation of 105 ft) is now submerged beneath Livingston Reservoir. Both early and late Barstovian fossil assemblages from the Flemming Formation have been collected from nearby localities (Prothero and Manning, 1987: fig. 1, table 1). Those localities yielding the early Barstovian Burkeville Fauna include the Point Blank Local Fauna, Trinity River Pit 1 (which has produced *Arctonasua* cf. *A. gracilis*), McMurray Pits 1 (which has produced *Edaphocyon pointblankensis*) and 2, and Stephen Creek; those yielding the late Barstovian Cold Spring Fauna include the Cold Spring Local Fauna and Sam Houston Local Fauna. The Stephen Prairie gomphothere is identified as *Serridentinus* (= *Gomphotherium*) *productus* (Earl Manning, personal commun.). Proboscideans are absent in the Burkeville Fauna (with one possible exception from the Burkeville Local Fauna that may be earliest late Barstovian), but are characteristic of the Cold Spring Fauna (Tedford et al., 1987). This suggests that the new procyonid from Stephen Prairie is late Barstovian in age.

SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1758
ORDER CARNIVORA BOWDICH, 1821
FAMILY PROCYONIDAE GRAY, 1825
SUBFAMILY PROCYONINAE GRAY, 1825

DIAGNOSIS: Procyoninae are derived compared with other procyonids such as *Amphic-*

tis, *Ailurus*, or *Simocyon* in having a Type B auditory bulla (Hunt, 1974) with an inflated entotympanic, greater separation of the posterior lacerate and posterior carotid foramina, a deep suprameatal fossa, loss of the alisphenoid canal, the mastoid process reduced, the paroccipital process reduced, and lack of an anterior loop of the internal carotid artery. Derived dental features include P4 with a more knoblike protocone and m1 with a distinct entoconid. Compared with the European, early Miocene, stem-procyonine *Broiliana*, the New World Procyoninae (crown clade Procyoninae: Potosini and Procyonini) are further derived in having P4 with a better developed parastyle, more posteriorly placed protocone, and a shorter metacone blade; M2 paracone and metacone more widely separated; m2 hypoconulid posterointernal, hypoconid more prominent, and anterior cingulum reduced; and mastoid and paroccipital processes further reduced.

COMMENT: Decker and Wozencraft (1991) provide a character analysis and phylogeny of the Recent genera of this subfamily (their Procyonidae).

TRIBE POTOSINI TROUESSART, 1904, NEW RANK

DIAGNOSIS: Premolars closely spaced and transversely broad; molars tend to become rounded; P4 with protocone anteriorly-posteriorly elongate, situated internal to and widely separated from the paracone, and with no hypocone on the internal cingulum; M1 with reduced internal cingulum and hypocone absent; M2 with reduced cusps; m1 with reduced, anteromedially situated paraconid; m1 talonid only slightly basined and with cusps poorly developed. Characteristics listed by Decker and Wozencraft (1991) as autapomorphies for the extant *Potos* and *Bassaricyon* include Steno's foramen between incisive foramina, ventral border of the infraorbital canal posterior to the dorsal border, malleus large, internal auditory meatus on the ventromedial edge of the petrosal, acromion process sharply angled, and the external pinnae short and rounded.

Bassaricyonoides Baskin and Morea, new genus

TYPE SPECIES: *Bassaricyonoides stewartae*, new species.

ETYMOLOGY: *Bassaricyon*, the Recent olingo; *-oides,* Greek, resembling.

INCLUDED SPECIES: The type and *Bassaricyonoides phyllismillerae*, new species.

DIAGNOSIS: A primitive, potosin procyonine that is intermediate in size between the Recent *Bassariscus astutus* and *Procyon lotor*. P4 with a metacone blade more reduced than in *Bassariscus*, but not as reduced as in *Bassaricyon*, and a low protocone opposite and broadly connected to the paracone. M1 and M2 with low cusps, hypocone and metaconule absent, and internal cingulum very reduced to absent. Protocone present on M1, very weakly developed on M2. The m1 has an open trigonid with a prominent, but low, anteromedian paraconid. The m2 has a metaconid, protoconid, hypoconid, and a posterointernal hypoconulid.

COMPARISONS: *Bassaricyonoides* possesses the dental characteristics enumerated above as diagnostic of the Potosini. It is more primitive than the extant *Bassaricyon* and *Potos* and the new genus described below in having P4 with a longer metacone blade; p2 lower than p4; and m1 with an open trigonid and larger paraconid. More detailed comparisons with other genera are presented with *B. stewartae* for the upper dentition and with *B. phyllismillerae* for the lower dentition.

Bassaricyonoides stewartae Baskin and Morea, new species

HOLOTYPE: UCR 16927 right maxillary fragment P4–M2 (fig. 6.1B; table 6.1) from Massacre Lake I Local Fauna (late Hemingfordian), Washoe County, Nevada.

ETYMOLOGY: Patronym for Jennifer A. Stewart.

REFERRED SPECIMENS: From the type locality: UCR 15449, left M1–M2 (fig. 6.1A); and 16453, right P3–P4.

DIAGNOSIS: A potosin that is approximately 15–20% smaller than *Bassaricyonoides phyllismillerae*. Diagnostic characters are those of the upper dentition for the genus.

DESCRIPTION: In UCR 16927, the P2 is represented by the alveolus for the posterior root; the P3 by two subequal-sized alveoli. The posterior half of P3, present on UCR 16453, has a small cusp with a minute posterior cingulum.
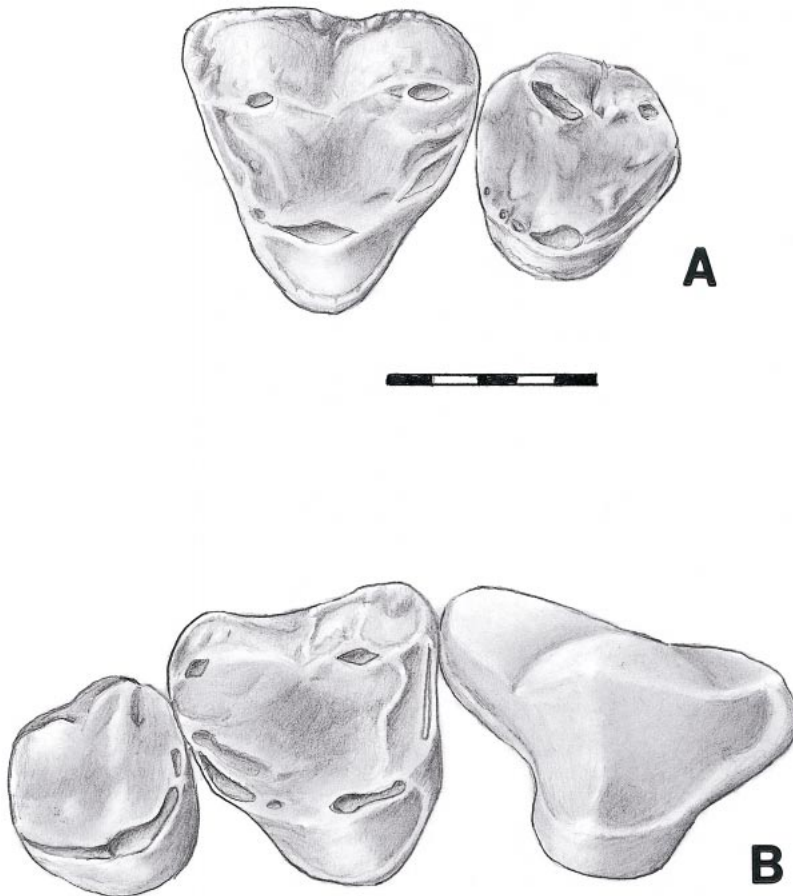
Fig. 6.1. *Bassaricyonoides stewartae*, new genus and species. **A,** UCR 15449: left M1–M2, occlusal view. **B,** UCR 16927 (holotype): right P4–M2, occlusal view. Scale = 5 mm.

TABLE 6.1
Dental Measurements (mm) of
Bassaricyonoides stewartae
(L = greatest anterior posterior dimension,
W = greatest transverse dimension).

	UCR 16927	UCR 15449	UCR 16453
P4L	8.3	—	7.4
W	6.2	—	6.0
M1L	6.7	6.5	
W	6.9	6.8	
M2L	5.1	4.5	
W	5.0	4.5	

The P4 has a low, short, metacone blade separated from the paracone by a shallow notch. The paracone is a tall, prominent cusp, with the apex situated posterior to the midline of the tooth. The parastyle is small and low, with a semicircular anterior margin. A thin ridge extends posteriorly from it to approximately halfway up the paracone. The protocone is a very low, anteroposteriorly elongate cusp opposite the paracone and separated from it by a shallow valley. A thin ridge extends from the protocone across this valley to the base of the paracone. There is no hypocone on the narrow posterointernal cingulum.

The M1 has a triangular (with rounded corners) occlusal outline and low cusps. There is a trigon basin between the three

principal cusps. The protocone is anteroposteriorly elongate, with its apex anterior to the midline of the tooth, and is approximately equal in height to the paracone and metacone. A postprotocrista extends to the posterior margin. No hypocone is present. There is a low and narrow cingulum on the internal base of the protocone. The paracone and metacone have wrinkled enamel, are subequal in size and separated by a wide, ''V''-shape notch. There is a low, narrow external cingulum.

The M2 has a subrounded occlusal outline with very poorly developed cusps. The metacone is separated from the smaller paracone by a narrow notch. There is a low, narrow external cingulum connecting the two cusps. The very low protocone is slightly posterior to the paracone and distinctly anterior to the metacone. The internal cingulum is very weakly developed. A postprotocrista extends to the middle of the posterior margin of the tooth, posterior to the metacone, creating a slight posteromedian shelf.

The infraorbital foramen is similar in size to that of *Bassariscus*, and is situated dorsal to the anterior half of the P4. In lateral view (occlusal surface ventral), P4–M2 lie along a concave-upward arc, as in *Procyon* or *Bassaricyon*. Relative to a horizontal M1, the P4 is angled upward anteriorly at 20° and the M2 is angled upward posteriorly at 35°.

COMPARISONS: When Morea (1981) described the Massacre Lake procyonid, he commented on the difficulty of establishing the familial relationships of this taxon based on its dentition alone. The triangular shape of the M1, with hypocone absent, and the large M2 preclude mustelid affinities. Omnivorous borophagine canids such as *Cynarctoides* and *Phlaocyon*, which at one time were included in the Procyonidae, have P4 with anteriorly situated protocone and M1 and M2 with prominent hypocones. Morea (1981) contrasted the dentition of *Bassaricyonoides* with that of *Procyon*, which has P4 with a hypocone, more reduced metacone, and a more anteriorly situated protocone, and has M1 and M2 with a metaconule and an internal cingulum. He noted the similarity of *Bassaricyonoides* to *Bassaricyon* and *Potos* and concluded that it was most likely closely

related to these two extant taxa, a conclusion supported by the present study.

Bassaricyonoides is distinguished from *Bassaricyon* in its more primitive dentition. Differences include having P4 with a longer metacone blade, a stronger parastyle, a backward tilting paracone, and a much smaller, more shelflike (as opposed to knoblike) protocone (but both are opposite the paracone); M1 with a better developed protocone on a more triangular internal margin with a narrow internal cingulum and a somewhat stronger external cingulum; and M2 with a more circular occlusal outline, but with a slight posteroexternal expansion, and lower, much more poorly developed cusps. *Potos* has a much more specialized (for frugivory) dentition than *Bassaricyonoides* or *Bassaricyon*, and has molars with cusps virtually absent. *Potos* has P4 more like that of *Bassaricyon* and M2 more reduced than in *Bassaricyon* or *Bassaricyonoides*. Further evidence supporting that *Bassaricyonoides* is a potosin procyonine is provided by the mandible from the early Hemingfordian Miller Local Fauna described below.

Other early Miocene procyonids include the stem procyonids *Amphictis* (Europe and possibly North America) and *Stromeriella* (Europe), the European stem procyonine *Broiliana*, and the North American procyonin *Edaphocyon*. *Bassaricyonoides* differs from these and other Miocene procyonines (including *Bassariscus*, *Probassariscus*, and *Arctonasua*) and resembles the Recent *Bassaricyon* in having molars with low, rounded to reduced cusps, molar length and width subequal (rather than distinctly wider than long), M1 and M2 internal cingulum and hypocone much more reduced to absent, and M2 with a rounded occlusal outline. *Bassaricyonoides* and *Stromeriella* are similar in size and have P4 protocone situated relatively posteriorly (although less so in *Stromeriella*) and with a broad connection to the paracone. *Bassaricyonoides* differs further from *Stromeriella* in having P4 with a shorter and broader metacone blade (shorter than the paracone vs. approximately equal in length), a less distinct parastylar region, paracone inclined more posteriorly with the apex situated posterior to the midline of the tooth, and protocone lower, more anteriorly-posteriorly

elongate (vs. knoblike) and closer to the paracone; M1 with parastyle absent and a very reduced internal cingulum (vs. the large broad internal cingulum of *Stromeriella*); and M2 relatively larger, with paracone and metacone further apart.

Bassaricyonoides is larger than *Broiliana*, as well as early Barstovian *Bassariscus antiquus* and *Probassariscus matthewi*. Moreover, *Bassaricyonoides* has P4 with a longer and lower, more posteriorly situated protocone and a relatively wider and shorter metacone blade, and M1 not transversely elongate and with a poorly developed internal cingulum and hypocone. *Bassaricyonoides* differs from *Probassariscus* in having P4 with a weaker parastyle and no hypocone and M1 with a weaker external cingulum and parastyle.

Bassaricyonoides further differs from the Hemingfordian and Barstovian *Edaphocyon* in its smaller size and in having P4 with a more posteriorly situated and much lower protocone, a broader parastyle region, and hypocone absent, and M1 lacking a metaconule. *Edaphocyon* has much stronger pre- and postprotocristae on M1 and M2. They are very reduced to absent in *Bassaricyonoides*. The P4 metacone blade is the same relative length in both. The Barstovian to Hemphillian *Arctonasua* has P4 with a posteriorly situated protocone, as in *Bassaricyonoides*, but differs in having a much more prominent parastyle, a greatly reduced metacone, and a much more bulbous protocone.

Bassaricyonoides stewartae differs from Recent *Nasua* and *Procyon* in its smaller size and in having P4 with a more posteriorly situated, lower and broader protocone, a less prominent parastyle, a better developed metacone blade, and no hypocone; M1 and M2 cusps are lower and rounder than in those taxa and there is no metaconule.

Trocharion albanense, from the Astaracian and Vallesian (MN7–MN9, equivalent to late Barstovian) of Europe, has been assigned to the mustelid subfamily Leptarctinae (Qiu and Schmidt-Kittler, 1982). Although the lower dentition (including the holotype) supports this allocation, other material assigned to *Trocharion* may have affinities with potosins such as *Bassaricyonoides* or perhaps *Parapotos*, the new genus

described below. As noted by Qiu and Schmidt-Kittler, the cranial fragment from Steinheim described by Helbing (1936: fig. 11) has a basicranium similar to that of *Nasua*. Qiu and Schmidt-Kittler (1982) assign the Steinheim basicranium to *Trochotherium*, which they include as a member of the musteloid stem group based on this specimen. The flattened bulla and broad mastoid process of the Steinheim specimen appear to be more similar to *Potos*. The upper dentition attributed to *Trocharion* (Qiu and Schmidt-Kittler, 1982: fig. 6) includes a P4 with a short metacone separated from the paracone by a carnassial notch, and an M1 lacking a hypocone (the cusp identified as a hypocone is the metaconule). The P4 and M1 appear to be intermediate in morphology between those of *Bassaricyonoides* and *Bassaricyon*.

Brachynasua is a procyonin procyonine from the Ensenadan (early Pleistocene) of Argentina. It is known from a maxilla with P2–M2 and an edentulous mandible. When *Brachynasua* was first described, Ameghino and Kraglievich (1925) suggested that it was related to *Potos*. *Brachynasua* does have features that are convergent with *Potos*, such as a shortened face and simplified dentition that may be adaptations for frugivory. However, these features developed independently and much earlier (early Miocene) in *Bassaricyonoides* and *Parapotos*, the base of the North American lineage that gave rise to *Bassaricyon* and *Potos*, than in *Brachynasua*. *Brachynasua* instead is derived from an endemic radiation of South American, late Miocene procyonins. Kraglievich and Olazábal (1959: 45, 56) concluded that although *Brachynasua* has a shortened rostrum, its dentition is similar to that of *Procyon* (and *Cyonasua*, which also have shortened rostra). Baskin (1990) suggested *Brachynasua* was more closely related to the Argentinean late Miocene and Pliocene genus *Cyonasua*. *Brachynasua* differs from *Bassaricyonoides* in having P1 absent, P4 with greatly reduced metacone blade, M1 with a better developed paracone and metacone, and M2 much more reduced.

Bassaricyonoides phyllismillerae, new species

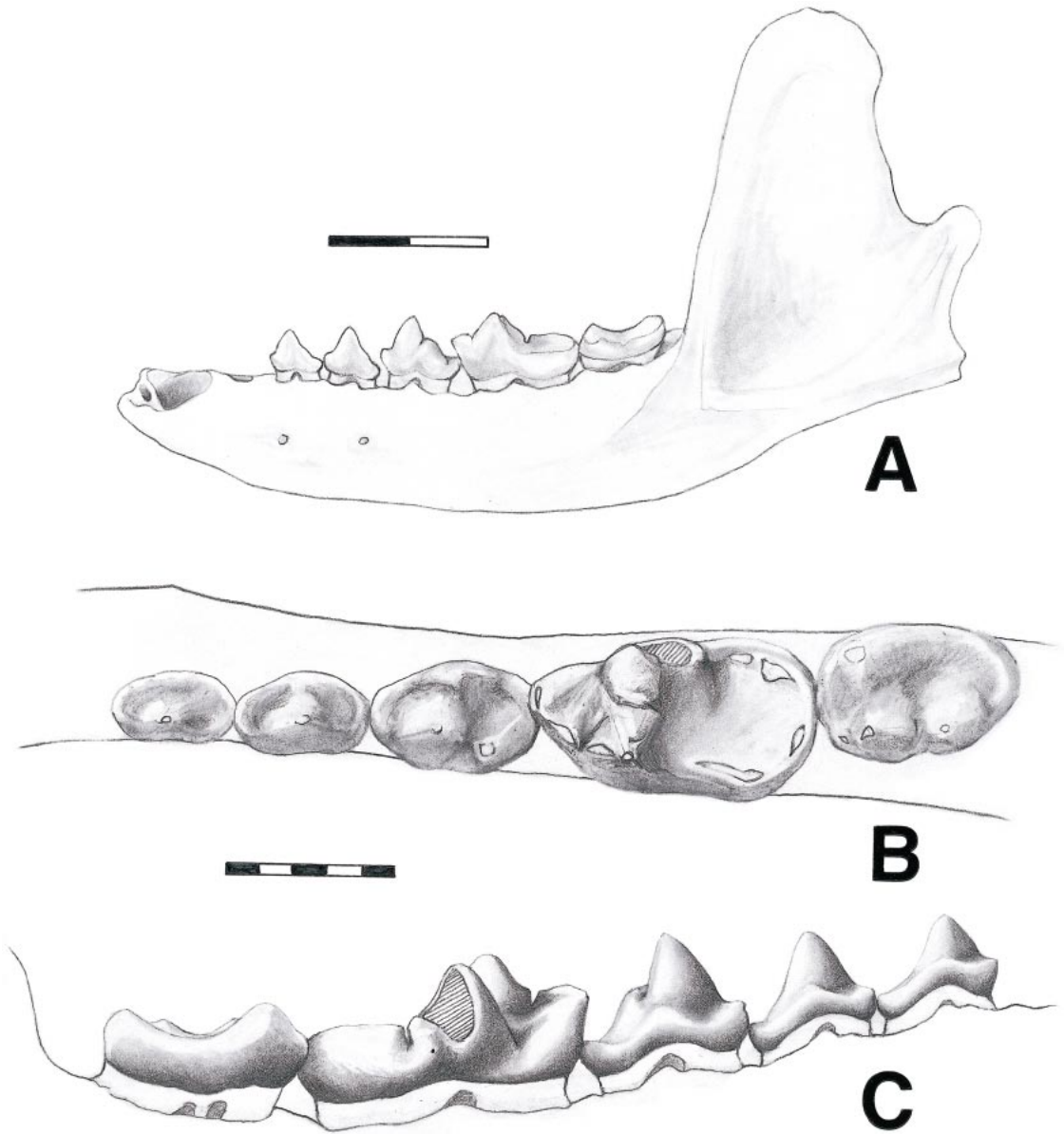HOLOTYPE: KUVP 130678, left mandible with p2–m2 from the Miller Local Fauna

Fig. 6.2. *Bassaricyonoides phyllismillerae*, new species, KUVP 130678: left mandible with p2–m2. **A,** Buccal view. **B,** Occlusal view of dentition. **C,** Lingual view of dentition. Scales = 10 mm for A, 5 mm for B, C.

(early Hemingfordian), Suwannee River, Dixie County, Florida (fig. 6.2; table 6.2).

ETYMOLOGY: Patronym for the late Phyllis Miller in recognition of her contributions to the collection of the Miller Local Fauna.

REFERRED SPECIMENS: Known from type specimen only.

DIAGNOSIS: A procyonid that is larger than *Probassariscus* and most *Bassariscus*, and approximately 15–20% larger than *Bassaricyonoides stewartae*. The premolars are closely spaced and relatively short and broad. The m1 has trigonid moderately open (primitive), the anteromedial paraconid low, but

TABLE 6.2

Dental Measurements of Type Specimens (mm, left to right) of *Bassaricyonoides phyllismillerae,* ?*Edaphocyon palmeri,* and *Parapotos tedfordi.* Parentheses indicate alveolar measurements.

L = greatest anterior posterior dimension, W = greatest transverse dimension, trl = trigonid length, from anterior side of paraconid to posterior side of protoconid, trw = trigonid width, taw = talonid width, Dm1 = depth of mandible below m1, Dp1 = depth of mandible below p1.

	KUVP 130678	KUVP 130679	F:AM 63289
c1L	(4.5)		11.5
W			7.0
p1L	(2.0)	(3.2)	(4.8)
W			
p2L	3.6	(5.3)	6.7
W	2.1		4.6
p3L	4.0	(6.3)	7.2
W	2.4		4.6
p4L	4.9	(6.6)	7.5
W	3.3		4.9
m1L	8.1	(8.3)	8.9
trl	4.2		4.3
trw	4.2		5.5
taw	4.5		5.4
m2L	5.6	6.5	5.5
W	3.8	4.2	4.6
p2-m2	26.1	39.1	33.4
Dm1	8.9	10.0	16.6
Dp1			18.6

prominent, and talonid with low rim, a very shallow basin, elongate (slightly longer than trigonid) and wider than trigonid (derived), a small hypoconid and no hypoconulid (primitive). The m2 has a short anterior cingulum, trigonid relatively low, metaconid taller than and slightly anterior to the protoconid, a prominent hypoconid, and a posterointernal hypoconulid.

DESCRIPTION: The incisors are closely appressed, with the alveolus for i2 situated behind those of i1 and i3. There is a very short postcanine diastema. The canine alveolus is ovate. The p1 is single rooted. The premolars are closely spaced, have anterior, interior, and posterior cingulids, and have an expanded posterointernal shelf, especially on p4. The p2 and slightly larger p3 are single cusped, with the cusp anterior to the midline of the tooth.

The p4 is wider posteriorly than anteriorly, with a prominent posterointernal heel. There

are two cingular cusps: one small and anterior, the other posterior. The posterior accessory cusp is on the posteroexternal margin of the main cusp.

The m1 has a short but relatively open trigonid, with paraconid-protoconid-metaconid forming a 70° angle (vs. 80° in *Probassariscus* and 60° in *Protoprocyon*). The protoconid is the largest and tallest cusp. It is slightly taller than the main cusp on p4. A shallow ''V''-shaped notch separates the protoconid from the anteriorly situated paraconid. The apex of the paraconid is situated close to the midline of the tooth, at a level approximately midway between the protoconid and metaconid. The metaconid is a large cusp that is taller than the paraconid and slightly shorter than and posterior to the protoconid. The talonid is broader than the trigonid and slightly basined. The rim of the talonid is low and the cusps on it are not very distinct. The rim is separated from the posterior side of the metaconid by a deep, narrow notch. The hypoconid is anteroposteriorly elongate. The possible entoconid and entoconulid are represented by wear facets, which are close together. There does not appear to be a hypoconulid.

The m2 has an ovate occlusal outline, with an elongate talonid and a short cingulid anterior to the protoconid and metaconid. The cusps are low. The metaconid is larger, taller, and slightly anterior to the protoconid. The talonid is moderately elongate, with a broad hypoconulid on the posterointernal margin. The hypoconid is similar in size and height to the protoconid and separated from it by a thin, shallow notch. The hypoconulid is equal in height to the hypoconid. There are two very small cuspules on the internal rim of the talonid. There is a small accessory rootlet on the internal margin at the anterior edge of the large posterior root.

The mandible is slender, becoming narrower anterior to p2, and curved ventrally. There is a large mental foramen beneath the anterior root of p2 and a smaller one under the posterior root of p3. The coronoid process is inclined slightly posteriorly. The masseteric fossa is wide and deep and has a strongly demarcated anterior border. Ventral to the masseteric fossa is a slightly concave, lateral inflection for the attachment of the an-

terior masseter. The ventral surface of the mandible below this structure is flattened.

DISCUSSION: The left mandible from Florida occludes reasonably well with the left M1–2 (UCR 15449) of *Bassaricyonoides stewartae*. Transparencies of the illustrations of the lower jaw and UCR 16927 appear to occlude well when the mandible is reduced in size by 20%. The low, elongate hypoconid of the m1 corresponds to the ovate talon basin of the M1. The low protocones of the M1 and M2 correspond to the shallow talonids with low cusps of the m1 and m2. The elongate protocone of the M1 fits the long broad talonid of the m1. The relatively short talonid of the m2 matches the small M2 protocone. The configuration of the m1 protoconid-paraconid blade of *B. phyllismillerae* matches the length and orientation of the P4 metacone blade of UCR 16927. These observations suggest the procyonids from Nevada and Florida are closely related. However, because of the difference in size and since there are no directly comparable elements from the two localities, they are considered separate species.

COMPARISONS: *Bassaricyonoides phyllismillerae* can be distinguished from European early Miocene *Amphictis* (Beaumont, 1976; Cirot and Wolsan, 1995) by its smaller size, less elongate mandible, anterior premolars that are broader, somewhat more complex, and more crowded (p2 is not separated from p3); p4 expanded posterointernally; m1 trigonid more closed and talonid only slightly basined, expanded medially, and the hypoconid (as well as the other talonid cusps) poorly developed; and m2 with a shorter anterior shelf region ("trigonid"). *Amphictis* has m1 with a deeply basined talonid with an anteroposteriorly elongate, trenchant hypoconid connected to the high posterior and internal walls with poorly developed cuspules. In *Amphictis* from the late Oligocene (Cirot and Wolsan, 1995), the m2 has an anterior cristid connecting the protoconid and metaconid, metaconid taller and slightly posterior to the protoconid, hypoconid equal in size to, but lower than, the protoconid, and the small hypoconulid on the posteroexternal margin close to the hypoconid. In the m2 of *Bassaricyonoides*, there is no anterior cristid, the anterior cingulum is not as well developed, the metaconid is slightly anterior to the protoconid, and the hypoconulid is situated posterointernally (derived procyonine features).

In the Orleanean *A. wintershofensis* (Dehm, 1950; Heizmann and Morlo, 1994), the premolars are slender and separated, p4 main cusp is lower than the m1 protoconid, and the m1 trigonid is open, and the m2 talonid is very elongate with a posterior heel (= hypoconulid) and has the hypocone much smaller than the hypoconulid. This species is closely related to the simocyonine procyonids, and may be ancestral to *Alopecocyon* (Beaumont, 1982). *Alopecocyon* occurs in the early Astaracian (Mein, 1989). It is larger than *Bassaricyonoides*, has narrower, more elongate premolars, m1 with more open trigonid with an anteriorly placed paraconid, and m2 with much more elongate talonid (characters of the Simocyoninae).

Bassaricyonoides phyllismillerae is similar in jaw size and overall cheek-tooth length to *Broiliana* and *Stromeriella*. All three have protoconid of m1 slightly taller than main cusp of p4. *Bassaricyonoides phyllismillerae* differs from *Stromeriella* in the absence of a diastema between p2 and p3, and in having p2 and p3 wider, with better developed cingulids; p4 broader and shorter with a prominent posterior accessory cusp; m1 metaconid taller than the paraconid, talonid wider transversely and less deeply basined, and a smaller and lower hypoconid; and m2 much longer and wider (m2:m1 length 70% vs. 50%), with better developed talonid cusps (especially the hypoconid) and a more anteriorly situated metaconid (vs. opposite the protoconid). The Agenian *S. aginense* differs from *B. phyllismillerae* in its larger size; the p4 has a small, poorly differentiated posterior accessory cuspule; the m1 has a more open trigonid and a shallower notch on the posterior margin of the metaconid that separates it from the talonid rim; and the m2 talonid is not greatly elongate, the hypoconid is small and indistinct, and the hypoconulid is posterocentral. *Bassaricyonoides phyllismillerae* differs further from the Orleanian *S. franconia* in lacking diastemata between p1 and p2 and p3 and p4, and in having m1 talonid not anteroposteriorly elongate and less deeply basined and in having a smaller hypoconid.

In *S. franconia*, m1 has paraconid situated a little more internally than in *Bassaricyonoides phyllismillerae* (it is in contact with the posterointernal margin of p4) and m2 has anterior cingulid longest medially (semicircle shaped), the cusps (protoconid, metaconid, and hypoconid) low and very small, the hypoconid much smaller and lower than the protoconid, and hypoconulid posterior to posterointernal with an indentation on the posteroexternal margin (similar to *Bassaricyon*).

Bassaricyonoides phyllismillerae differs from *Broiliana* in having shorter and broader, less secant premolars. The p2 and p3 have better developed anterior, posterior, and medial cingulids and the p4 is much shorter and broader, especially posteriorly. The m1 is relatively longer (28% vs. 23%) relative to p1–m2 length. The m1 trigonid has a similar shape in *B. phyllismillerae* and *Broiliana*, but in *B. phyllismillerae* the trigonid is not closed internally by a low cingulum and the talonid is somewhat longer and much broader and less basined and lacks a distinct hypoconid and entoconid. The m2 has a much shorter anterior cingulid on the trigonid, a larger, more distinct hypoconid, a better developed internal rim of the talonid, and a posterointernal (vs. posteroexternal) hypoconulid, and lacks a paraconid.

The earliest procyonid in North America is from the late Arikareean, upper Harrison Formation. The specimen (AMNH 81029), a left mandible with a badly damaged m1 mainly represented by the talonid, was identified as *Bassariscus* sp. (Cook and Macdonald, 1962). The mandible is much more slender than that of *B. phyllismillerae* and is similar to specimens of *Bassariscus* from the early Barstovian Lower Snake Creek Fauna of Nebraska. However, the m1 trigonid appears to be more open and the m2 more elongate than in *Bassariscus*, suggesting assignment to cf. *Amphictis*. As in *Bassaricyonoides*, m2 also has an accessory mediointernal accessory rootlet. A third rootlet is also present in a few specimens of *Bassariscus* from Barstovian localities in the AMNH collections. A cast of *Stromeriella* (1937 II 13010) also apparently shows this rootlet.

An *Amphictis*-like taxon occurs in the early Hemingfordian Runningwater Formation

of Nebraska (Tedford et al., 1987) and Calvert Formation of Delaware (Emry and Eshelman, 1998), which are close in age to the Miller Local Fauna. The Runningwater *Amphictis* (as represented by F:AM 49192) has more slender, elongate premolars than *B. phyllismillerae* and has a more open trigonid, better developed hypoconid, and a shorter, narrower, more basined talonid on m1. The m2 hypoconid is much smaller than the hypoconulid.

The mandible of *B. phyllismillerae* is similar in overall size to that of the early Barstovian *Bassariscus antiquus* and *Probassariscus matthewi*. In *Bassaricyonoides*, the premolar and m1 trigonid cusps are somewhat more inflated, the premolars are relatively shorter and broader; the m1 is relatively larger and has the talonid longer and wider and much less basined, with much smaller cusps; and the m2 has a much lower protoconid and metaconid, metaconid anterior to the protoconid, a shorter and less well-developed anterointernal shelf, a less inflated hypoconid and hypoconulid, and a less basined talonid. The m1 trigonid has a similar morphology in all three genera. *Bassaricyonoides* can be further distinguished from *Bassariscus* in having m1 that lacks a hypoconulid and m2 that is broader and less elongate. The ratio of m2:m1 length in *B. phyllismillerae* is similar to that of *Bassariscus astutus*. *Probassariscus matthewi* and *Bassaricyonoides* both have a relatively broad talonid on m2. *Probassariscus matthewi* has m1 with an entoconulid and m2 with a small, low entoconid (derived). In *Bassariscus* and *Bassaricyonoides* these two cusps are absent.

The early Hemingfordian *Edaphocyon lautus* and the early Barstovian *E. pointblankensis* are known only from upper dentitions. The morphology of the P4 indicates that the lower carnassial should have had a somewhat closed trigonid, a derived characteristic (Baskin, 1982), unlike the more primitive m1 trigonid of *B. phyllismillerae*. Additionally, *Edaphocyon* is larger and has a more elongate muzzle, as indicated by the slender anterior premolars separated by diastemata. This is evident in the second procyonid mandible from the Miller locality referred below to ?*Edaphocyon*. This specimen further differs from *B. phyllismillerae* in having m2

with a trigonid possessing a paraconid, and with a talonid that is more deeply basined and elongate.

The Barstovian to Hemphillian *Arctonasua* is much larger than *Bassaricyonoides*, with rounder and more bulbous cusps. The m1 of *Arctonasua* has a closed trigonid and a talonid with distinct hypoconid, entoconid, and entoconulid. The m2 has a hypoconid, posteromedian hypoconulid, and entoconid.

The Clarendonian *Protoprocyon* is slightly larger than *Bassaricyonoides*, but with a more slender mandible and narrower coronoid process. The paraconid of m1 is offset posteriorly and internally producing the more closed trigonid characteristic of the more derived procyonines (Baskin, 1982, 1989). The talonid is expanded labially, a derived character, and has a distinct hypoconid, entoconid, and entoconulid. The m2 is derived in possessing a posteromedial hypoconulid, an entoconid equal in size to the hypoconulid, and a prominent hypoconid (the largest cusp on the tooth). (By *lapsus calami*, Baskin [1982: 73] erred in the diagnosis of *Arctonasua*; the m2 metaconid, not hypoconid, is larger than the protoconid, a primitive procyonine characteristic.)

In *Protoprocyon* the entoconid and entoconulid of m1 are close together and form a narrow wall. This may lead to the character state seen in *Paranasua*, *Procyon*, and *Nasua*. In *Procyon*, the m1 usually has the entoconulid absent. However in some specimens, a small entoconulid is present, suggesting that it is being lost in the *Procyon-Nasua* lineage. *Procyon* has m2 with an entoconid. In the m2 of *Nasua*, the entoconid is shifted posteriorly and the hypoconulid is reduced to absent. This causes some specimens of *N. nasua* to appear to have the primitive m2 morphology.

The Recent *Bassaricyon* is similar in size to *Bassaricyonoides*. The premolars of *Bassaricyon* are similar in morphology (widened posteriorly), but lack an internal shelf. *Bassaricyonoides* differs from *Bassaricyon* in possessing crowded incisors, m2 with a taller trigonid, more elongate talonid (especially posterointernally), a more anteroposteriorly elongate hypoconid, and m1 with a wider, less basined talonid, smaller hypoconid and entoconid, and in having a tricuspid, open

trigonid. In *Bassaricyon*, m1 paraconid is very reduced to absent. If present, it is situated close to the metaconid, causing the trigonid region to be much shorter than the talonid.

Parapotos, new genus

TYPE AND ONLY SPECIES: *Parapotos tedfordi*, new species.

ETYMOLOGY: Greek, *para,* near; plus *Potos*, the kinkajou.

DIAGNOSIS: The robust canine has a weak internal groove; lower premolars overlap; p4 is lower than p3, and has a prominent heel; m1 with a low, anteromedian paraconid and a circular, shallow-basined talonid; and m2 subround with a very short anterior cingulid (trigonid) and a large, basined talonid.

COMPARISONS: *Parapotos* is easily distinguished from all other procyonids by its large size, massive mandible with a large canine, combined with relatively small, but cusped, molars. *Parapotos* is more derived than *Bassaricyonoides* in possessing p2 taller than p4, and m1 with a shortened trigonid (indicating P4 had a reduced metacone blade). *Parapotos* is more primitive than *Bassaricyon* and *Potos* in having a well-developed paraconid on m1. More detailed comparisons are presented below.

Parapotos tedfordi, new species

HOLOTYPE: F:AM, 63289, left mandible with c, p2–m2; from Stephen Prairie (?late Barstovian), San Jacinto County, Texas (fig. 6.3; table 6.2).

ETYMOLOGY: Patronym for Richard H. Tedford, in recognition of his important contributions to the systematics of fossil and Recent carnivorans and for encouraging others in the study of fossil mammals.

RERERRED SPECIMENS: Known from type specimen only.

DIAGNOSIS: Same as for the genus.

DESCRIPTION: The mandible is very deep, deeper anteriorly than posteriorly. The symphysial area is very large and thickened and extends posteriorly to a level of the p1–p2 border. There are two mental foramina: a smaller circular one below p1 and a larger, ovate one below p3. The alveoli indicate that the incisors are closely appressed, i2 lies be-
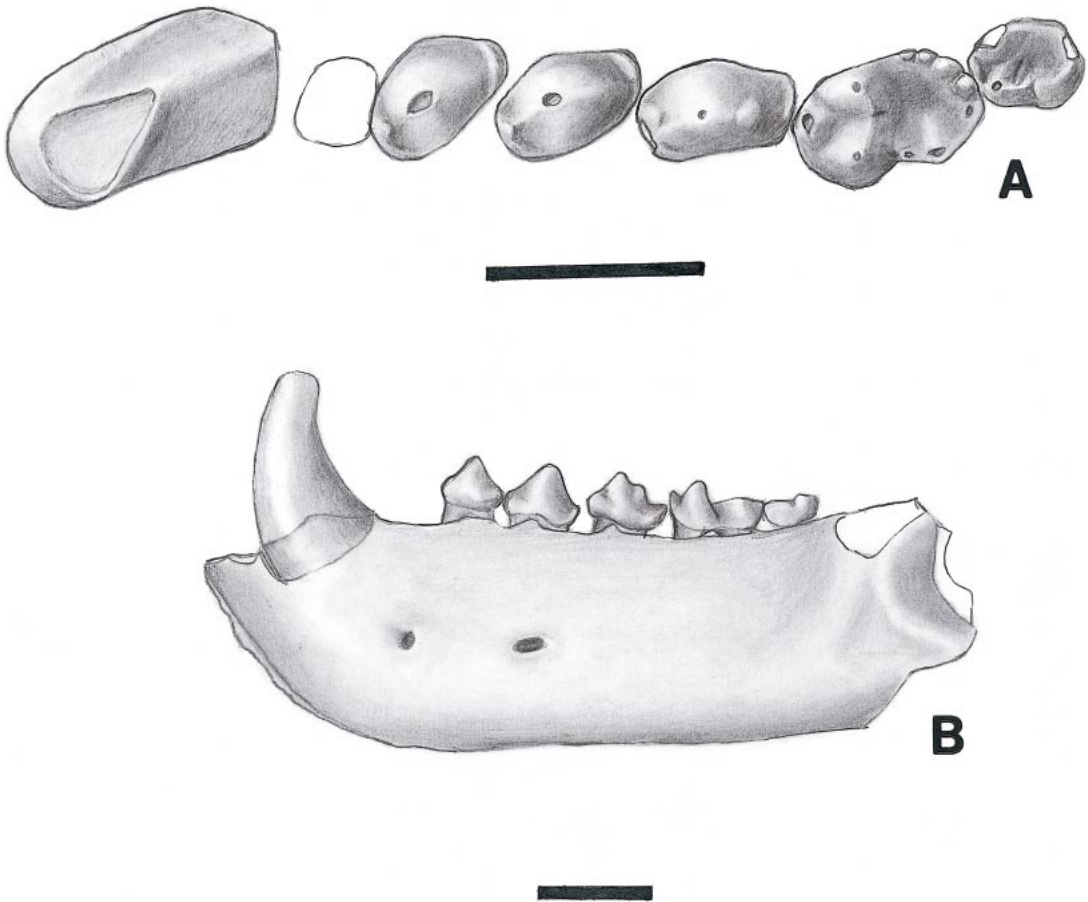
Fig. 6.3. *Parapotos tedfordi*, new genus and species, F:AM 63289: left mandible with c1, p2–m2. **A,** Occlusal view of dentition. **B,** Buccal view. Scales = 10 mm.

hind i1 and i3. The canine is massive, with a shallow groove on its posterointernal margin. The premolars are crowded and overlap because of offset of p1–p3. p1 is single rooted, but has a relatively large alveolus. The protoconid of p2–p4 is situated lateral to the midline of the tooth, closer to the external margin. The anterior cingulid, interior cingulid, and posterior heel become progressively better developed from p2 to p4. These premolars are widest medially.

The p2 is offset at approximately 45° to the anteroposterior axis of the jaw. The protoconid is above the anterior root.

The p3 has a stronger anterior cingulid and longer posterior heel than p2.

The p4 is lower than the p2 or p3. The anterior end is blunt. A small anterior cin-gular cusp, posterior accessory cusp, and posterior cingular cusp and a well-developed talonid heel are present.

The m1 has convex and slightly concave inner and outer margins, respectively. The short, triangular trigonid has subequal protoconid and metaconid opposite each other. The protoconid is approximately equal in height to the protoconid of p4. A lower paraconid is situated on the anteromedian margin. The paraconid is separated from the protoconid and metaconid by "V"-shaped notches. A "Y"-shaped depression is situated between the three cusps of the trigonid. The talonid is longer and slightly narrower than the trigonid. The basined talonid is bordered by a low rim including the anteroposteriorly elongate hypoconid. The internal and pos-

terointernal rim consists of four small cusps. There is a small wear facet in the position of the hypoconulid.

The m2 has a subround occlusal outline, is double rooted, and situated next to the internal margin of the mandible. The trigonid is very short. There is a small, median cusp on the anterior cingulid. The metaconid is larger than and posterior to the protoconid. The talonid is basined and has a distinct hypoconid. There are two small cusps (?a twinned hypoconulid) on the posterior margin. The larger one is situated posteriorly, closer to the external border, adjacent to the hypoconid. The smaller one is posterointernal.

COMPARISONS: *Parapotos* is a procyonid because it has m2, which, although small, is double-rooted and relatively elongate compared with the m1, has talonid longer than trigonid, and has both a hypoconid and hypoconulid, unlike most mustelids, which have a single talonid cusp. This assignment is also supported by the weak internal groove of the canine, a feature characteristic of *Bassaricyon* and *Potos*. *Parapotos* does have features seen in some mustelids. A massive mandible that deepens anteriorly is present in paleomustelids such as *Potamotherium* or *Brachypsalis*. These differ from *Parapotos* in having the m1 with an open, bladelike trigonid and a smaller talonid. Mustelids with a double-rooted m2 include paleomustelids such as *Brachypsalis* and the neomustelids *Leptarctus* or *Taxidea*. In these, the m2 trigonid is equal in length to or longer than the talonid, and the m2 is much shorter relative to the m1.

Stromeriella also has a small m2, but differs in having a more slender mandible, unenlarged canine, slender premolars sometimes separated by diastemata, m1 with an internally situated paraconid and more elongate talonid, and m2 talonid rim lacking cusps other than the very low hypoconid and with a very low heel.

The m1 trigonid of *Parapotos* resembles that of *Arctonasua minima* (Baskin, 1982) and certain members of the *Cyonasua* group in having a low, anteromedian paraconid. An isolated m1 (F:AM 25378) of *A. minima* (from the type locality, the early Barstovian Observation Quarry) has a similar occlusal outline, but has a strong hypoconid, hypoconulid, and entoconid. *Parapotos* differs from these in having weakly developed cusps on m1, especially of the talonid, and on m2, and in having a reduced m2, characters that indicate it is a member of the Potosini. *Arctonasua* and *Cyonasua* have m1 with a well-developed entoconid and entoconulid and m2 with a long heel with a prominent posterointernal hypoconulid. *Arctonasua* and more derived procyonins also differ from *Parapotos* in having p4 distinctly taller than m1.

Of the Potosini, *Parapotos* most closely resembles *Bassaricyon* and *Potos* and differs from *Bassaricyonoides phyllismillerae* in having the following derived characteristics: p2 and p3 as tall or taller than p4 and m1 with a shortened trigonid and with paraconid reduced to absent (corresponding to a reduced metacone blade on P4). *Parapotos* and *Potos* share the following derived characteristics: mandible massive, deeper anteriorly and with a large symphysial region, canine large, low p4 with a broad heel, and m2 oval in outline and reduced in length, with both trigonid and hypoconulid greatly reduced to absent (corresponding to a reduced M2). *Parapotos* differs from *Potos* in having an unfused mandibular symphysis, p1 present, p2 double rooted, and m1 and m2 with distinct (but small) cusps. Alternatively, a sister taxon relationship between *Bassaricyon* and *Potos* is suggested by the following synapomorphies: upper and lower canines with external and internal grooves, m1 paraconid greatly reduced to absent, and other cusps of molars weakly developed to absent.

TRIBE PROCYONINI GRAY, 1825, NEW RANK

DIAGNOSIS: Primitive Procyonini are distinguished from primitive Potosini in having the following apomorphies: M1 with a more posteriorly situated hypocone, M1 with a better developed metaconule, and bulla with a more inflated entotympanic. Characteristics listed by Decker and Wozencraft (1991) as autapomorphies for the extant *Procyon*, *Nasua*, *Nasuella*, and *Bassariscus* include nasiolabialis fossa present, orbital wall of palatine inflated, vomer attached to posterior part of palate, interosseus crest of ulna large, and banded tail rings present.

Edaphocyon Wilson, 1960

?*Edaphocyon palmeri*, new species

HOLOTYPE: KUVP 130679, right mandible with m2; from the Miller Local Fauna (early Hemingfordian), Suwannee River, Dixie County, Florida (fig. 6.4; table 6.2).

ETYMOLOGY: Named for Mr. Bob Palmer for his exceptional generosity in acquiring the Miller Local Fauna for the University of Kansas.

REFERRED SPECIMENS: Known from type specimen only.

DIAGNOSIS: A medium-sized procyonine larger than *Bassariscus antiquus* and smaller than *Arctonasua minima*. The mandible is elongate and slender, with a pronounced diastema between p2 and p3. The m2 has a very reduced paraconid and a deeply basined talonid, with an indistinct entoconid, a prominent hypoconid, and a posterointernal hypoconulid.

DESCRIPTION: The p1 is single rooted but relatively long. The other premolars are double rooted. There is a 1.1-mm diastema between the root of p1 and the anterior root of p2 and a 4.5-mm diastema between the posterior root of p2 and the anterior root of p3, where the mandible narrows on the dorsal margin. The m2 has a short, shallow trigonid basin. A preprotocristid extends first at an approximately 45° angle from the anterior side of the protoconid to the anteromedian margin of the tooth and then directly medially, forming the anterior wall of the trigonid. The preprotocristid terminates in a small cusp (apparently a very reduced paraconid) just internal to the midline of the tooth. The protoconid is heavily worn, but was apparently somewhat smaller and lower (plesiomorphic) than the metaconid. The metaconid is separated from the swollen termination of the preprotocristid (paraconid) by a V-shaped valley. The talonid is very elongate, deeply basined, with a prominent hypoconid and posterointernal hypoconulid. A deep wear facet is present on the posterior margin of the tooth. The entoconid is indistinct, represented by a swelling with a small wear facet on the high internal wall of the talonid. There is a narrow cingulid that extends from the anteroexternal base of the protoconid around the anterior margin and between the proto-

conid and hypoconid. The mandible is long, slender, and gently curved ventrally, with three mental foramina.

COMPARISONS: Until more material is obtained, the generic identification of this specimen must remain tentative. The m2 that is approximately 78% the length of m1, with greatly reduced paraconid and elongate talonid, indicates this specimen is a procyonid. The elongate, slender jaw compares best, as discussed below, with the medium-sized procyonid *Edaphocyon*, which is only known from upper dentitions. Procyonids with an elongate rostrum, as was apparently present in ?*E. palmeri*, are *Edaphocyon*, *Arctonasua*, and *Amphictis*. The two previously described species of *Edaphocyon*, which are known only from upper dentitions, have elongate slender premolars and diastemata between P1–2 and P2–3 (Baskin, 1982). The mandible of ?*E. palmeri* is slightly shorter than the corresponding upper dentition of the contemporaneous, early Hemingfordian *E. lautus*, closer in size to the early Barstovian *E. pointblankensis*. The deeply basined talonid on the m2 of ?*E. palmeri* corresponds to the well-developed protocone on M2 of *E. lautus* or *E. pointblankensis*. These upper dentitions of *Edaphocyon* have a pronounced diastema between P1 and P2, which should correspond to a pronounced diastema between p1 and p2, and is absent in ?*E. palmeri*.

The m2 of ?*Edaphocyon palmeri* possesses a paraconid. This primitive musteloid feature is also present in *Broiliana*, and probably *Bassariscus antiquus* and *Probassariscus matthewi*. It is absent in other *Bassariscus*, *Arctonasua*, and more derived procyonins, and in *Bassaricyonoides phyllismillerae* and the other potosins. Baskin (1989) was uncertain whether this cusp is a true paraconid or a neomorph formed from a swollen anterointernal cingulum. In *Bassariscus antiquus* and *Probassariscus matthewi*, this cusp is at the anterior apex of the anterior cingulid, approximately equidistant between the protoconid and metaconid, and is not clearly connected to the protoconid. Other reasons for this uncertainty include the fact that this cusp, when present adjacent to the metaconid in genera such as *Broiliana*, is connected to the protoconid by a convex anterior cingulid rather than a straight preprotocristid, and its
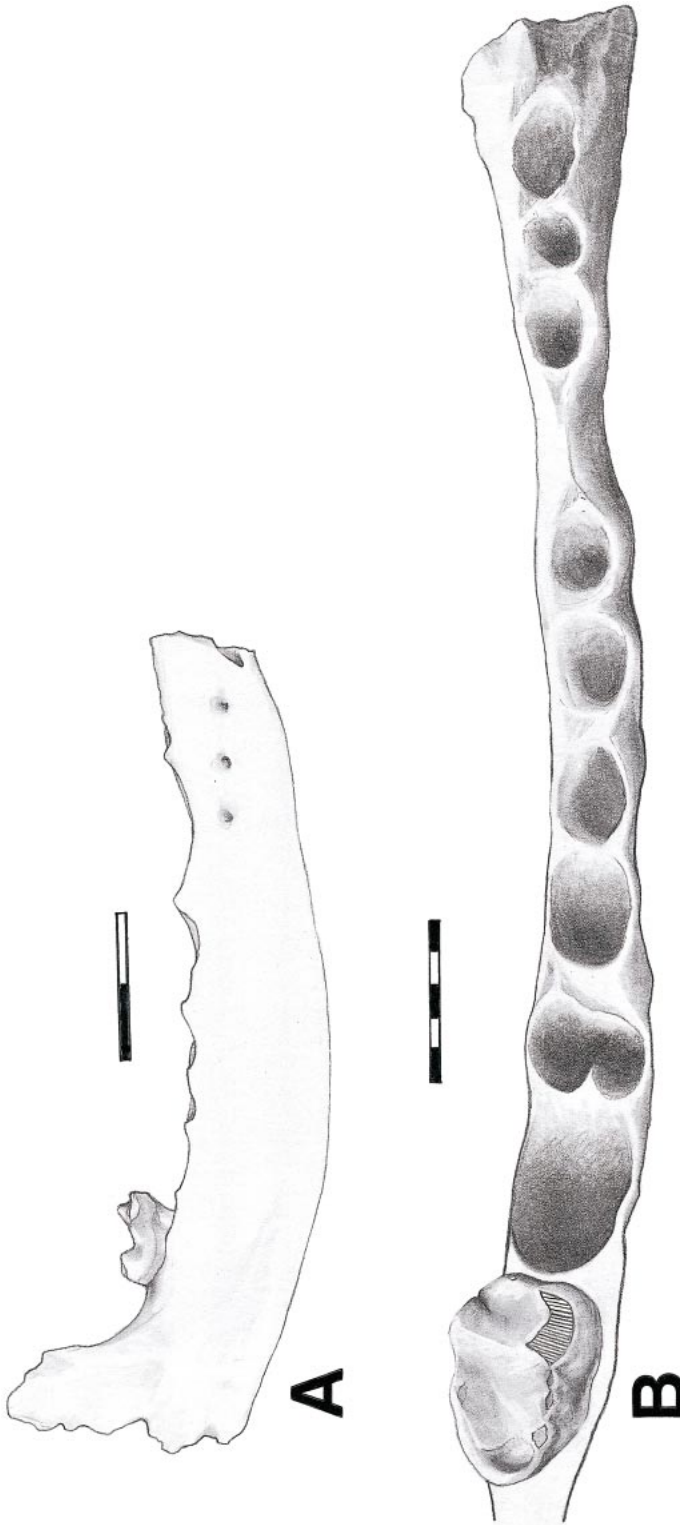
Fig. 6.4. ? *Edaphocyon palmeri*, new species, KUVP 130679: right mandible with m2. **A**, Buccal view. **B**, Occlusal view. Scales = 10 mm for A, 5 mm for B.

absence in most mustelids and possible absence in European *Amphictis*. However, the m2s of the primitive musteloid *Mustelavus*, the paleomustelid *Brachypsalis*, and the neomustelid *Leptarctus ancipidens* have a small paraconid. These and the m2 trigonid in ?*E. palmeri* suggest that a paraconid is present on m2 in primitive procyonines and mustelids and is lost independently in both lineages. The presence of a mure closing the internal margin of the talonid is a derived feature absent in *Broiliana*, potosins, and *Bassariscus antiquus*. A prominent entoconid is present in more derived procyonins, such as *Protoprocyon*.

The Barstovian to Hemphillian genus *Arctonasua* (Baskin, 1982) has moderately to very inflated cusps, unlike ?*E. palmeri*. The two Barstovian species, *A. minima* and *A. gracilis*, have an elongate mandible, with diastemata between the anterior premolars as in ?*E. palmeri*. The m2 is unknown in the early Barstovian *A. minima*, the smallest species, which is larger than the Florida specimen (p2–m2 = 45 mm) and has a more massive mandible (depth below m1 = 13 mm). The late Barstovian *A. gracilis* differs from ?*E. palmeri* in its much larger size and in having m2 with a relatively shorter trigonid and relatively longer talonid, a prominent posteromedial hypoconulid (lost in the derived species *A. fricki*), and a distinct entoconid. As in ?*E. palmeri*, there is a narrow cingulid on the anteroexternal corner of the base of the protoconid, the preprotocristid appears (the anterior margin of m2 is somewhat broken) to terminate in a paraconid, the metaconid is taller than the protoconid, and the lingual margin of the talonid is not open. The m2:m1 length ratio of 81% for *A. gracilis* is similar to that for ?*E. palmeri*. The m2 is unknown in the early Barstovian *A.* cf. *gracilis*, which has a very reduced p1 and a very long p1–p2 diastema, unlike ?*E. palmeri*.

Amphictis also has a slender mandible with spaced anterior premolars. Measurements given for postcanine tooth row length and m2 length and width (Viret, 1929) are similar to those of the Florida specimen. The m2 of *Amphictis* (Beaumont, 1982; Heizmann and Morlo, 1994; Cirot and Wolsan, 1995) appears to have a similar trigonid region, but differs from ?*E. palmeri* in having a more prominent hypoconid, a more laterally situated hypoconulid, a less deeply basined talonid, and a lower internal margin of the talonid. The mandible of ?*E. palmeri* is larger than, but similar in proportions to, the Agenian *Broiliana* cf. *B. nobilis* (Bonis, 1973). Some specimens of *Broiliana* have a diastema between p2 and p3. The m2 of *Broiliana* differs from ?*E. palmeri* in having the paraconid adjacent to the metaconid and the rim of the talonid open internally and a posterointernal hypoconulid.

Bassaricyonoides phyllismillerae, also from the Miller Local Fauna, has a much shorter tooth row. The m2 is more derived than that of ?*E. palmeri* in having a much shorter trigonid region with no paraconid and more primitive in having a much shorter hypoconulid heel.

Bassariscus antiquus is much smaller and has m2 talonid open lingually, not closed by a wall as in ?*E. palmeri*. The m2 of ?*E. palmeri* is broadly similar to that of *Probassariscus matthewi*, but is much larger. It is more primitive than that of *Probassariscus* in possessing a better-developed trigonid and in lacking an entoconid (although with an internal wall blocking the opening to the lingual margin). If this m2 is characteristic of *Edaphocyon* and the internal wall of the m2 talonid of ?*E. palmeri* is not formed by fusion of the entoconid with the hypoconulid, then the m2 entoconid evolved independently in *Probassariscus* and in *Edaphocyon* and more derived procyonines.

The Clarendonian *Protoprocyon* has a much shorter p2–m2 length, even though m2 length is approximately the same in both genera, indicating the relative enlargement of this tooth in *Protoprocyon* (m2:m1 length ratio = 91%). Additionally, m2 morphology is much more derived in *Protoprocyon*. It has small, subequal protoconid and metaconid, large hypoconid, posteromedian hypoconulid and a prominent entoconid equal in height to the hypoconulid. The ventral margin of the jaw has an inflection beneath the anterior margin of the coronoid process in contrast to the smoothly curved ventral margin of ?*E palmeri*.

NORTH AMERICAN PROCYONINE DIVERSITY

Van Valkenburgh (1999: 463) noted that the "history of carnivorous mammals is characterized by a series of rise-and-fall patterns in which declining clades are replaced by phylogenetically distinct, but functionally similar clades." Most fossil (Baskin, 1982) and Recent procyonines have hypocarnivorous dentitions that reflect either omnivorous or frugivorous diets. The exceptions are the mesocarnivorous *Bassariscus* and *Probassariscus*. In the early and medial Miocene of North America, the typical procyonid (i.e., small hypocarnivoran) niche was occupied mainly by hypocarnivorous borophagine canids. Morphological and, presumably, ecological similarity to procyonines led Simpson (1945), following Wortman and Matthew (1899) and McGrew (1938), to include the known hypocarnivorous borophagines (*Cynarctoides*, *Cynarctus*, and *Phlaocyon*) in the Procyonidae. Hypocarnivorous borophagines have P4 short and usually with a hypocone, M1–M2 with a discrete hypocone, M2 enlarged, and m2 elongated (Wang et al., 1999), as do most procyonines. Hypocarnivory evolved independently in at least four lineages of borophagines, most importantly in the Phlaocyonini and Cynarctina (table 6.3). Approximately one-third (20 species in six genera) of the borophagines are hypocarnivorous (Wang et al., 1999), with perhaps 15 species fully hypocarnivorous. In marked contrast to the other borophagines, these hypocarnivores, except for one or two species, are represented by "no more than a handful of specimens" (Wang et al., 1999: 338), yet most are better represented than the Tertiary Procyoninae. In the Miocene, true procyonines that are hypocarnivorous are represented by perhaps 15 species in eight genera, with most taxa represented by a single specimen.

All extant procyonines are to some degree arboreal (McClearn, 1992). It is not known whether the hypocarnivorous borophagines or the extinct procyonines were arboreal. Wortman and Matthew (1899) briefly described the postcranial skeleton of *Phlaocyon leucosteus* (Wang et al., 1999: fig. 35) and noted similarities with that of *Procyon*. The forelimb is described as having the humerus the same length but more slender, and a radius and ulna of about the same diameter, but 15% shorter than in *Procyon*. Iwaniuk et al. (1999) conclude that the brachial index (radial length/humerus length) is one of the most important indicators of arboreal locomotion. The relatively short radius (r/h = 0.75) of *P. leucosteus* suggests that some hypocarnivorous borophagines may have resembled procyonines in locomotion as well as diet.

The North American late Eocene through Pliocene may be characterized by five chronofaunas (Tedford et al., 1987; Webb and Opdyke, 1995): the White River (late Duchesnian–early Arikareean), Runningwater (late Arikareean–early Hemingfordian), Sheep Creek (late Hemingfordian–early Barstovian), Clarendon (late Barstovian–early Hemphillian), and late Hemphillian chronofaunas. The differences in faunal composition that distinguish these chronofaunas are related to influxes of immigrant taxa and to climate change, probably mainly the latter for the small hypocarnivorans, since there are few immigration events of these ecomorphs. Borophagines are exclusively North American. The procyonines first immigrated to North America in the early Hemingfordian and have since been represented mainly by endemic taxa. The phlaocyonins are the dominant hypocarnivorans in the late Arikareean and early Hemingfordian, the cynarctins in the Barstovian, and the procyonines in the Clarendonian to Recent (table 6.3; fig. 6.5). The question is whether the diversity of each clade was determined mainly by competition (active displacement) or was caused by chance or factors such as climate (passive displacement).

The early Tertiary had been marked by an abundance of small frugivorous mammals (e.g., primates, dermopterans) that inhabited subtropical to tropical environments, which largely disappear from North America by the late Eocene. Modern carnivoran families first appear in the late Eocene, but do not become widespread until the Oligocene. The early Oligocene cooling event had its greatest effect on floras of the Pacific northwest (Wing, 1998). The early Oligocene (Orellan) of North America lacks small hypocarnivorans. From the middle to late Oligocene (Whitney-

TABLE 6.3
Temporal Ranges for Species of Hypocarnivorous Phlaocyonini, Cynarctina, and Procyoninae

PHLAOCYONINI	
Phlaocyon latidens	early Arikareean
P. achoros	middle Arikareean
P. annectens	late late Arikareean
P. multicuspis	late late Arikareean
P. leucosteus	late late Arikareean–late Hemingfordian
Cynarctoides acridens	early late Arikareean–early early Barstovian
C. emryi	late late Arikareean–early Hemingfordian
C. luskensis	late late Arikareean
C. gawnae	early Hemingfordian
CYNARCTINA	
Paracynarctus kelloggi	early Hemingfordian–late Barstovian
P. sinclairi	early Barstovian
Cynarctus galushai	early–late Barstovian
?C. marylandica	early Barstovian
C. saxatilis	late Barstovian
C. voorhiesi	late late Barstovian
C. crucidens	Clarendonian
PROCYONINAE	
Bassaricyonoides phyllismillerae	early Hemingfordian
?Edaphocyon palmeri	early Hemingfordian
Edaphocyon lautus	early Hemingfordian
E. pointblankensis	early Barstovian
Arctonasua minima	early Barstovian
A. gracilis	Barstovian
A. floridana	Clarendonian
A. sp. A	late Barstovian
A. sp. B	Clarendonian
A. eurybates	late Hemphillian
A. fricki	late Hemphillian
Parapotos tedfordi	late Barstovian
Protoprocyon savagei	Clarendonian
Paranasua biradica	Clarendonian
cf. *P.* sp.	early Hemphillian
Procyon sp.	late Hemphillian–Recent
Nasua sp.	late Hemphillian–Recent

an through middle Arikareean) to earliest Miocene (early late Arikareean), hypocarnivorous borophagines are rare, represented by one or two species at a time. *Oxetocyon cuspidatus* from the Whitneyan and early Arikareean is the earliest hypocarnivorous borophagine. The first hypocarnivorous phlaocyonin is *Phlaocyon latidens*. *Cynarctoides* also appears in the early Arikareean, but is only incipiently hypocarnivorous at this stage.

With warmer climates in the early Miocene (Wing, 1998), diversity of hypocarnivorous phlaocyonins peaks with six species in the late Arikareean (fig. 6.5). Another small hypocarnivoran is the late Arikareean arctoid *Nothocyon*. In the early Hemingfordian, the diversity of hypocarnivorous borophagines is maintained at six, with the appearance of the earliest cynarctin, *Paracynarctus kelloggi*. However, the beginning of the Hemingfordian is also marked by a major dispersal event from the Old World to North America (Tedford et al., 1987; Woodburne and Swisher, 1995) and the total diversity of small hypocarnivorans in the North American fossil record increased to a maximum. Immigrant hypocarnivorans include the first
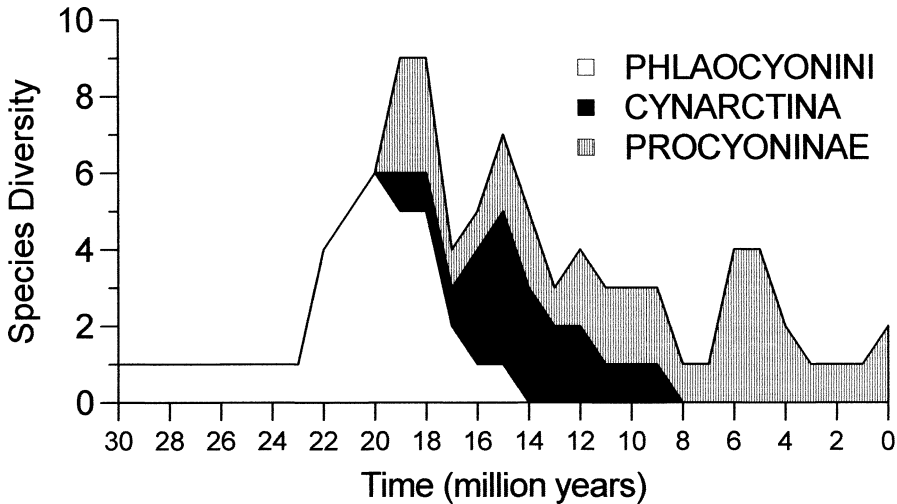
Fig. 6.5. Patterns of species diversity for the hypocarnivorous Phlaocyonini, Cynarctina, and Procyoninae.

North American procyonines (table 6.3) and the leptarctine mustelids (*Craterogale* and *Leptarctus*). Leptarctines may have occupied the arboreal frugivore niche (Lim, 1999) associated with the extant potosins. *Leptarctus* is well represented in the fossil record through the early Hemphillian. The early Hemingfordian peak in small hypocarnivoran diversity may result from biogeographic differences. Hypocarnivorous borophagines are rare in Gulf Coast faunas, known only from a few isolated teeth from the middle Arikareean to early Hemingfordian (Wang et al., 1998). They are much better represented in the midcontinent. Although never abundant, hypocarnivorous procyonines have over half their Miocene fossil record from Gulf Coast localities. Procyonines today have their greatest diversity in the New World tropics to subtropics, and the mainly Gulf Coast fossil distribution suggests that this was true in the past as well (Baskin, 1982). Additionally, extant procyonines occur mostly in forested habitats, environments that are poorly represented in the North American Neogene fossil record. These observations may account for the fact that procyonids have the poorest fossil record of any North American carnivoran family.

In the late Hemingfordian (ca. 17 Ma), there is a sharp drop in diversity for the Borophaginae (Wang et al., 1999: fig. 143),

largely caused by a dramatic decline in the Phlaocyonini (fig. 6.5). Six species of hypocarnivorous borophagines are present in the early Hemingfordian Runningwater Formation of Nebraska; only two are present in the overlying Box Butte and Sheep Creek Formations. The transition from the Runningwater to Sheep Creek chronofauna is associated with the evolution of mammals with more open-country adaptations, notably the grazing horses (Hulbert and MacFadden, 1991), presumably indicating the increasing importance of grasslands (Webb and Opdyke, 1995; Jacobs et al., 1999). The only procyonid recorded from the late Hemingfordian is *Bassaricyonoides stewartae* from Nevada. The lower procyonid diversity may be an artifact of smaller sample size, since there are few late Hemingfordian faunas from the Gulf Coast.

There are three species of hypocarnivorous procyonines and five of hypocarnivorous borophagines in the early Barstovian. The early Barstovian rise of the cynarctins appears to be an example of passive replacement (Van Valkenburgh, 1999), because they do not diversify until after the Hemingfordian decline of the phlaocyonins. Two of the three procyonines are from the Gulf Coast, suggesting they had little impact on cynarctin diversity. The early Barstovian is also marked by the first appearance of two me-

socarnivorous procyonine genera, represented by *Bassariscus antiquus* from Nebraska and *Probassariscus matthewi* from Nebraska and Nevada, at least one of which is an immigrant from the Old World. Late Barstovian hypocarnivoran diversity is similar with three procyonines and four borophagines. The late Barstovian decline in small hypocarnivoran diversity may be associated with a cooling and drying climate, leading to the spread of open, drought-tolerant vegetation (Wing, 1998).

Grass-dominated ecosystems become widespread in the Clarendonian and continue into the Hemphillian (Jacobs et al., 1999). In the Clarendonian, there are four species of hypocarnivorous procyonines, as well as the mesocarnivorous *Bassariscus* spp. Hypocarnivorous borophagines decrease to the single species *Cynarctus crucidens*, the last cynarctin. It is unlikely that this minor diversification of procyonids caused the extinction of the cynarctins, which had been in decline for over three million years. The lack of competition, however, may have contributed to success of the procyonines.

In the Hemphillian, procyonines are represented by *Bassariscus*, two large species of *Arctonasua* from Florida, Nebraska, and Oklahoma, and ?*Paranasua*, from Kansas. The first definite record of the extant *Procyon* is from the late Hemphillian Bone Valley of Florida and possibly from California. The first probable record of *Nasua* is from the late Hemphillian of Florida. The last hypocarnivorous borophagine is the Hemphillian *Carpocyon limosus*, an epicyonine, which independently evolved hypocarnivory.

By Blancan time, *Procyon* and *Bassariscus* are, with one exception, the only procyonines in the United States, probably having achieved a distribution similar to that of the present. *Bassariscus* occurs in California, Texas, Kansas, Washington, Arizona, and Nebraska. *Procyon* occurs in Kansas, Texas, Florida, California, and Washington. *Nasua* is known from an isolated p4 from the early Blancan of the Texas Panhandle. Pleistocene records of procyonines include *Bassariscus* and *Procyon*. Today *Procyon* is the only genus that occurs widely in northern temperate latitudes. *Nasua* occurs in southern Arizona and New Mexico southward; *Bassariscus* is more widespread than *Nasua*, occurring through most of the desert southwest and extending northward to Oregon.

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