A GENERIC REVISION OF THE PROTOLABIDINI (MAMMALIA, CAMELIDAE), WITH A DESCRIPTION OF TWO NEW PROTOLABIDINES

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ABSTRACT

A revised diagnosis of the Protolabidini characterizes the tribe as having a narrow rostrum and laterally expanded anterior nares. *Tanymykter*, new genus, possess the above derived features and is included in the Protolabidini as the primitive sister taxon to *Protolabis*. The morphological features that separate *Tanymykter* from *Protolabis* are all primitive except for the derived condition of closely appressed P^1_1 roots. Based upon new material from the Milk Creek Formation, morphological distinctions between *Protolabis* and *Procamelus* are clarified. The principal derived features of *Protolabis coartatus* that differ from *Procamelus* are extreme constriction of the rostrum, lateral expansion of the anterior nares, P_1 and P_2 small and sometimes absent, and a mandibular angle with extreme lateral flare and a prominent mesial tuberosity. Although the above derived features are less pronounced, they are still present in *Protolabis heterodontus* and other undescribed samples in the collection of the American Museum of Natural History. Thus, Stirton's species, *coartatus*, which has previously confused the generic concept of *Procamelus*, is transferred to *Pro-tolabis*. The small size of the cranium and coronoid process is correlated with the strong lateral and mesial flare of the mandibular angle in *P. coartatus*. This reflects increased emphasis on the masseter and pterygoid muscles in mastication and less emphasis on the temporalis. In contrast, the large coronoid process in *Procamelus* indicates greater emphasis on the temporalis muscle.

Oxydactylus exilis Matthew is transferred to *Michenia* because it shares the derived features of a narrow rostrum, incisiform upper canine, and a shallow symphysis. A new species, *Michenia yavapaiensis*, with P_1 unerupted, P_2 small, unerupted or absent, and tall-crowned molars is described from the Milk Creek Formation. Finally, a cladogram of proposed relationships of the Protolabidini is presented, including *Tanymykter*, new genus, *Protolabis* and *Michenia* with supporting evidence for this tribe being a monophyletic group. The relationship of other members of the Camelinae to the Protolabidini is also discussed. A short section detailing the stratigraphic framework of the Milk Creek Formation, Yavapai County, Arizona is included.

INTRODUCTION

During the Miocene, camels of the Tribe Protolabidini were common in western North America. Members of this tribe have been found in deposits ranging in age from late Arikareean to Clarendonian. The Protolabidini may be characterized by progressive constriction of the rostrum, a weak to strong buccinator fossa, marked lateral expansion of the anterior nares, and a progressive shortening of the metapodials with the length of the metacarpus[1] ranging from subequal to significantly shorter than the metatarsus.

The genera of the Protolabidini include *Protolabis* Cope, 1876, *Michenia* Frick and Taylor, 1971, and *Tanymykter*, new genus. Although well known since its first description,

Protolabis has frequently been confused with Procamelus and Miolabis, a fact pointed out by Frick and Taylor (1971, pp. 4-5). In that paper the authors briefly discussed the characters that distinguish *Protolabis* from *Procamelus* and *Miolabis*, and clarified the taxonomy with respect to *Miolabis*. *Michenia* is less well known due to its recent description, although it includes material from the Avawatz Mountains referred to *P. coartatus*, and one species (*M. exilis*) previously referred to that taxonomic scrapbasket, *Oxydactylus*. Judging from the abundant material of *Michenia* in the F:AM collection, this genus is probably well represented but unrecognized in other collections. *Tanymykter* is based on a species also long referred to *Oxydactylus*, despite significant morphological differences with the genotypic species, *O. longipes*.

Our initial objective in writing the present paper was to describe the protolabidines from the Milk Creek Formation in Arizona. However, after an analysis of the character po-

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[1] Although Frick and Taylor (1971, p. 21) reported that the length of the metacarpus (AMNH 14259) slightly exceeded that of the metatarsus in *Michenia agatensis*, a reexamination of the metacarpus shows, when an allowance is made for its crushed and restored condition, the length of the metacarpus could be either equivalent or greater than that of the metatarsus.

larities in *Michenia* and *Protolabis*, it became apparent that the primitive sister taxa to both of these genera could be found only in taxa referred to *Oxydactylus*. Recognition of certain derived features in species referred to *Oxydactylus* necessitated their transfer to the Protolabidini and a broadening of the concept of this tribe. A final result of this study is, therefore, a revised definition of the Protolabidini as a monophyletic group, based on shared derived characters.

ACKNOWLEDGMENTS

ABBREVIATIONS

The following abbreviations are used for institutions throughout the text:

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History

AMNH (M), the American Museum of Natural History, Modern Mammals

CIT, formerly the California Institute of Technology; the collection is now at the Los Angeles County Museum

CM, Carnegie Museum

F:AM, Frick American Mammals, Department of Vertebrate Paleontology, the American Museum of Natural History

UALP, University of Arizona Laboratory of Paleontology

UCMP, University of California, Museum of Paleontology, Berkeley

UTBEG, University of Texas, Bureau of Economic Geology

MEASUREMENTS AND STATISTICS

N, sample size

OR, observed range

P, probability from students t-distribution

S, standard deviation

T, students t-statistic

V, coefficient of variation

X, mean

( ) indicate approximate measurement

STRATIGRAPHY

The Milk Creek Formation crops out in the Walnut Grove Basin about 15 miles directly south of Prescott, Arizona. The basin is drained by Milk Creek, a tributary of Hassayampa Creek. The Milk Creek Formation has been partially mapped on the Kirkland and Mount Union Quadrangles by Plafker (MS) and Hook (MS), in unpublished master's theses, and by McKee and Anderson (1971) and Anderson and

Blacet (1972). Anderson and Blacet (1972) formalized the usage of Milk Creek Formation, a name first proposed by Hook (MS). Hook's Milk Creek Formation included only the Mio-Pliocene sediments of the Walnut Grove Basin; Anderson and Blacet's (1972) Milk Creek Formation includes sediments and intercalated basalts and latites.

Hook (MS) gave a detailed description and

stratigraphic section of the sediments of the Milk Creek Formation. According to Hook, the sediments include approximately 2300 ft. of "predominantly siltstone and fine-grained sandstone and interbedded layers of medium and coarsegrained sandstone and tuff [p. 9]." On the basis of lithology and structure, Hook divided his Milk Creek Formation into three members. The lower member consists predominantly of 496 ft. of interbedded conglomerate, conglomeratic and silty sandstone, and tuff. The lower member is in places conformably overlain by basalt with a maximum thickness of 342 ft. Hook's middle member consists of 1062 ft. of argillaceous siltstones and sandstones with beds of clay and coarse, resistant sandstone and tuff. The upper member is 747 ft. thick and composed of "interbedded layers of siltstone, sandy and argillaceous siltstone, coarse-grained, resistant sandstone, and conglomerate [p. 12]." Locally, the sandstones of the upper member are strongly crossbedded. The vertebrate fossils described in this paper were obtained from Hook's upper member.

The accompanying stratigraphic columns (fig. 1) are partial sections of Hook's upper member of the Milk Creek Formation, and show the relative positions of the various quarries. Section A was measured by the senior author and Section B was drawn from information supplied by Ted Galusha. The sections are in the SW. ¼, SW. ¼, sect. 5, T. 11 N., R. 21 W. Mount Union Quadrangle, Arizona. Section A is about 500 ft. northwest of Section B. The upper part of the two sections are easily correlated by means of a gray-white resistant marker sandstone. The correlation at the base of the unit was established by tracing beds from the Shield's Ranch Quarry, at the level of the Manzanita Quarry, to Goldie's Honeypot Quarry, a distance of about one-half mile. Manzanita Quarry lies about 10 ft. stratigraphically below Goldie's Honeypot Quarry, and thus the section thickens by about 33 ft. between Manzanita and Goldie's Honeypot.

We believe that the alternating siltstones, sandstones, and occasional mudstones in these two sections are largely fluvial. The 37 ft. of tabular planar crossbedded sandstone atop section A, and the 17.5 ft. of slope-forming sandstone below this, however, is aeolian in origin (Honey, MS). In Section B, the 10 ft. of sandstones both above and below the white limey layer at Deep Springs Quarry are physically correlative with the aeolian sands to the west in Section A, and the sands immediately below the white-limey layer exhibit large-scale tabular planar crossbedding. This large-scale crossbedding disappears east of Deep Springs Quarry. In several places in Section A, isolated bones were found weathering out of the cliffs just below the gray-white resistant marker sandstone, providing strong evidence for direct association of some fossils with aeolian sediments. The fossils of Milk Creek Quarry also occur in sandstone. The fossils in Shield's Ranch, Manzanita, and Goldie's Honeypot Quarries occur in claystones and siltstones, however. Further, the fossils in the last quarry show evidence for sorting in a current of water (Honey, MS), possibly a current associated with overbank deposition.

SYSTEMATICS

ORDER ARTIODACTYLA OWEN, 1848

SUBORDER TYLOPODA ILLIGER, 1811

FAMILY CAMELIDAE GRAY, 1821

SUBFAMILY CAMELINAE GRAY, 1821

TRIBE PROTOLABIDINI ZITTEL, 1895

INCLUDED GENERA: *Protolabis* Cope, 1876; *Michenia* Frick and Taylor, 1971; and *Tanymykter*, new genus.

REVISED DIAGNOSIS: The Protolabidini differ from the Camelopini, Camelini, and Lamini in shorter cranial (postorbital) length relative to facial length; greater rostral constriction; lateral expansion of anterior nares; maxillary fossa never pocketed; paroccipital process rarely extends below level of auditory bulla in contrast with other Camelinae except *Camelus*; distance between upper canines equal to or less than distance between upper I^3s; I^{1-2} present in primitive species; $P^1_{\bar{1}}$ with double roots versus single root in other Camelinae; and length of metacar-

A (Section above Goldies Honeypot Quarry)

Top of cliffs

Gray—white sandstone with tabular planar cross beds

Gray—white resistant marker sandstone

37'

Gray—white sandstone with large scale tabular planar cross beds; forms cliffs

resistant ledges

17.5' — Gray—white sand and sandstone; forms gentle slope

Gray—white sandstone; forms discontinuous ledge — 2' Gray—white sandstone; medium

0.5'

7.5' Tan sandstone; cross bedded

2' Tan sandstone; fine to coarse; forms resistant ledge

8' Tan sandstone; alternating fine and coarse grained cross beds

6.5' Tan mudstone with interbedded fine sands and sandy silts; some small scale trough and wedge planar cross strata

6.5' Green—brown mudstone with sandy stringers toward top; forms slope

5.5' Light tan sandstone; fine to coarse layers; white pumice? fragments; forms steep slope

6.5' Tan siltstone, locally with root casts; forms slope

6' Green—gray sandstone; fine; calcareous; forms slope

2.5' Sandstone, coarse
Dark tan sandstone; silty, calcareous

3' Tan speckled sandstone; fine, calcareous

Goldies Honeypot Quarry
1' Green—gray siltstone
White siltstone; calcareous; 0.5'
1' Green—gray sandy siltstone; calcareous

4' Green—gray sandstone; fine to medium; calcareous; resistant; contains root casts

2.5' Tan sandstone; medium; friable; forms recess

11.5' Tan sandstone; medium to coarse; friable; weakly bedded

A

B (Section above Manzanita Quarry)

Gray sand and sandstone; mostly covered

35'

Milk Creek Quarry

Discontinuous calcareous ledges

Light tan sandstone; medium; friable; forms covered slope

3.5' Dark green mudstone

Gray—white resistant marker sandstone

10' Light tan sandstone; medium; calcareous; resistant

Deep Springs Quarry
White limey layer

10' Gray sandstone; coarse; locally cross bedded with lenses of granules, pebbles and cobbles

5' Siltstone and sandstone; thinly interbedded

10' Gray sandstone; coarse; locally cross bedded, especially at base

30' Gray sandstone, alternating with layers of buff and greenish siltstone and clayey sandstone; forms slope

5' Gray sandstone; coarse

gray sandstone ledge 0.5'

5' Sandstone and siltstone, clayey and calcareous

2' Grey sandstone; blocky
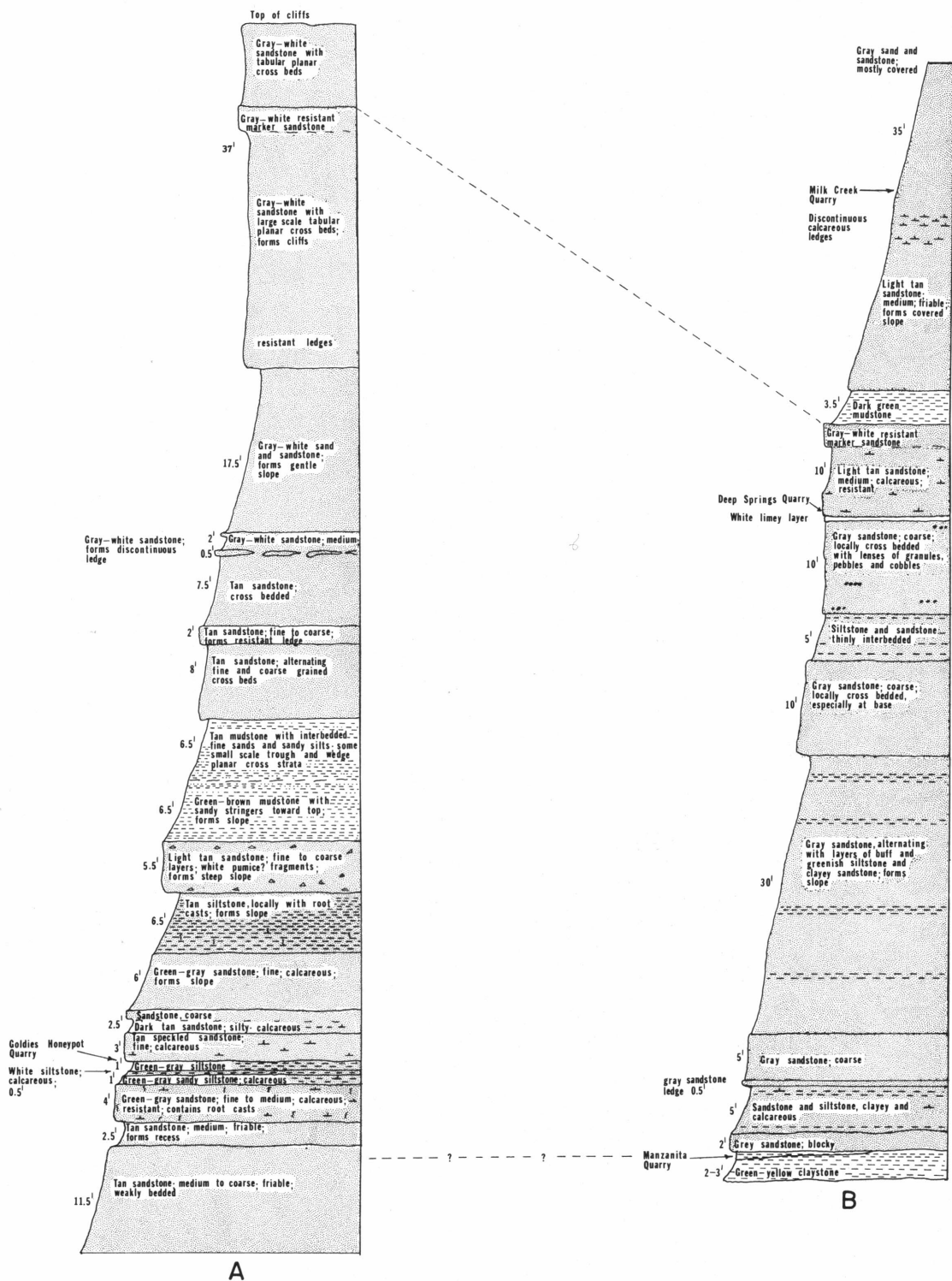
Manzanita Quarry

2-3' Green—yellow claystone

B

FIG. 1. Stratigraphic sections of part of Hook's (1956) Upper Member of the Milk Creek Formation. A. Section above Goldies Honeypot Quarry. B. Section above Manzanita Quarry. Vertical scale 1″=5.7′. No horizontal scale.

pus either subequal or less than metatarsus except in the recent *Lama* and *Camelus*.[1]

TANYMYKTER, NEW GENUS

TYPE: *Tanymykter brachyodontus* (Peterson, 1904)

ETYMOLOGY: From the Greek *tany*, long; *mykter*, nose.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Early Hemingfordian of Wyoming and the medial Hemingfordian of Nebraska.

DIAGNOSIS: Differs from *Oxydactylus* in longer, narrower rostrum, with anterior palatine vacuities usually more elongate; I^{1-2} generally weaker and often more laterally situated; C/ always larger than I^3; P_{1-2} diastema longer; mandible with weaker mesial inflection of angle; cervical vertebrae less elongate; limbs proportionally shorter with humerus longer relative to radius, phalanges longer relative to metapodials, and length of metapodials less than basal length of skull.

Differs from *Protolabis* in generally weaker buccinator fossa and generally wider rostrum; basisphenoid with two strong, elongate tuberosities; P^2 with stronger metastyle and parastyle; P^3 lingual cingulum usually stronger and unbroken; upper and lower molars more brachyodont and anteroposteriorly shorter, with stronger buccal ribs above and stronger metastylids and lingual ribs below; mandibular angle ventrally unexpanded; metacarpals unfused and metatarsals weakly fused; proximal phalanx more convex dorsally and distal articular surface more grooved and less anteriorly expanded.

Differs from *Michenia* in less constricted rostrum and shallower buccinator fossa; relatively longer braincase; stronger I^3 and C/C; more robust symphysis; and stouter metapodials.

DISCUSSION: Peterson (1904, p. 434) named the genus *Oxydactylus*, basing his diagnosis

upon the characters of the genotypic species *O. longipes*, and a referred species, *O. brachyodontus*. In many skull, dental, and mandibular features the two species are primitive and closely resemble each other, and in addition possess primitive phalanges and unfused metapodials. These (and other) shared primitive characters were used to diagnose the genus *Oxydactylus*. We feel, however, that the differences in rostral, vertebral, and limb proportions in *O. longipes* and "*O.*" *brachyodontus* have considerable phylogenetic significance, and justify separating the two species at the generic level. We agree with McKenna (1966, p. 6), that the morphological boundaries of *Oxydactylus* have been stretched "past the breaking point," and we have separated *O. brachyodontus* as the primitive sister taxon to *Protolabis*.

Tanymykter brachyodontus (Peterson, 1904)
Figures 3-4; Table 1-2

Oxydactylus brachyodontus Peterson, 1904, p. 469, pl. 11, pl. 12, fig. 4, pl. 13, pl. 14, figs. 3-5.

TYPE: CM 664, skull with I^{2-3}, C, P^{1-4}, M^{1-3}; mandible with complete dentition; cervical vertebrae 1-7; distal ends of right and left humeri; right and left ulnae and radii; all carpals, metacarpals, and phalanges, left femur; right tibia; calcaneum; astragalus, cuboid, and metatarsals, from the Upper Harrison beds[2] of Peterson, 1906 (= the Marsland Formation of Schultz, 1938) Nebraska: (figured by Peterson 1904, pl. 11, pl. 12, fig. 4, pl. 13, pl. 14, figs. 3-5).

DISTRIBUTION: From the Upper Harrison beds of Peterson, 1906 (= Marsland Formation of Schultz, 1938) Sioux County, Nebraska and from deposits approximately temporally equivalent to the Upper Harrison beds of Peterson in Goshen and Platte Counties, Wyoming.

REFERRED MATERIAL: From the Upper Harrison beds, Sioux County, Nebraska CM 562, "nearly complete skeleton" (Peterson 1904, p. 469).

From deposits approximately temporally equivalent to the Upper Harrison beds in Wyoming: F:AM 36594, 16 mi. district, S of Lusk, Goshen County, skull and mandible with complete dentition; atlas, partial axis, two fragmentary cervical vertebrae, proximal right

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[1] In both the recent *Lama* and *Camelus* the metacarpus is sometimes shorter than the metatarsus and the metapodials tend to be subequal in length. Following Webb's (1965, pp. 44-45) subdivision of the Camelinae into four tribes, two of which included *Lama* and *Camelus*, we assume that these two Recent taxa are derived from members of this subfamily in which the length of the metacarpus always exceeds that of the metatarsus.

[2] The Upper Harrison beds are here presumed to be equal to the "Lower Marsland" as interpreted by McKenna in a footnote (1965, p. 14).

femur, distal left femur, right fragmentary metacarpus; left tibia; right astragalus; two proximal phalanges; F:AM 36597, east side of road to Jay-EM Goshen County, skull with complete dentition, atlas; distal left humerus; left radius-ulna; right metacarpus; proximal right femur; proximal left tibia; left calcaneum; proximal right metatarsus and distal metapodial; F:AM 36542, 3 mi. SW of Guernsey, Platte County, partial skull with I^1-M^3, axis, third cervical, left tibia, left tarsals except for astragalus, left metatarsus, and proximal phalanx.

DESCRIPTION AND COMPARISON: Peterson (1904, p. 469-471), provided a brief description of *Oxydactylus brachyodontus* and compared this species with *Oxydactylus longipes*. Here, we point out the significant differences whereby *Tanymykter brachyodontus* (Peterson) differs with *Oxydactylus longipes* (figs. 2-4).

Tanymykter brachyodontus and *O. longipes* differ mainly in their relative limb and vertebral proportions. *Tanymykter brachyodontus* retains the primitive condition of relatively short cervical vertebrae and limbs. Peterson (1904, p. 469) noted the "comparatively short and heavy" cervicals of "*O.*" *brachyodontus* as distinctive from the elongate vertebrae of *O. longipes*. Peterson also noted that the cervical spines were heavier in "*O.*" *brachyodontus* and the spine of the axis was also more steeply inclined than in *O. longipes*. We have not seen these features duplicated in specimens in the F:AM collection. However, on elongate axes referred to *Oxydactylus*, we have noted that the inferior keel extends forward, as a low but sharp ridge, well anterior to the opening of the vertebrarterial canal. On referred cervicals of *Tanymykter* the inferior keel terminates as a rounded ridge slightly posterior to the vertebrarterial canal.

Peterson (1904, p. 470) stated that "the limbs of *O. brachyodontus* (No. 664) are elongated and rather lighter in comparison with the cranium, than in *O. longipes*." Although this statement is true, we think that it is more significant that the limbs of *T. brachyodontus* are proportionally shorter than those of *O. longipes*. These proportional differences are seen most clearly when the lengths of the various limb elements are compared with those of the skulls of the two species. Because the occiput and anterior border of the premaxilla are broken in the type skull of *T. brachyodontus*, we measured the distance from the back of the I^3 to the external auditory meatus, and compared this length with the total lengths of various limb elements. In the type of *T. brachyodontus* the I^3—external auditory meatus/radius ratio is 88 vs. 68 in *O. longipes*. Similarly, the I^3—external auditory meatus distance is 93 percent of the length of the femur and 78 percent of the length of the tibia in the type of *T. brachyodontus*, vs. 68 and 60 percent in the type of *O. longipes*. Thus, the limbs of *O. longipes* are proportionally longer relative to the skull than are those of *T. brachyodontus*. In the type of *O. longipes* the metatarsus is associated with the skull, while the type of *T. brachyodontus* has the metacarpus associated with the skull. Thus, the metapodial/skull length ratios cannot be directly compared in the types. However, the type of *O. longipes* is closely matched by a skull (F:AM 50753) which has an associated metacarpus and metatarsus. In F:AM 50753 the metacarpus and metatarsus are virtually equal in length, and the metacarpus is approximately 18 percent longer than the basal length of the skull (from the anterior border of the premaxillary to the anterior edge of the foramen-magnum). In contrast, the length of the metacarpus of the type of *T. brachyodontus* is less than the distance from the I^3 to the external auditory meatus which makes it less than the basal length of the skull. Specimens in the F:AM collection show that the metacarpus in *Oxydactylus* ranges from 5 to 21 percent longer than the basal length of the skull, whereas the metacarpus of *Tanymykter* ranges from 3 to 10 percent shorter than the basal length of the skull. Moreover, specimens in the F:AM collection show that the humerus is longer relative to the radius and the first phalanx is longer relative to the metapodial in *Tanymykter*. In the F:AM collection metatarsal V is variably present in both genera.

The type skulls and dentitions of *T. brachyodontus* and *O. longipes* possess many primitive features and are morphologically similar. For this reason plus the fact that the skull of *T. brachyodontus* is incomplete, Peterson could point out only a few features whereby they differed. Our analysis reveals additional distinguishing features of the skull of *T. brachyodontus*, which are described below.

The type skull of *T. brachyodontus* has a relatively longer, narrower rostrum than that of the type skull of *O. longipes*. Referred specimens show that the rostral width/length ration in *Oxydactylus* is nearly always greater than in *Tanymykter*. Similarly, the rostral length/cheek tooth length ratio is also nearly always greater in *Tanymykter*, again demonstrating the relative elongation of the rostrum in this genus. Much of this elongation in *Tanymykter* occurs in the premaxillaries; thus, the lengths of the anterior palatine foramina also aveaage longer than in *Oxydactylus*. The lateral surface of the maxilla above the P^1 on the type of *O. longipes* is inflated and shows little evidence of a buccinator fossa. In contrast, the lateral surface of the maxilla of the type of *T. brachyodontus* is more depressed and shows a weak development of the buccinator fossa. Referred specimens of *T. brachyodontus* (F:AM 36594, fig. 4) show greater development of this fossa and consequently have an even narrower rostrum. The above skull also shows marked lateral expansion of the anterior nares, a derived feature in common with other protolabidines.

The maxillary of the type skull of *T. brachyodontus* is broken in the region of the maxillary fossa. Referred specimens (F:AM 36534, 36597) exhibit a large, well-developed maxillary fossa. This fossa is subcircular and has well-defined posterior, dorsal, and ventral rims. Although the fossa is confined entirely to the maxillary, the dorsal border crowds against the nasals. A broad, low elevation separates the maxillary fossa from the much shallower buccinator fossa. A marked concavity immediately beneath the nasals on the type skull of *T. brachyodontus* indicates that the maxillary fossa was similarly strongly developed in this specimen. The maxillary fossa of the type of *O. longipes* is much shallower and lacks well-defined posterior dorsal and ventral rims. We suspect, however, that the depth of the maxillary fossa is variable in both taxa. For example, one skull (F:AM 50733), which is referred to *O. longipes*, has the fossa more strongly developed and possesses a well-defined dorsal border. Similar variation in fossa depth are seen in *Protolabis*.

The sagittal and lambdoidal crests are slightly weaker on the referred skulls of *T. brachyodontus* than on those of *O. longipes*.

The auditory bullae of the referred *T. brachyodontus* are slightly more inflated than those of the type of *O. longipes*. In the type of *O. longipes* the paroccipital process projects slightly below the ventral border of the lateral plate of the bulla. In the referred specimens of *T. brachyodontus* the paroccipital process is level with, or slightly above, the ventral border of the lateral bullar plate.

The basioccipital of the referred specimens of *T. brachyodontus* is notable in possessing a strong, narrow median ridge that separates the moderately to well-developed depressions for the origin of the rectus capitus ventralis muscle. Immediately anterior to these depressions are two rugose, elongate tubercles. The basioccipital of *O. longipes* is somewhat distorted, but it apparently did not possess the strong median ridge and well-developed rectus capitus ventralis troughs. The two anterior tuberosities, however, were apparently present. In other cranial features *T. brachyodontus* and *O. longipes* are closely comparable.

The incisors of both *Tanymykter* and *Oxydactylus* are small. However, those of *Tanymykter* are always weak, laterally compressed, and concave lingually. Many specimens referred to *Oxydactylus* have incisors which are larger and subcylindrical in cross section, and the I^3 is usually larger than the C. Referred specimens of *Tanymykter* often have the incisors more laterally situated than in *Oxydactylus*.

There are no significant differences in the cheek teeth morphologies in the two genera. Although Peterson (1904, p. 469) stated that the P^1 of *T. brachyodontus* had a single root, reexamination of the type specimen reveals that the P^1 roots are fused. The length of the P_1-P_2 diastema (26.2 mm.) in *T. brachyodontus* is greater than that (14.4 mm.) in the type *O. longipes*. Although the length of the diastema is variable, it is almost always longer in *Tanymykter* than in *Oxydactylus*. Furthermore, the type mandible of *O. longipes* possesses a lingual inflection on the angle which is stronger than that in the type of *T. brachyodontus*, and referred specimens of *Oxydactylus* also show stronger mesial inflections of the mandibular angle.

DISCUSSION: In discussing the affinities of *Oxydactylus*, Peterson (1904, p. 472) con-
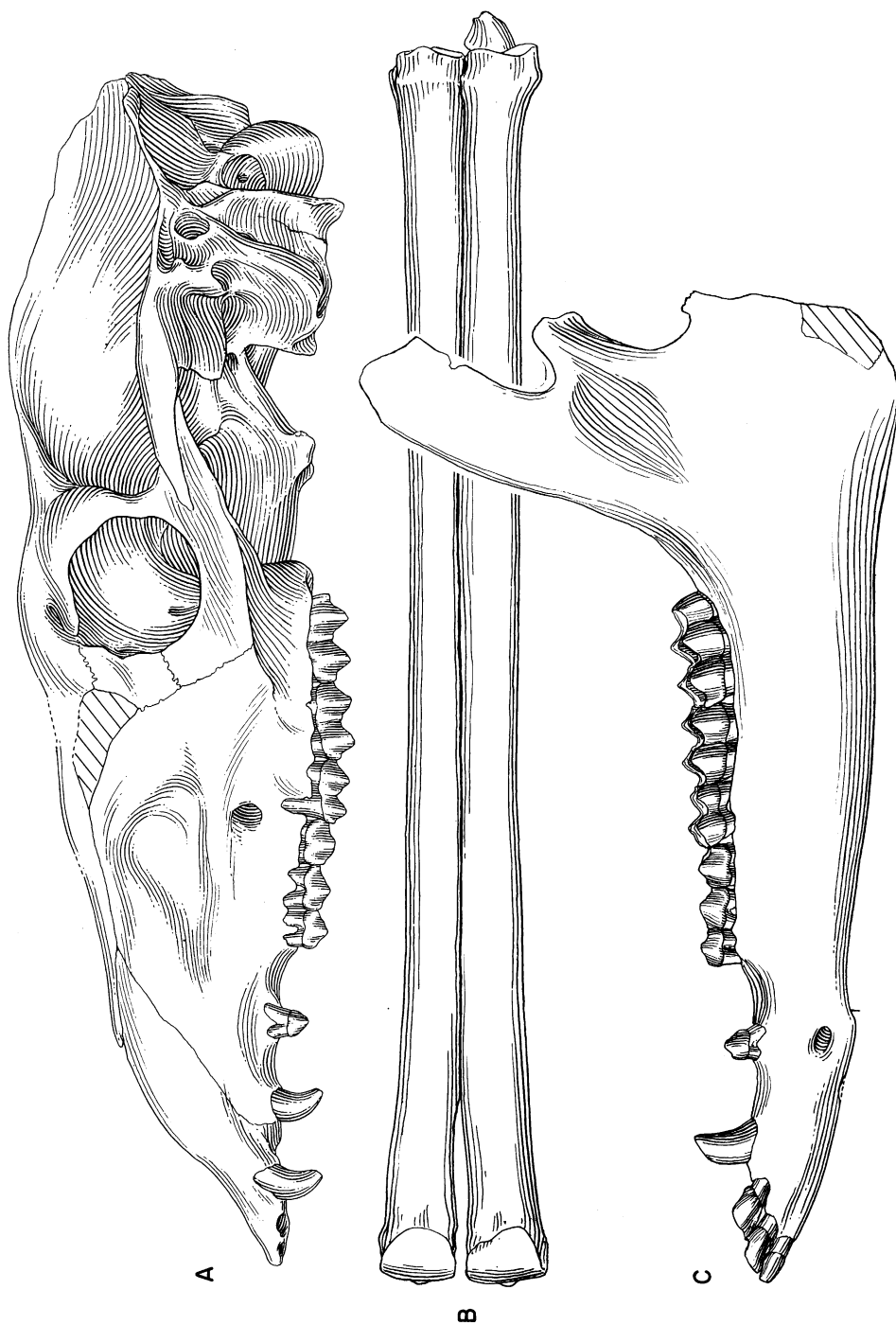
FIG. 2. A-C. *Oxydactylus longipes*, type, CM 918, from the Upper Harrison beds, (Hemingfordian) Sioux County, Nebraska. A. Lateral view. B. Anterior view. C. Lateral view. All X½.
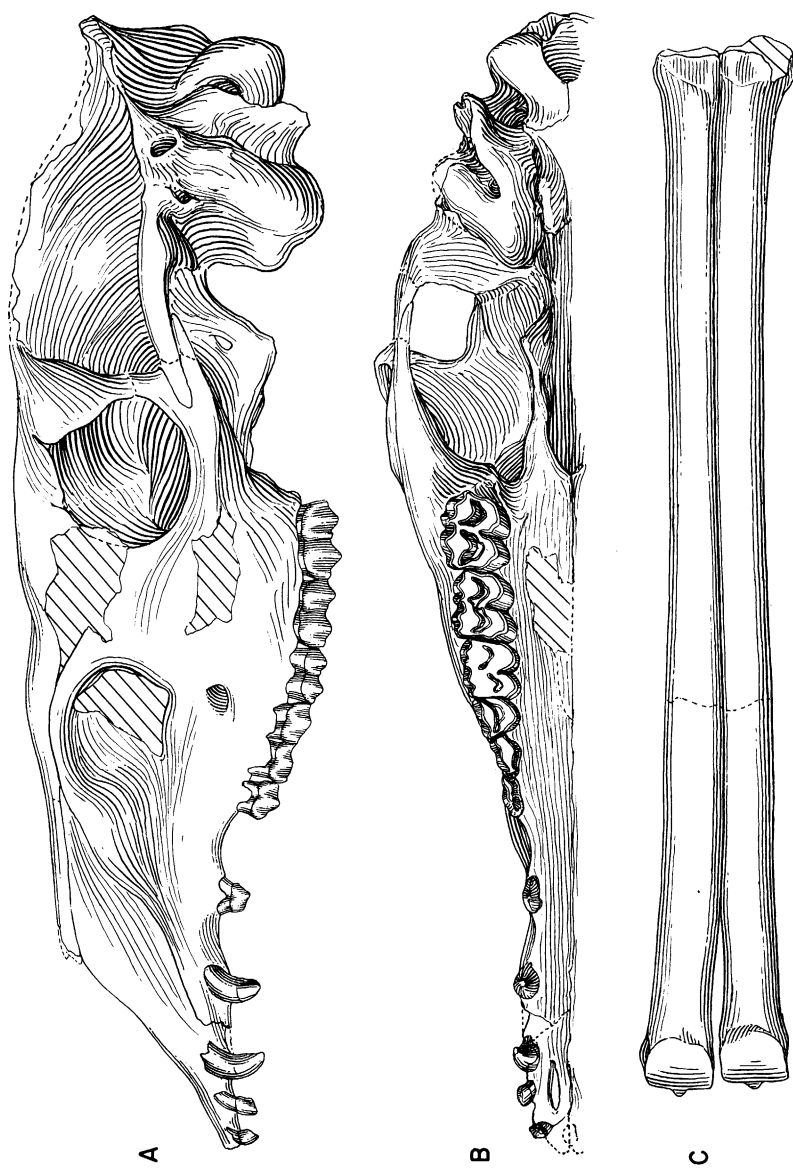
FIG. 3. A-C. *Tanymykter brachyodontus* (Peterson), F:AM 36597 from the Lusk area (Hemingfordian), Wyoming. A. Lateral view. B. Palatal view. C. Right metacarpus, anterior view, reversed. All X½.

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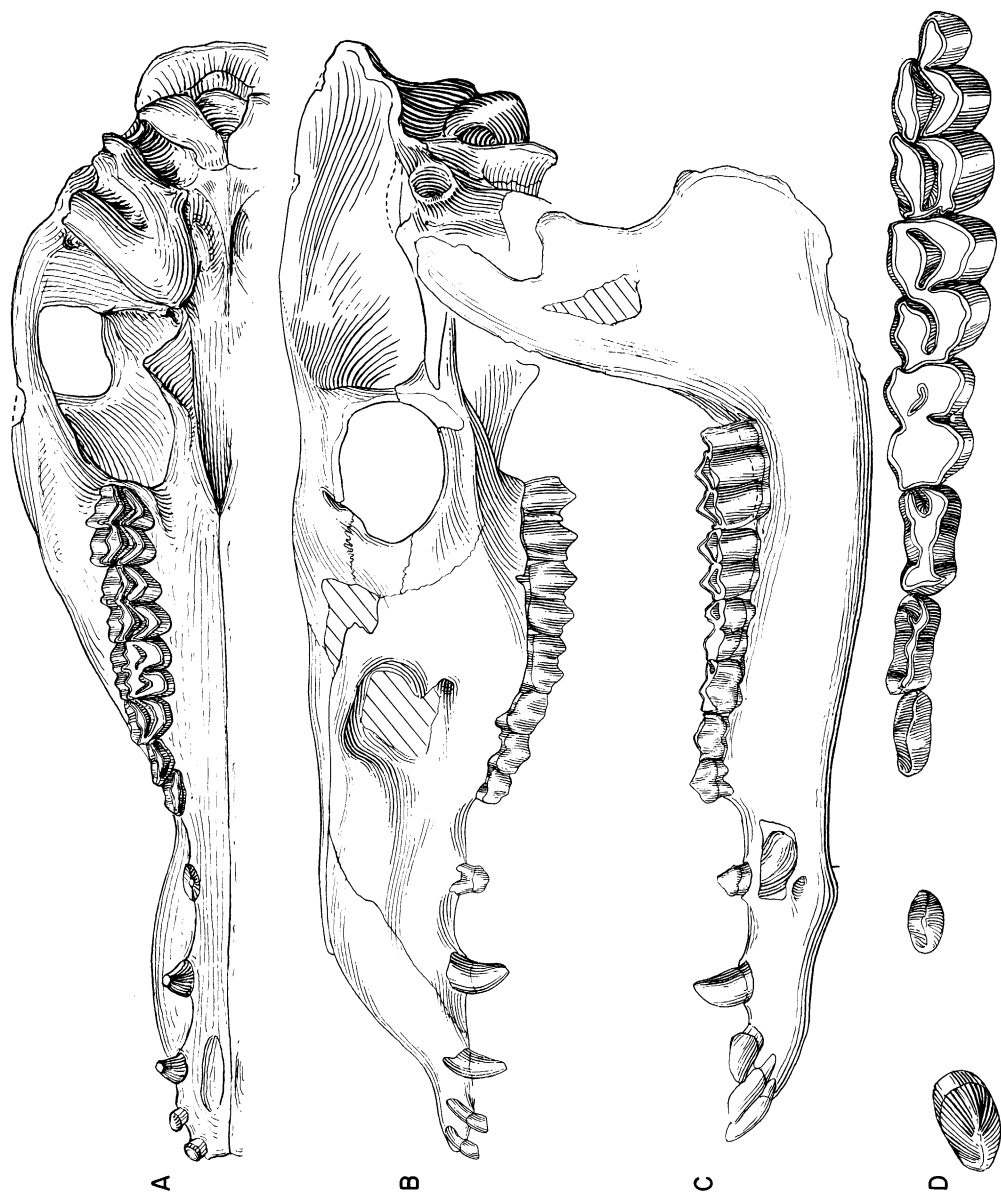
FIG. 4. A-D. *Tanymykter brachyodontus* (Peterson), F:AM 36594 from the Lusk area (Hemingfordian), Wyoming. A. Palatal view. X½. B. Lateral view. X½. C. Lateral view. X½. D. Occlusal view. X1.

TABLE 1

Measurements (in Millimeters) of the Skull and Upper Dentition of *Tanymykter brachyodontus* (Peterson) from Nebraska and Wyoming

	CM 664[a]	F:AM 36597[b]	F:AM 36594	F:AM 36542
Occipital crest to incisive border (vertex)	—	301.0	293.0	—
Foramen magnum to incisive border (basilar)	—	290.0	277.0	—
Postorbit to anterior incisive border (facial)	—	210.0	199.0	202.0
Postorbit to occipital crest (cranial)	—	(92.)	(89.)	—
Anterior border foramen magnum to posterior edge M^3	—	109.7	94.1	—
Palatal width between I^3	—	19.0	21.3	19.7
Palatal width between P^2	(21.)	(27.9)	20.9	—
Palatal width between M^3 posterior moiety	—	—	42.3	—
Palatal width narrowest part of rostrum	—	(20.2)	19.0	18.3
I^3-C diastema length	12.7	16.5	13.1	12.5
C-P^1 diastema length	15.8	14.0	15.0	14.4
P^{1-2} diastema length	20.2	18.8	18.4	21.8
Upper canine length	(7.2)	6.3	7.8	5.7
P^1 length	5.8	8.1	7.1	6.0
P^2 length	11.8	11.7	11.6	9.9
P^2 width	5.3	5.2	6.3	4.6
P^3 length	11.2	9.5	11.7	11.9
P^3 width	—	6.9	7.5	6.8
P^4 length	11.5	11.1	12.0	10.9
P^4 width	11.7	11.1	11.5	10.2
M^1 length	14.8	13.7	15.0	13.0
M^1 width	16.4	16.3	16.2	15.7
M^2 length	17.8	15.6	18.8	17.1
M^2 width	17.0	16.8	17.6	15.6
M^3 length	19.2	18.5	19.5	19.6
M^3 width	17.5	17.1	16.9	15.4
P^{2-4} length	35.0	32.7	32.6	32.1
M^{1-3} length	54.5	51.0	55.8	51.0
P^2-M^3 length	88.8	83.5	86.0	81.6

[a]CM 664 is the type of *Tanymykter brachyodontus* (Peterson).
[b]F:AM 36597, F:AM 36594, and F:AM 36542 are referred.

cluded that *O. longipes* was closely allied with *Aepycamelus* (=*Alticamelus*) by virtue of the small cranium and elongated cervicals and limbs. Authors since Peterson have accepted this view and have classified *Oxydactylus*, including *O. brachyodontus*, within the Aepycamelinae (=Alticamelinae). The present authors concur with the original view of Peterson and believe that *O. longipes* is the sister taxon

of *Aepycamelus*. However, the characters of "*Oxydactylus*" *brachyodontus* show a close relationship to other camelids, specifically *Protolabis*, and we have, therefore, removed "*Oxydactylus*" *brachyodontus* from the Aepycamelinae.

Evidence indicates that *Tanymykter brachyodontus* is the primitive sister taxon to *Protolabis*. Unlike *Oxydactylus longipes* the

TABLE 2

Measurements (in Millimeters) of the Mandible and Lower Dentition of *Tanymykter brachyodontus* (Peterson) from Nebraska and Wyoming

	CM 664[a]	F:AM 36594
Mandible length	(240.)	235.1
Distance mental foramen below top of ramus	15.3	14.1
Depth jaw between P_1 and P_2	22.0	22.4
Depth jaw at P_1	18.1	23.5
Depth jaw below anterior moiety of M_3	37.6	30.0
C-P_1 diastema	19.8	18.7
P_{1-2} diastema	26.5	20.5
Lower canine length	7.8	9.8
P_1 length	6.7	7.8
P_2 length	10.4	11.7
P_2 width	4.1	4.5
P_3 length	11.6	12.1
P_3 width	4.7	5.7
P_4 length	12.3	13.2
P_4 width	6.7	7.3
M_1 length	15.0	14.7
M_1 width	11.8	11.1
M_2 length	18.5	17.5
M_2 width	13.0	13.1
M_3 length	(30.)	25.7
M_3 width	13.4	13.7
P_{2-4} length	34.2	38.6
M_{1-3} length	63.8	60.5
P_2-M_3 length	99.0	100.3

[a]CM 664 is the type of *Tanymykter brachyodontus* (Peterson).

proportionally longer rostrum of *T. brachyodontus* with longer premaxillaries and longer anterior palatine foramina and a weakly developed buccinator fossa are derived features, seen in the camelines. The narrower rostrum and the more laterally expanded anterior nares in *T. brachyodontus* are derived features that are shared with *Protolabis*. Furthermore, *T. brachyodontus* lacks the derived features seen in *Oxydactylus longipes* which link it with *Aepycamelus*, namely, the elongate cervicals and limbs, with metapodials longer than the basal length of the skull. *Tanymykter brachyodontus* and *Protolabis* retain the primitive condition of short cervicals and limbs, with metapodials shorter than the basal length of the

skull. If fused, the metapodials of *T. brachyodontus* would in fact be indistinguishable from those of many *Protolabis* specimens. Another feature reflecting relationship to *Protolabis* is seen in the shape of the I^{1-2}. As mentioned before, the incisors of *Tanymykter* are weak, laterally compressed, and strongly concave lingually. These incisors are virtually identical with those of *Protolabis*. In addition, some referred specimens of *T. brachyodontus* (F:AM 36594, fig. 4) have the incisors laterally situated, forming near parallel rows, as in *Protolabis*. Interestingly, were it not for the brachyodont molars, the palate of *T. brachyodontus* (F:AM 36594) would be indistinguishable from that of *Protolabis*. The more elongate P_{1-2} diastema and relatively deep rectus capitus ventralis troughs are also similar to these features in *Protolabis*.

The only feature in which *T. brachyodontus* is derived relative to primitive species of *Protolabis* is in the appressed roots of P_1. We conclude, on the basis of their shared derived characters of narrow rostrum and the lateral expansion of the anterior nares, that *Tanymykter* and *Protolabis* are sister taxa.

PROTOLABIS COPE, 1876

TYPE SPECIES: *Protolabis heterodontus* (Cope, 1874).

INCLUDED SPECIES: *Protolabis coartatus* (Stirton, 1929); *Protolabis barstowensis* Lewis, 1968.

KNOWN DISTRIBUTION: From early Hemingfordian to Clarendonian of the western United States.

REVISED DIAGNOSIS: *Protolabis* differs from *Procamelus* in smaller size; less inflated braincase; weaker sagittal and lambdoidal crests; maxillary fossa not pocket-like; shorter paroccipital processes terminating above ventral border of auditory bullae; greater rostral constriction; retention of I^1-I^2 in primitive species; I^3 and C rarely transversely compressed and without sharp anterior and posterior edges; P^1_1 double rooted, recurved, and caniniform, but never bladelike; P_2-P_4 shorter and more brachyodont with P_2 sometimes lost in most derived species; molars lower crowned, narrower and less anteroposteriorly expanded;

weak to strong lateral flare and weak to strong mesial tuberosity or shelf on angle of mandible; angular process more subdued; coronoid process shorter with less rugose muscle attachments; and metapodials proportionally lighter with metatarsus longer than metacarpus.

Protolabis differs from *Tanymykter* in stronger buccinator fossa and generally narrower rostrum; basisphenoid without well-developed elongate tuberosities; P^2 with weaker metastyle and parastyle and discontinuous lingual cingulum; P^3 lingual cingulum weaker and generally discontinuous, upper and lower molars taller crowned and anteroposteriorly longer, with weaker buccal ribs above and weaker metastylids and lingual ribs below; mandibular angle more ventrally expanded; metapodials fused; proximal phalanx less convex dorsally and distal articular surface less grooved and more anteriorly expanded.

Differs from *Michenia* in larger size; longer braincase; stronger I^1-I^3 in primitive species; stronger and more caniniform $\overset{c}{c}$; more anteroposteriorly expanded M_3^3; deeper, more ventrally produced symphysis; deeper horizontal ramus; and relatively stouter metapodials. See p. 418.

DISCUSSION: As discussed by Frick and Taylor (1971, p. 3), *Protolabis* was originally diagnosed by Cope (1876 p. 144) as a camel retaining a full set of upper incisors, whereas *Procamelus* Leidy (1858 p. 89), was defined by Cope as a camel that had lost the first two upper incisors. This criterion of the presence or the absence of upper incisors has been considered diagnostic by authors since Cope; indeed, other dental and skeletal features have usually assumed secondary significance. The assumption that *Protolabis* always retains a complete set of upper incisors has led to a problem in distinguishing between *Protolabis* and "*Procamelus*" *coartatus*. Recently, Frick and Taylor (1971, p. 5) have added the differences in the metapodial proportions and molar expansion to the differential diagnosis of *Protolabis* and *Procamelus*. In the present paper these and other differences will be examined and evaluated more fully, to clarify the distinctions between these two genera. Skull, dental, mandibular, and metapodial morphological features are herein considered; a complete anatomical study

of the two genera is quite beyond the scope of the present paper.

The skulls of *Protolabis* average smaller than those of *Procamelus*. The sagittal and lambdoidal crests are usually weaker, and the braincase is less inflated, in *Protolabis*. The stronger crests and more inflated braincase in *Procamelus* result in a greater postorbital length relative to facial length. In the specimens measured little overlap was found in the postorbital/preorbital ratio. This ratio ranged from 34 percent to 44 percent in *Protolabis*, vs. 44 percent to 59 percent in *Procamelus*.

Both *Protolabis* and *Procamelus* possess a maxillary fossa. The development of this fossa, however, differs between the two genera. In *Protolabis* the fossa varies in shape from anteroventrally elongate to subcircular, and may cover a wide area on the maxillary centered above the infraorbital foramen, and just beneath the nasal. This fossa varies from a deep depression with well-defined rims, to a very shallow concavity. It is never pocket-like. In contrast, the fossa in *Procamelus* is usually deeply depressed and pocket-like. A few *Procamelus*, however, have only a shallow trough with a posterodorsal slit at the position of the pocket. The maxillary fossa in *Procamelus* is also over the infraorbital foramen, but is generally situated lower on the maxillary than in *Protolabis*. Both genera usually have a shallow trough trending anteroventrally from the maxillary fossa.

The paroccipital process of *Protolabis* is more weakly developed than in *Procamelus* and almost never projects below the ventral edge of the lateral plate of the auditory bulla. In contrast, the paroccipital process of *Procamelus* is much more strongly developed and almost always projects below the lateral plate of the bulla. The troughs on the basioccipital for the origin of the rectus capitus ventralis muscle are generally more strongly developed and deeper in *Protolabis*. In later occurring *Protolabis* skulls the troughs often occur as deep, elongate depressions on either side of a sharp median ridge. *Procamelus* tends to have shallower troughs separated by a wider, more rounded median ridge. Immediately anterior to each trough is a tuberosity, probably for the origin of the longus capitus. These tuberosities are

often elongate and strongly developed in *Procamelus*, whereas in *Protolabis* they tend to be weakly developed.

Constriction of the rostrum posterior to the canine is a progressive feature in *Protolabis*. This constriction is associated with the pronounced development of a buccinator fossa on the ventrolateral border of the maxillary anterior to the P^2. Examination of many specimens in the F:AM collection reveals that rostral constriction and buccinator fossa development is least in the early, primitive samples and greatest in the late, derived samples. The palate narrows rapidly immediately posterior to the canine, reaching maximum constriction between the P^1 and P^2. This is in part correlated with the deepening of the buccinator fossa to a maximum depth between the P^1 and P^2. Palatal constriction is less pronounced and occurs more posteriorly in *Procamelus*. This correlates both with the weaker development of the buccinator fossa and a much larger P^1. In *Procamelus*, only slight constriction occurs immediately behind the canine, and most of the narrowing is behind the large P^1. This results in the rostrum of *Procamelus* being more constant in width anterior to the P^1, whereas the rostrum of *Protolabis* flares greatly anterior to this point. Generally, in *Procamelus* the rostral width between the canines is either equal to or greater than the width between the I^3s. In contrast, the intercanine distance in *Protolabis* is always equal to or less than the inter-I^3 distance. An examination of many specimens shows that the rostrum of *Procamelus* is almost always wider than that of *Protolabis*; even specimens of primitive taxa of *Protolabis* have rostra relatively narrower than those of most *Procamelus*.

Protolabis was originally diagnosed as having a full set of upper incisors, and these teeth are present in all but the most derived taxa. In general, the I^1 and I^2 are small and peglike. Occasional loss of I^1 or both I^1 and I^2 occurs as individual variation in earlier samples, but by the Clarendonian both of these teeth are usually lost or unerupted. This was recognized by Frick and Taylor (1971, p. 4), when they referred Cope's specimen of *"Procamelus occidentalis"* from the "Santa Fe marls" of New Mexico to *Protolabis*. It is uncertain if these teeth are always lost, or unerupted, but it is clear that in many adult individuals of *Protolabis* the first two superior incisors are absent. Their former positions are occasionally indicated by healed alveoli. Extreme constriction of the rostrum occurs in association with the loss of I^1 and I^2; both are derived features of *Protolabis* that attain maximum specialization in *P. coartatus*.

In his analysis of variation in *Procamelus grandis*, Webb (1969, p. 158) noted differences in the character of the caniniform teeth which he attributed to sexual variation. Specifically, Webb considered specimens with large, conical, recurved teeth to be males, and those with laterally compressed, bladelike, caniniform teeth females. These observations were confirmed by the examination of a large number of *Procamelus* specimens in the Frick collection, but no comparable consistent dichotomy was observed for *Protolabis*. In all the *Protolabis* specimens examined, the I^3 and C are conical and recurved, and never as compressed as in *Procamelus*; moreover, they lack the sharp anterior and posterior flanges that are characteristic of the females of *Procamelus*. The lower canine of *Protolabis* is occasionally bladelike and consequently, small procamelines are sometimes difficult to distinguish from *Protolabis* by this character alone. In all *Procamelus* examined, the P_1 is bladelike, caniniform, and recurved, whereas in *Protolabis* it is low crowned, blunt, and less recurved. Although lateral compression of the caniniform teeth does not appear to be a sexual character in *Protolabis*, the size of these teeth is believed to reflect sexual dimorphism, with the larger, heavier toothed specimens from each sample presumed to the males.

The presence of a double-rooted $P_{\overline{1}}^1$ in *Protolabis* and a single-rooted $P_{\overline{1}}^1$ in *Procamelus* is useful in separating the two genera. Webb (1969, p. 148) included the presence of a double-rooted $P_{\overline{1}}^1$ in his diagnosis of *Protolabis*, but because he considered *coartatus* to be a member of *Procamelus*, Webb could not always use this character to separate the two genera. In *Protolabis* the roots vary from widely flared to closely appressed or fused. If the roots are fused, however, a mesial or lateral groove indicates this fusion, and a cross section of the

tooth usually shows the individual roots. In contrast, *Procamelus* has a single-rooted, caniform P^1_1. Generally, the P^1_1 of *Procamelus* is transversely compressed with sharp anterior and posterior edges, though in some of the larger specimens the P^1 is robust and conical. In *Procamelus* the P^1 is often as large as the I^3, which itself is only slightly smaller than the canine. On the other hand, the P^1 (like the P_1) of *Protolabis* is not caniniform, and never as large as the I^3, and has a low, blunt crown.

Protolabis exhibits a progressive reduction in the size of the P_2-P_4. P_2 shows the greatest reduction, and in its most derived state, is very small and occasionally lost. Patton (1969, pp. 151, 162-163) noted premolar reduction as characteristic of the *Protolabis* lineage, but based much of his hypothesis on species now referred to *Miolabis* by Frick and Taylor (1971, p. 4).

In general, P_2 of *Protolabis* is lower crowned than that of *Procamelus*, and has a low, central protoconid. In *Procamelus*, the protoconid is higher and has steep crests descending anteriorly and posteriorly. Patton (1969, p. 156) noted that *Procamelus* occasionally has reduced premolars, as seen in his figure 16 of *Procamelus occidentalis*. Nevertheless, Clarendonian specimens of *Protolabis* usually have a more highly reduced P_2. Reduction in size is also usually applicable to P_3 and P_4. P_3 and P_4 of *Protolabis* are also lower crowned and generally have a less expanded talonid than those of *Procamelus*. With wear, the talonid of P_3 and P_4 of *Procamelus* acquires a more pronounced buccal bulge than in *Procamelus*. In *Procamelus* the width of the posterior cusps of P_3 and P_4 is almost always greater than that of the middle cusps, a fact pointed out by Webb (1969, p. 158). In *Protolabis* the central cusp tends to be equal in width or wider than the posterior cusps. There are exceptions though, including the type of *P. angustidens*, in which the posterior cusps of P_4 (but not P_3) are wider than the middle cusp. Also, the degree of lingual inflection of the anterior cusp of P_3 and P_4 was found to be variable in both genera; however greater inflection was generally present in *Protolabis*.

No morphological features are known that can be consistently used to distinguish the molars of *Protolabis* and *Procamelus*. Both genera overlap to some degree in the development of ribs, styles, and stylids, and in the flatness of the buccal walls above and the lingual walls below. However, there are significant differences in the proportions of the molars. Frick and Taylor (1971, p. 5) pointed out that the molars of *Procamelus* are more anteroposteriorly elongate and higher crowned than those of *Protolabis*. Specifically, in a similar wear stage M^1_1 and M_2 of *Procamelus* are longer relative to the length of M^3_3 than those of *Protolabis*. The molars of *Procamelus* also tend to be relatively wider than those of *Protolabis*.

Mandibular rami of *Protolabis*, particularly those of earlier samples, tend to have shorter, more upright symphyses than those of *Procamelus*. In general, the mandible of *Procamelus* has a long symphysis which forms a rather shallow angle with the horizontal body of the ramus. In dorsal view, the posterior border of the relatively short symphysis in *Protolabis* is found to be either beneath or anterior to P_1; on the longer, shallower symphysis of *Procamelus* the posterior border unites either beneath or posterior to P_1. However, there are occasional exceptions with some individuals of *Protolabis* having a long, shallow symphysis. The ventral border of the mandibular ramus in *Protolabis* is generally less convex and straighter than in *Procamelus*. Immediately behind the symphysis the lower border of the ramus is concave in both genera, but in *Protolabis* this concavity extends posteriorly for a greater distance than in *Procamelus*.

Lateral flare of the posteroventral border of the mandibular angle occurs repeatedly to varying degrees in many individuals of *Protolabis*. This flare is greatest in latest known samples. An occasional jaw of *Procamelus* in the Frick collection also exhibits a slight flare of the mandibular angle, but this condition occurs rarely and never to the same degree as in *Protolabis*. An even more consistent feature in *Protolabis* is the development of a mesial flaring or tuberosity immediately anterior to the lateral flaring on the posteroventral border of the mandibular angle. This mesial flare appears to be invariably present in later samples. Mes-

ial inflection of the mandibular angle occurs very rarely in *Procamelus*, and when present, it is manifested only as a slight bending of the bottom part of the ramus. Never is the development of the mesial tuberosity as strong as in *Protolabis*, which in its derived state occurs as a prominent anterodorsally trending shelf. This mesial tuberosity is evidenced on the lateral surface of the mandible by a small concavity on the lower border just anterior to the lateral flare. This concavity is absent in *Procamelus*.

The angular process of the mandible in *Protolabis* is usually less developed than in *Procamelus*. In *Procamelus* it is often very knoblike and mesially inflected, whereas in *Protolabis* it tends to be subdued with only a slight mesial inflection in some specimens. Consequently, the notch on the back part of the jaw in *Protolabis* is shallower than in *Procamelus*. Furthermore, the coronoid process in *Protolabis* is anteroposteriorly narrower and does not extend as high above the condyle as in *Procamelus*. In *Protolabis*, the coronoid process generally has less rugose muscle attachments along its length, and this is correlated with a relatively smaller temporal fossa.

As discussed by Frick and Taylor (1971, p. 5), the length of the metatarsus in *Protolabis* is always greater than the length of the metacarpus, whereas the reverse is true in *Procamelus*. Moreover, the metapodials of *Protolabis* are much shorter and less robust than those of *Procamelus*, with the length of the metapodials in *Protolabis* always less than the basal length of the skull and proportionally shorter than in *Procamelus*.

Protolabis coartatus (Stirton, 1929)
Figures 5-9, Tables 3-6

Procamelus near *gracilis* Merriam, 1916, p. 189, figs. 30a-b, 31a-c, 32, 33.
Procamelus coartatus Stirton, 1929, p. 295, figs. 2-4.
Procamelus cf. *gracilis* Stirton, 1929, p. 297, fig. 5.
Protolabis notiochorinos Patton, 1969, p. 152, figs. 14-15, table 11.

TYPE: UCMP 19820, rostral part of skull with I^3, C, and P^1; mandible with complete dentition; distal end of humerus; radius-ulna; all carpals except for cuneiform; metacarpal; and proximal and median phalanges from Stewart Valley (early Clarendonian), Cedar Mountain region, Nevada.

KNOWN DISTRIBUTION: Early Clarendonian of Stewart Valley and Fish Lake Valley, Nevada, Clarendonian of Lapara Creek, Texas, and Milk Creek, Arizona.

REFERRED MATERIAL: From Fish Lake Valley beds, Esmeralda County: UCMP 29608, palate with roots of P^2-P^4, partial M^1 and M^2 (Stirton, 1929, fig. 4); UCMP 29605, fragmentary right ramus; UCMP 29612, palate with left P^3-P^4, left M^1-M^3, right P^2-P^4, right M^1-M^3 (Stirton, 1929, fig. 5).

From Lapara Member of Goliad Formation: UTBEG 31152-332, mandible with P_4-M_3, roots of P_2-P_3, P_1 alveolus (Patton, 1969, figs. 14-15); UTBEG 31081-261, 31081-295, 31081-612, 31081-525, UTBEG 31132-319, all metapodials.

From Manzanita Quarry, 10 feet below Goldie's Honeypot Quarry, Milk Creek Formation (Clarendonian), Milk Creek area, Yavapai County, Arizona: F:AM 73290, palate with P^2 (broken)-M^2; F:AM 73300, partial mandible with I_1-I_3, C-P_3 (all broken) and P_4-M_3; F:AM 73257, left partial ramus with P_3-M_3 (P_4 broken); F:AM 73266, partial mandible with I_1 (root) -I_2, I_3-P_1 (all broken) and P_3 (root)-M_3; F:AM 73265, right partial ramus with P_3 (broken)-M_3; F:AM 73297, right partial ramus with P_2-P_3 alveoli and P_4-M_3; F:AM 73299, symphysis with I_1 (broken)-C and P_1 (broken); F:AM 73366, right partial ramus with C-P_1 and P_3-M_3 (P_4 broken); F:AM 73375, right partial ramus with incomplete symphysis with C(alveolus) and P_2 (unerupted)-M_1 and M_2-M_3 broken; F:AM 99634, left partial ramus with symphysis with I_1-C (broken alveoli), P_3 (root)-M_3; F:AM 73374, left partial ramus with P_2-M_2 and M_3 broken; F:AM 73299, left ramal fragment with M_3; F:AM 73333, immature palate with dP^2-M^1; F:AM 73332, right immature partial mandible with dP^2-dP^4; F:AM 99631, right immature partial maxilla with dP^2-M^1 (all broken); F:AM 73335, right immature partial maxilla with dP^2-M^1; F:AM 73337, right immature partial maxilla with dP^2-M^1 (M^2 broken) and right and left immature partial rami with dP_2-M_2; F:AM 99629, left immature partial maxilla with dP^3-M^1 (all broken); F:AM 73346, left immature partial maxilla with M^1-M^2 broken

and right and left immature partial rami with dP_3-dP_4 and M_1-M_2 broken; F:AM 73347, right immature ramus with dP_2dP_3 and dP_4 broken; F:AM 73342, right and left immature partial rami with incomplete symphysis with dI_2-dI_3, dC root and dP_2 (aleveolus)-dP_4; F:AM 73339, right immature partial ramus with dP_2 alveolus-dP_4 and M_1 broken; F:AM 73343, left immature partial ramus with symphysis with dI_1-dC, dP_3 (broken)-M_1; F:AM 73341, left immature partial ramus with dP_2-M_1 and M_2 broken germ; F:AM 99624, right immature partial ramus with dP_4-M_1; F:AM 99619, right immature partial ramus with dP_3-dP_4 and M_1 broken; F:AM 73345, right and left immature partial rami with dP_3-dP_4 and M_1 broken; F:AM 99623, left immature partial ramus with dP_3(broken)-dP_4 and M_1 broken germ; F:AM 73348, left immature partial ramus with dP_2-dP_4 and M_1 broken; F:AM 99620, right and left immature partial rami with dP_4-M_1 and M_2 broken; F:AM 73355, immature partial mandible with $?I_1$ germ and dP_3-M_1 and M_2broken germ; F:AM 73310, right incomplete metacarpus; F:AM 73311, left metacarpus; F:AM 73312, left metacarpus; F:AM 73313, full length broken mesial half of left metacarpus; F:AM 73315, left metacarpus; F:AM 73323, right metacarpus; F:AM 73343, right incomplete metatarsus; F:AM 73297, right metatarsus; F:AM 73360, left metatarsus; F:AM 73318, left distal end humerus and radius and ulna; and F:AM 73319, right crushed radius and ulna, and associated broken proximal end metacarpus.

Shields Ranch Quarry (=Stein Gallery, UALP locality 1-7), Milk Creek Formation, same horizon as Manzanita Quarry (Clarendonian), Milk Creek area, Yavapai County, Arizona: F:AM 73296, left premaxilla-maxillary fragment with I^2(alveolus)-P^1; F:AM 99626, right partial maxilla with M^1-M^2 and M^3 broken; F:AM 99627, right partial maxilla with M^1-M^2; F:AM 73369, right partial ramus with P_3-M_3; F:AM 73268, right and left partial rami with incomplete symphysis with C(broken)-P_1, P_3-M_1 and M_2-M_3 both broken; F:AM 74468, mandible with I_1-M_3; F:AM 73392, left partial ramus with symphysis, I_1-I_3 (all broken), C (alveolus)-P_1, P_3 (root)-P_4 and M_1-M_2 broken; F:AM 99632, left partial ramus with M_1M_3 all broken; F:AM 99639, right ramal fragment

with symphysis and I_1-C; F:AM 73334, right immature partial maxilla with dP^3 (alveolus)-M^1 and right immature partial ramus with dP_3-M_1 all broken; F:AM 99630, right and left immature maxilla with dP^2-M^2; F:AM 99628, right immature partial maxilla with dP^2 (root)-dP^4; F:AM 73331, left immature partial maxilla with dP^2 (root)-dP^4; F:AM 73344, right immature partial ramus with dP_2 (root)-M_1; F:AM 99625, right immature partial ramus with dP_3-M_1; F:AM 99621, right immature partial ramus with dP_3 (alveolus)-M_3 (erupting); F:AM 73357, right partial ramus with dP_3 (alveolus)-M_2; F:AM 99641, right immature partial ramus with dP_4-M_2 all broken; F:AM 73423, left metacarpus; F:AM 99647, left incomplete metacarpus; F:AM 99648, left proximal one half metacarpus; F:AM 99651, distal part of metacarpus; F:AM 73412, left metatarsus; F:AM 73412A, right proximal one half metatarsus; F:AM 73317, right metatarsus; F:AM 99646, right incomplete metatarsus; UALP 9404, partial right ramus with P_4, M_1, M_2 (broken); UALP 9405, mandibular symphysis with I_1-I_3, C, P_1 (roots); UALP 9386, right M^1-M^2; UALP 9374, right articulated astragalus, calcaneum, navicular and cuboid; UALP 3628, right metatarsal; UALP 9375, right distal tibia and metatarsal; UALP 9376, left metatarsal; UALP 9378, right proximal metacarpal; UALP 9379, distal metapodial; UALP 9380, left astragalus; UALP 9391, left distal humerus; UALP 9392, left distal humerus; UALP 9393, left proximal radius-ulna, right distal radius-ulna, right distal tibia; UALP 9394, left astragalus; UALP 9395, right distal radius-ulna; UALP 9397, right radius-ulna; UALP 9398, left distal humerus; UALP 9399, left proximal radius; UALP 9400, left distal tibia, proximal phalanx; UALP 9401, right proximal radius-ulna; UALP 9396, left distal tibia; UALP 9402, left distal radius-ulna; and UALP 9403, left distal radius-ulna.

Trail Prospect, Milk Creek Formation, same horizon as Shields Ranch Quarry (Clarendonian), Milk Creek area, Yavapai County, Arizona: F:AM 73291, right partial maxilla with P^2-P^3 broken and P^4-M^3 (M^1 and M^3 broken); and F:AM 73356, left immature ramus with I_1, dI_2-dC roots and dP_3-dP_4 broken and M_1.

Goldie's Honeypot Quarry (UALP locality 7498), Milk Creek Formation, 5 feet above

Shields Ranch horizon, Milk Creek area, Yavapai County, Arizona: UALP 9022, partial skull with I^3 (root), C, P^1, P^3-P^4, M^1 (broken), M^2 and M^3 (broken); UALP 9023, right partial palate with M^1-M^3; UALP 9034, left partial palate with dP^3-dP^4 and M^1; UALP 9010, right partial dentary with P_2-P_4 and M_1 (broken); UALP 9032, mandibular symphysis with I_1-I_3 roots and C; UALP 9016, left partial ramus with dP_3 (roots), dP_4 and M_1; UALP 9005, left dentary and symphysis with right dI_1-dI_2, right I_1, left dP_3 (roots), left dP_4 and left M_1-M_2; UALP 9012, right dentary with dP_3-dP_4 and M_1-M_2; UALP 9006, right fragmentary dentary with dP_2-dP_4; UALP 9015, right fragmentary dentary with dP_3-dP_4 and M_1; UALP 9019, right fragmentary dentary with dI and dP_3-dP_4; UALP 9007, left fragmentary dentary with dP_3-dP_4; UALP 9009, mandible with dI_2-dI_3, I_1, I_2 (erupting), dC, dP_3 (roots), dP_4, M_1 and M_2 (broken); UALP 9011, right partial dentary with P_1, P_3-P_4, M_1-M_2 and M_3 (broken); UALP 9017, left partial dentary with C (root), P_1, P_2 (alveolus), P_3-P_4; (broken) and M_1-M_3; UALP 9013, left partial dentary with dP_2 (alveolus), dP_3 (broken), dP_4 and M_1-M_2; UALP 9014, right partial dentary with dP_2 (alveolus), dP_3 (broken), dP_4 and M_1; UALP 9008, right partial dentary with P_3-P_4 and M_1-M_3; UALP 9024, left partial palate with dP^3-dP^4 and M^1-M^2; UALP 9443, partial rostrum with I^3, C, P^1, and P^3-P^4; UALP 9114, left astragalus; UALP 9108, left proximal metacarpal; UALP 9107, left proximal metacarpal; UALP 9129, left astragalus; UALP 9106, distal metapodial; UALP 9110, left distal radius-ulna; and UALP 9125, right distal tibia.

Cliff Prospect, Milk Creek Formation, stratigraphically between the Milk Creek Quarry and Shields Ranch Quarry horizons (Clarendonian), Milk Creek area, Yavapai County, Arizona: F:AM 93314, left metacarpus.

Deep Spring Quarry (=Johny Post, UALP locality 1-1a), about 69 feet above Manzanita Quarry and 34 feet below Milk Creek Quarry, Milk Creek Formation (Clarendonian), Milk Creek area, Yavapai County, Arizona: F:AM 73438, articulated skull with I^3-M^3 and mandible with I_1-I_3 alveoli, C-P_1 and P_3-M_3; F:AM 73379, articulated skull with I^3-P^1 and P^2-M^3 and mandible with I_1 (alveolus)-M_3; F:AM 73437, skull with I^1-P^1 alveoli, P^2-M^3, mandi-

ble with I_1, I_2-C alveoli and roots and P_1-M_3, and atlas, axis, three other cervical vertebrae, metatarsus and phalanges; F:AM 73378, skull with I^3-M^3; F:AM 73378A, right femur; F:AM 73385, skull with I^3-M^3; F:AM 73285, skull with I^3-M^3; F:AM 73390, skull with I^3 (alveolus)-M^3; F:AM 73377, skull with I^3-C alveoli, P^1 broken and P^2-M^3; F:AM 73439, left partial maxilla with P^2-P^4 all erupting and M^1; F:AM 73309, mandible with I_1 alveolus, I_2-I_3, C alveolus and P_1-M_3; F:AM 73384, mandible with I_2, C and P_3-M_3; F:AM, 73376, mandible with I_1-C alveoli, P_1 unerupted and P_2-M_3; F:AM 73306, right ramus with symphysis, I_1-P_1 and P_3-M_3; F:AM 73308, mandible with I_3-M_3; F:AM 73383, mandible with incomplete symphysis and P_3-M_3; F:AM 73307, left partial ramus with P_3 (broken)-M_3; F:AM 99635, left partial ramus with P_4-M_3 all broken; F:AM 99638, left partial ramus with P_4-M_3 all broken; F:AM 99640, right ramal fragment with M_3; F:AM 99637, right partial ramus with P_2-M_2 all broken; F:AM 99633, right ramal fragment with P_4-M_2 all broken; F:AM 99636, left ramal fragment with incomplete symphysis, I_1-I_3 alveoli and C-P_2 all broken; F:AM 99625, left immature partial ramus with dP_3-M_1; F:AM 73415, right and left articulated radii through third phalanx; F:AM 73413, left articulated metacarpus through third phalanx; F:AM 73414, right metacarpus; F:AM 73416, right and left metacarpi and two or more associated individuals including F:AM 73416A, crushed and broken metapodial; F:AM 73416B, left humerus; F:AM 73416C, left radius and ulna; F:AM 73416D, crushed radius and ulna; F:AM 73420, right metacarpus and articulated phalanges; F:AM 73422, left metacarpus; F:AM 73421, left metacarpus; F:AM 73417, left metacarpus; F:AM 73418, left metacarpus; F:AM 73419, right metacarpus; F:AM 73428, left metatarsus; F:AM 99645, left broken metatarsus; F:AM 73429, right metatarsus and right calcaneum; F:AM 73431, right metatarsus; F:AM 73430, right metatarsus; F:AM 73435, right metatarsus; F:AM 73434, right metatarsus; F:AM 73433, left metatarsus; F:AM 99644, broken metatarsus; F:AM 99643, crushed metatarsus; F:AM 73432, broken metatarsus; F:AM 73425, right humerus; F:AM 73424, right humerus; F:AM 73426, left radius

and ulna; F:AM 73427, left crushed femur; F:AM 99652, right tibia; F:AM 73413, scaphoid and magnum; F:AM 73436, partial pelvis; F:AM 99655, left partial humerus; F:AM 99656, right and left radius and ulna; F:AM 99657, left femur; F:AM 101454, right crushed femur; F:AM 101472, right femur; F:AM 101473, right femur; F:AM 101474, right and left crushed femora, associated with F:AM 101473 of a larger individual; F:AM 101475, left crushed femur; F:AM 101476, left femur; UALP 5023, partial skull with P^1-P^4 and M^1-M^3; UALP 1441a, right articulated humerus, radius-ulna, metacarpal, 2 proximal phalanges and sesamoid; UALP 1441b, left articulated scapula (glenoid fossa), humerus, radius-ulna, scaphoid, lunar, cuneiform, magnum, unciform, trapezoid, pisiform, metacarpal, 2 proximal phalanges, 2 medial phalanges, 2 distal phalanges, and 3 sesamoids; UALP 9355, distal left tibia; UALP 9356, left astragalus and calcaneum; UALP 9357, right proximal femur; UALP 9358, left proximal and distal femur; UALP 9359, right? metatarsal; UALP 9360, left distal humerus; UALP 9361, 2 proximal phalanges, UALP 9355-UALP 9361 apparently associated; UALP 9362, right proximal humerus; UALP 9363, left proximal metatarsal, 1 proximal phalanx, 2 medial phalanges, 2 distal phalanges; UALP 9364, right metacarpal, 2 proximal phalanges, 2 medial phalanges and 1 distal phalanx; UALP 9365, right distal radius-ulna, right proximal metacarpal, 2 proximal phalanges; UALP 9366, left astragalus and calcaneum, 1 distal metapodial, 5 proximal phalanges, 2 medial phalanges and 1 distal phalanx; UALP 9367, right astragalus and calcaneum, left distal tibia and 2 distal phalanges; UALP 9369, right proximal femur; UALP 9370, right astragalus; UALP 9371, right calcaneum; and UALP 9372, right astragalus, proximal left metatarsal, left cuneiform, proximal phalanx and medial phalanx.

Milk Creek Quarry, about 103 feet above the Manzanita Quarry level, Milk Creek Formation (Clarendonian), Milk Creek area, Yavapai County, Arizona: F:AM 73292, anterior part of skull with C-M^3 and F:AM 73292A, associated left partial ramus with P_2-M_3; F:AM 73293, crushed anterior part of skull with I^3-M^3; F:AM 73284, partial palate with P^2(broken)-M^2 and M^3 broken; F:AM 73295, partial palate with P^1-M^2; F:AM 73303, partial mandible with C, P_1 root and P_2(root)-M_3 (P_3-M_1 broken); F:AM 73302, left partial ramus with symphysis, I_1-M_2 and M_3 broken; F:AM 73267, right partial ramus with symphysis, I_1-P_1 and P_3-M_3; F:AM 73298, left partial ramus with P_1 (root)-M_2 and M_3 broken; F:AM 73301, left partial ramus with P_3-M_1 roots and M_2-M_3; F:AM 73304, right partial ramus with P_2-M_2 and M_3 broken; F:AM 73263, right and left partial rami with P_3-M_3; F:AM 73264, right partial ramus with P_3 (broken)-M_3; F:AM 73264A, left partial ramus with P_2(germ), P_3-M_2 and M_3 (broken); F:AM 99642, right partial ramus with P_2 (alveolus)-M_2 and M_3 broken; F:AM 73289A, left partial ramus with P_2 (broken)-M_3; F:AM 73271, left partial ramus with P_3-M_1 and M_2-M_3 broken; F:AM 73274, symphysis with I_1-C and P_1 broken; F:AM 73272, symphysis with I_1-I_3 and C-P_1 broken; F:AM 73273, symphysis with I_1 (broken)-C and P_1 root; F:AM 73271B, symphysis with C(root)-P_1 broken; F:AM 73336, right immature partial maxilla with dP^2-dP^3 and dP^4-M^1 broken; F:AM 73389, right immature ramal fragment with dP_2(broken)-dP_3 and dP_4 broken; F:AM 73303, right incomplete metacarpus; F:AM 73316, right and left incomplete metacarpi; F:AM 73289B, left incomplete metatarsus; F:AM 73321, right articulated distal end humerus and proximal half radius and ulna; F:AM 73320, left crushed radius and ulna; F:AM 73624, left proximal part of radius and ulna; and F:AM 73322, left distal end tibia.

REVISED DIAGNOSIS: Differs from *P. heterodontus* and *P. barstowensis* in extreme transverse constriction of rostrum posterior to P^1; I^1-I^2 lost; P^2-P^3 without parastyle; molars with less sharp styles and less prominent ribs; P_1 short, peglike, occasionally suppressed or absent, with closely appressed roots; P_2 very small and occasionally absent, with closely appressed and sometimes fused roots; P_3-P_4 relatively smaller and simpler; molars (especially M_3) anteroposteriorly shorter; mandibular ramus with prominent lateral flare on angle of mandible; and prominent mesial tuberosity or shelf on ventral angle of mandible.

DESCRIPTION AND COMPARISON: Knowledge of the cranial structure of *Protolabis coartatus* has heretofore been based on the fragmentary

rostral and palatal remains from Stewart and Fish Lake valleys. The many complete and partial skulls which exist in the collections at the American Museum of Natural History and the University of Arizona now make possible a more thorough description of the cranial anatomy of this species. Because all skulls have suffered some postmortem distortion, the following description is based upon the examination of all specimens.

The length of the skull of *P. coartatus* is intermediate between that of *P. barstowensis* and the skull described from New Mexico by Cope (1877, p. 329) under the name of *Procamelus occidentalis*. The basal length averages 318.4 mm. All the Milk Creek specimens exhibit some dorsoventral flattening, but the face appears to have been relatively deep with little maxillary inflation anterior to the orbits. Anterior to the cheek teeth, the muzzle is strongly constricted. The skull is wide across the orbits with marked postorbital constriction immediately in front of the braincase. The braincase

is unexpanded and short relative to the length of the skull; it is only slightly more inflated than that of *P. heterodontus* and is approximately the same size as the above specimen that Cope described from New Mexico.

The anterior rostral region is best preserved in the type (UCMP 19820) from Stewart Valley. As Stirton (1929, p. 295) observed, the rostrum is distinctive for its extreme lateral constriction. This constriction is most apparent in the palatal view, where the roof of the palate narrows continuously from I³ to a point about midway between P¹ and P². The narrowest point of the rostrum posterior to P¹ is marked by a sharp maxillary crest on each side of the roof of the mouth; it is between these crests that the palatal width was measured. On the type specimen of *P. coartatus* the narrowest palatal width is 8.5 mm., whereas the width of some referred specimens from Milk Creek measures as little as 5.0 mm. These measurements are less than half of those of *P. heterodontus* and *P. barstowensis*. The palate of the
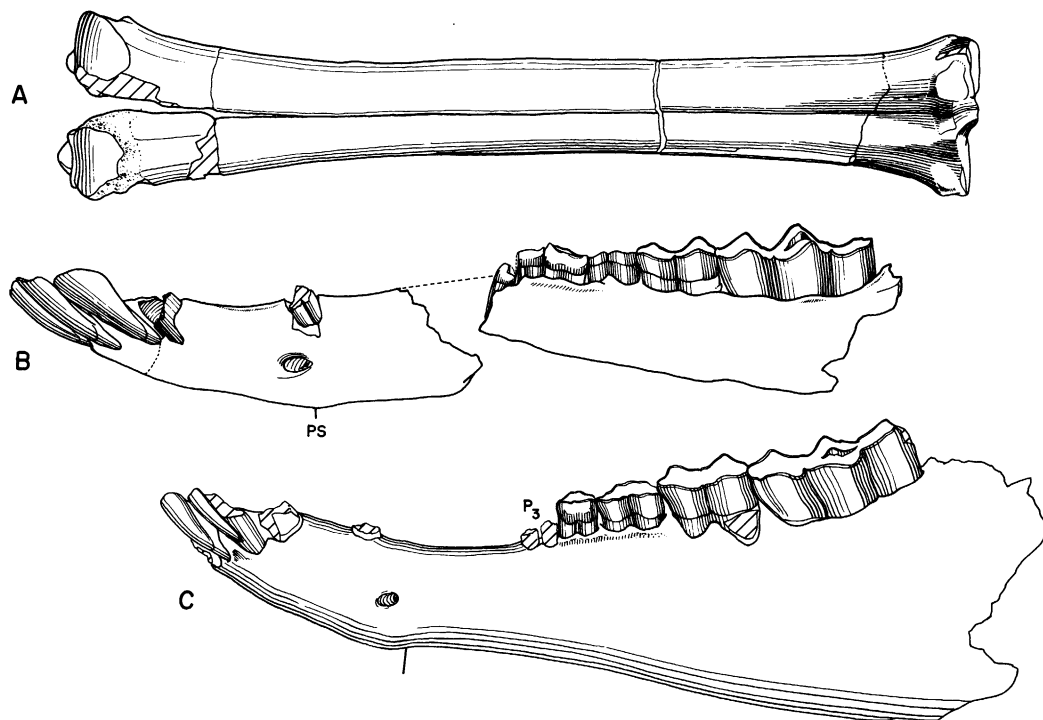

Fig. 5. A-C. *Protolabis coartatus* from Manzanita Quarry (Clarendonian), Arizona. A. F:AM 73315, metacarpus, anterior view. B. F:AM 73300, lateral view. C. F:AM 73266, lateral view, reversed. All X½.

type and several of the referred specimens are undistorted, demonstrating that this constriction is real. This palatal narrowing is associated with the pronounced development of the buccinator fossa on the ventrolateral border of the maxilla, above and behind P^1. When the fossa is undistorted, it is arcuate in outline, beginning above the canine and arching posteriorly in a smooth curve about halfway up the face, descending and disappearing above P^4. The fossa is deepest between P^1 and P^2, and its surface tends to be relatively smooth. A partial skull (AMNH 9118) from northeastern Colorado referred to P. heterodontus also shows this fossa well developed.

Above the buccinator fossa the premaxillary and maxillary bones flare and roll outward and upward, reaching their maximum expansion immediately behind the external nares. In dorsal view the rostrum narrows rapidly posteriorly, reaching its maximum constriction above the maxillary fossa and anterior to the nasofrontal suture. Vertical crushing has obscured the details of this fossa in most specimens except F:AM 73379 from Milk Creek. The maxillary fossa is high on the maxillary bone, beginning at a point above the anterior edge of P^2. The fossa increases in depth posteriorly, reaching a maximum depth above and immediately behind the infraorbital foramen. Posteriorly, the maxillary fossa decreases in depth and disappears above the anterior lobe of M^3. The superior border of the fossa is marked by a shallow groove separating the maxillary and nasal bones. The maxillary fossa of P. coartatus is broad and open and resembles that of the partial skull of P. heterodontus (AMNH 9118). Some Protolabis specimens in the F:AM collection were observed to have a more deeply depressed maxillary fossa with a well-defined rim. The infraorbital foramen is situated above the anterior moiety of M^1, as in the type of P. heterodontus. As mentioned above, P. coartatus has a relatively deep face, measuring approximately 72.0 mm. from the palatal border at a point behind P^1 to the top of the nasals (F:AM 73379).

In the type rostrum of P. coartatus the premaxillary-nasal suture measures 52.5 mm.; in some of the Milk Creek specimens it may be as short as 28.0 mm. The nasals contact each other along a suture 86.0 mm. in length (F:AM 73438). Near the posterior end of each nasal are one or two small foramina. Skulls of P. coartatus measure from 145.0 to 160.0 mm. across the frontals between the orbits. On the anterodorsal border of the orbits is a mesially directed notch about 16.0 mm. long. Because of crushing the true dimensions of the orbits cannot be determined, but they appear to be about the same as those of P. heterodontus.

The zygomatic arch in P. coartatus measures about 15.0 mm. dorsoventrally at the widest point and is of similar proportions to that of P. heterodontus. It varies from relatively flat to slightly arched. Anteriorly, a strong zygomatic ridge extends onto the face to a point above the posterior moiety of M^2. This ridge is higher on the face and more strongly developed than in P. heterodontus (AMNH 9426). The anterior edge of the zygomatic process of the squamosal contacts the maxilla less than halfway forward along the ventral edge of the orbit. In some skulls (F:AM 73438 and UALP 1449), a single large subsquamosal foramen is present on the posterior root of the zygomatic arch.

The supraoccipital tilts posterodorsally and widens laterally, with the maximum width between the paroccipital processes. The lambdoidal crest is strong. The median occipital ridge is narrow at the top and widens ventrally to equal the width across the top of the foramen magnum. At its junction with the foramen magnum, the median ridge occasionally bears two small tubercles. On a nearly undistorted occiput (UALP 1449), the height of the foramen magnum measures 22.3 mm., and the width 25.0 mm. In form, the occipital condyles of P. coartatus are similar to those of P. heterodontus. The basal articular surfaces are convex posteriorly and concave anteriorly. They fail to meet at the midline and are slightly upturned at their junction with the basioccipital. The deeply excavated mastoid fossae lie laterally to the condyles, and are separated by a distance of 34.0 mm. in an undistorted occiput (F:AM 73285). This compares with a measurement of 47.0 mm. in a referred skull of P. heterodontus (AMNH 4432).

The basisphenoid in P. coartatus possesses two troughs for the insertion of the rectus cap-
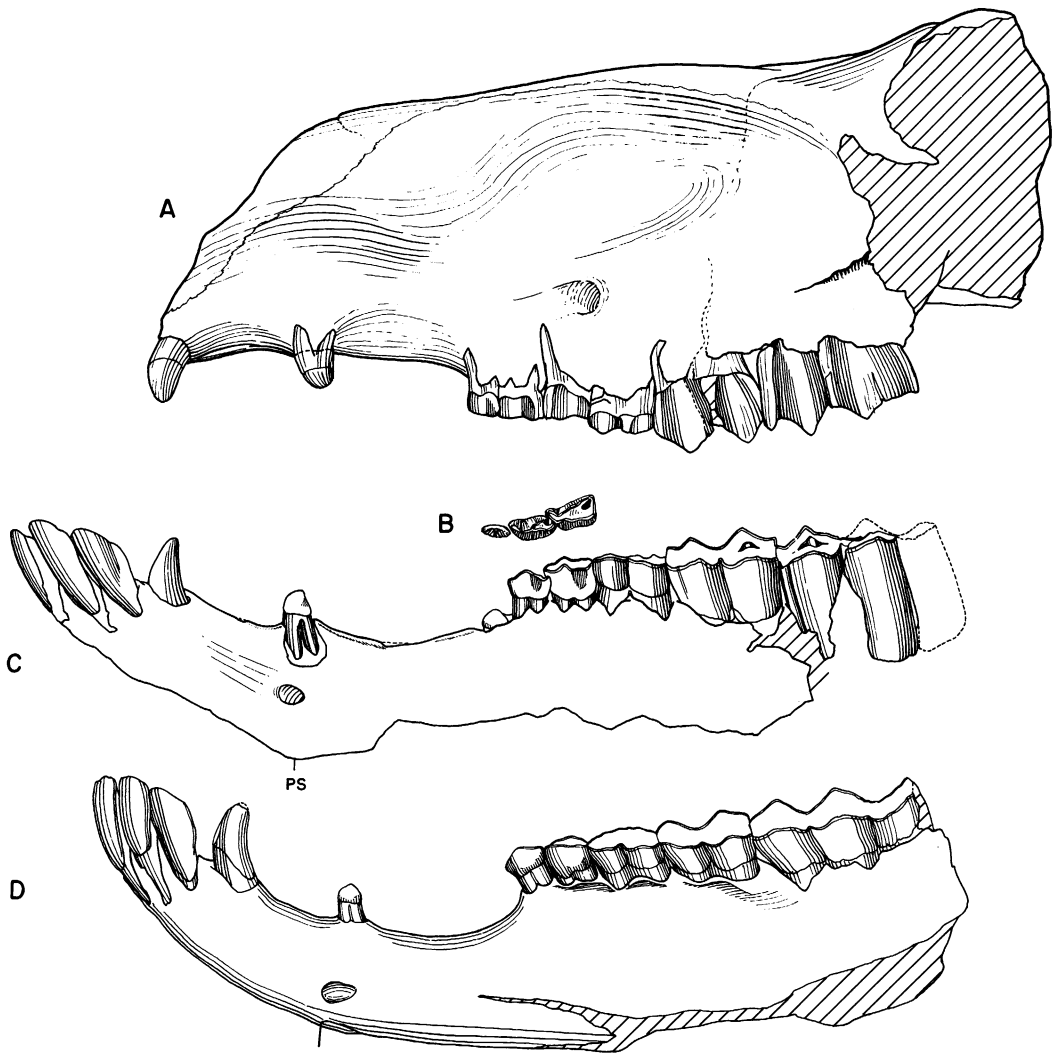
FIG. 6. A-D. *Protolabis coartatus* from Milk Creek Quarry (Clarendonian), Arizona. A. F:AM 73292, lateral view. B-C. F:AM 73302. B. Occlusal view. C. Lateral view. D. F:AM 73267, lateral view. All X½.

itus ventralis muscle. The troughs are separated by a narrow anteroposterior ridge and vary from elongate to circular. They are occasionally very deeply depressed, as in *P. heterodontus*. The troughs decrease in depth posteriorly until meeting the occipital condyles. In *P. heterodontus* the basisphenoid troughs end before reaching the condyles, resulting in a narrow width of undepressed basioccipital anterior to the condyles.

Between the basioccipital and the base of the bulla is a compound foramen (UALP 1449) representing the conjoined posterior lacerate foramen and posterior opening of the carotid canal. The posterior part, representing the posterior lacerate foramen, is the larger of the two. In *P. heterodontus* these two foramina are separated by a thin wall of bone. About 7.0 mm. posteromesially from the posterior lacerate foramen is the hypoglossal foramen. The hypo-

glossal foramen in *P. coartatus* is situated near the rim of the condyloid fossa, just beneath the anterior lip of the occipital condyle, and at the same level as the posterior lacerate foramen. It is situated similarly in *P. heterodontus*, but in some skulls of *Protolabis* it is deeper inside the condyloid fossa. At the bottom of the condyloid fossa and against the medial wall is the condyloid foramen. In both *P. coartatus* and *P. heterodontus* the condyloid foramen is about the same size as the hypoglossal foramen.

The tympanic bulla of *P. coartatus* is smaller than that of *P. heterodontus* (AMNH 9432), and the lateral plate is also less inflated in *P. coartatus*. The distance between the center of the external auditory meatus and the bottom of the bulla measures 44.8 mm. in *P. heterodontus* (AMNH 9432) and 34.0 mm. in *P. coartatus* (UALP 3632). The latter is a relatively small individual of *P. coartatus*, the larger specimens being too crushed for accurate measurements. In both species the external auditory meatus is nearly circular without a prominent outward projecting lip. The base of the medial plate of the bulla is slightly wider in *P. heterodontus* than in *P. coartatus*. In both *P. heterodontus* and *P. coartatus* the anterior edge of the bulla projects slightly anterior to the basioccipital-basisphenoid suture. Anterior to the bulla and lateral to the basisphenoid is a pair of mesial and lateral pterygoid processes, separated by a deep valley. The lateral process is prominent and pyramidal in shape. The interpterygoidal valley runs anteriorly into the foramen ovale.

Crushing and erosion have obscured the morphological details of the orbital region in *P. coartatus* but those of the palate are known in detail. The anterior border of the internal nares is V-shaped and lies behind the posterior border of M^3, with the distance varying up to 11.0 mm. Lateral to the tip of the "V" are two small, variably expressed tubercles. The position of the anterior palatine foramen is variable, generally being between the M^1s, but is also sometimes between P^4 and M^1 (UCMP 29602), or between the anterior moieties of the M^2s (UALP 9022). In the specimens measured the width of the palate between the posterior lobes of M^3 varies from 45.2 mm. to 55.3 mm. The

width of the palate between P^2 varies from 16.8 mm. to 22.0 mm. As was pointed out by Henshaw (1940, p. 20), the restored width of *P. coartatus* specimen (UCMP 29612) is probably too great. These palatal widths are slightly greater than in *P. heterodontus* (F:AM 32880) from northeastern Colorado.

UPPER DENTITION: The rostrum of the type of *P. coartatus* lacks the first two upper incisors, and it was for this reason that the species was originally allocated to *Procamelus*. The referred specimen from Fish Lake Valley (UCMP 29608) and most of the Milk Creek specimens also lack the first two upper incisors. However, specimens (F:AM 73296 and 73377) from Milk Creek have shallow alveoli for I^2, and F:AM 73293 has the root of I^1 preserved. Most specimens, however, lack any indications of the presence of these teeth. When present, these teeth in the Milk Creek sample were diminutive and usually lost early during the life of the individual. Evidence is insufficient to determine whether these are deciduous or permanent incisors, but in F:AM 72393, one of these incisors was present in an old individual. Earlier occurring *Protolabis* specimens occasionally exhibit reduction and loss of the anterior incisors, as can be seen in a referred specimen (F:AM 32880) of *P. heterodontus* from northeastern Colorado. In this specimen there is a diminutive I^2 but no I^1.

I^3 and C of *P. coartatus* are robust, recurved, and subcircular to circular in cross section. They are indistinguishable from those of *P. heterodontus* and *P. barstowensis*. The canine is slightly larger than I^3 and separated from it by a diastema varying in length from 4.2 mm. to 12.0 mm. In *P. heterodontus* I^3-C diastema varies in length from 8.1 mm. to 12.7 mm. In the Milk Creek sample the muzzle is longer and the length of C-I^1 diastema varies from 15.4 mm. to 26.0 mm.

P^1 in *P. coartatus* is small and blunt with two roots. The roots vary from widely flared in the referred specimen from Fish Lake Valley (UCMP 29608), to closely appressed in the type, and even fused in one specimen from Milk Creek (UALP 9022). In the last specimen P^1 is entirely unlike the large caniniform P^1 of *Procamelus*. The Milk Creek sample is signifi-

Fig. 7. A-B. *Protolabis coartatus*, F:AM 73438, from Deep Spring Quarry (Clarendonian), Arizona. A. Lateral view, reversed. B. Lateral view. All X½.
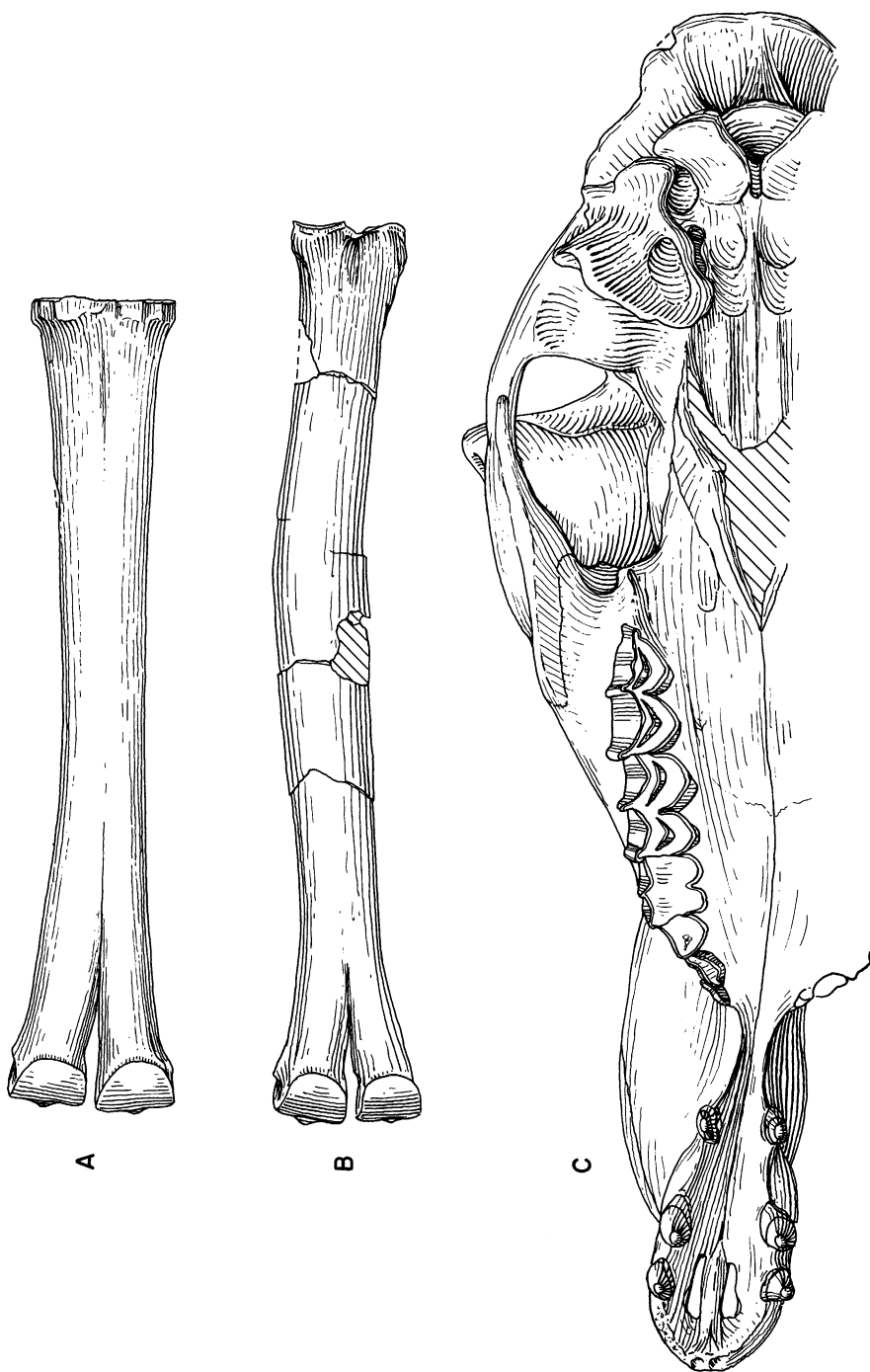
Fig. 8. A-C. *Protolabis coartatus* from Deep Spring Quarry (Clarendonian), Arizona. A. F:AM 73416, metacarpus, anterior view. B. F:AM 73434, metatarsus, anterior view, reversed. C. F:AM 73488, palatal view, reversed. All X½.

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TABLE 3

Measurements (in Millimeters) and Statistics of Skulls and Upper Dentition of *Protolabis coartatus* Referred from Milk Creek, Arizona, Compared with Measurements of the Type and Referred Remains of *Protolabis coartatus* (Stirton) from Nevada and *Protolabis heterodontus* (Cope) from Colorado

	N	OR	X	S	V	UCMP 19820[a]	UCMP 29612[a]	UCMP 29608[a]	AMNH 8296[b]	AMNH 9426[b]	F:AM 32880[b]
Occipital crest to incisive border (vertex)	4	331.0-337.5	334.7	2.7838	0.8316	—	—	—	—	—	—
Foramen magnum to incisive border (basilar)	4	311.0-321.8	318.45	5.0209	1.5766	—	—	—	—	—	—
Postorbit to anterior incisive border (facial)	4	232.1-266.0	245.67	14.383	5.854	—	—	—	—	—	—
Postorbit to occipital crest (cranial)	4	93.9-103.5	99.05	4.234	4.274	—	—	—	—	—	—
Anterior border foramen magnum to posterior edge M^3	4	99.0-123.0	109.8	9.922	9.037	—	—	—	—	129.4	—
Outside width across orbits	4	146.5-160.0	150.27	6.512	4.333	—	—	—	—	—	—
Palatal width between I^3	2	19.3-27.9	23.6	—	—	23.6	—	—	—	—	21.7
Palatal width between P^2	6	16.8-25.3	20.18	3.339	16.547	—	—	—	—	—	30.0
Palatal width between M^3 posterior moiety	8	43.4-55.3	50.01	4.414	8.825	—	—	—	—	—	60.7
Palatal width narrowest part of rostrum	8	5.0-8.7	6.07	1.368	22.53	8.6	—	8.7	—	—	18.3
I^3-C diastema length	12	4.3-7.8	6.07	1.206	19.866	12.5	—	5.8	8.1	—	12.1
C-P^1 diastema length	13	15.7-25.9	20.03	3.171	15.832	17.5	—	19.9	16.2	—	12.8
P^{1-2} diastema length	10	23.6-50.5	34.53	8.057	23.33	—	—	—	—	—	27.8
Upper canine length	12	8.0-11.7	9.82	1.128	11.499	8.0	—	—	10.3	—	—

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TABLE 3 — (Continued)

	N	OR	X	S	V	UCMP 19820[a]	UCMP 29612[a]	UCMP 29608[a]	AMNH 8296[b]	AMNH 9426[b]	F:AM 32880[b]
P¹ length	13	5.1-7.7	6.25	0.754	12.08	6.6	—	6.0	6.6	—	5.7
P² length	14	7.8-11.1	8.79	0.9706	11.039	—	8.6	—	—	—	10.4
P² width	10	4.6-5.9	5.05	0.422	8.36	—	4.5	—	—	—	4.5
P³ length	16	9.9-13.1	11.36	0.8294	7.304	—	10.7	—	—	—	13.7
P³ width	14	6.2-10.0	7.39	0.9351	12.651	—	6.8	—	—	—	7.0
P⁴ length	19	10.0-14.2	12.37	1.306	10.559	—	11.3	—	14.4	—	14.5
P⁴ width	16	9.7-12.6	11.19	0.8497	7.591	—	10.4	—	14.4	—	11.8
M¹ length	16	13.8-21.3	18.23	2.099	11.512	—	17.7	—	19.8	—	22.0
M¹ width	15	14.8-18.7	17.16	1.344	7.831	—	16.8	—	19.2	—	19.0
M² length	23	20.7-32.6	26.38	3.160	11.982	—	25.0	—	28.2	—	31.3
M² width	19	15.2-21.6	18.46	2.016	10.924	—	17.2	—	21.5	—	19.6
M³ length	15	31.6-42.0	34.32	3.45	10.052	—	31.6	—	35.2	—	37.7
M³ width	13	17.1-23.6	19.90	2.135	10.782	—	16.9	—	19.0	—	17.8
P²⁻⁴ length	13	27.0-38.3	31.51	2.924	9.2826	—	33.0	—	—	—	38.8
M¹⁻³ length	14	69.9-90.1	76.24	6.567	8.614	—	75.2	—	82.7	—	90.7
P²-M³ length	11	93.0-121.6	105.72	8.854	8.375	—	107.9	—	—	—	125.0

[a]UCMP 19820 is the type of *Protolabis coartatus* (Stirton, 1929) and UCMP 29612 and 29608 are referred.
[b]AMNH 8296 is the type of *Protolabis heterodontus* Cope, 1874 and AMNH 9426 and F:AM 32880 are referred.

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cant in showing all graduations of P^1 root from widely flared to fused. Individuals with completely fused roots are rare, and only one was found in which a cross section of the tooth failed to reveal evidence of a double root.

The length of the premolar row and the individual lengths of the premolars are highly variable in *P. coartatus*. The sample from the stratigraphically highest Milk Creek Quarry has relatively larger premolars than the sample from the stratigraphically intermediate Deep Spring Quarry. The premolars of *P. coartatus* from the stratigraphically highest level (Milk Creek Quarry) are similar in size to those of *P. heterodontus* from northeastern Colorado. In *P. coartatus* however, the morphology is simpler. P^2 is double rooted with a high, central, basally swollen paracone separated by a buccal groove from a buccally inflected metastyle. In *P. heterodontus* the metastyle is slightly more developed. The parastyle is absent in *P. coartatus*, whereas *P. heterodontus* retains a vestigial parastyle. A weak lingual cingulum runs along the base of P^2 in *P. coartatus*.

Like P^2, P^3 of *P. coartatus* has a bulbous paracone that is separated by a groove from a buccally inflected metastyle. Again the parastyle is absent; in contrast P^3 of *P. heterodontus* has a prominent, buccally inflected parastyle. Consequently, P^3 of *P. heterodontus* has a shallow anterior groove formed by the inflection of the parastyle, which fails to extend to the base of the tooth. Mesially, P^3 of *P. coartatus* sometimes possesses a basal swelling which is continuous with two crests running from the anterior and posterior edges of the tooth. These crests do not join to form a fossette. Although stronger in *P. heterodontus*, these crests also do not join to form a fossette.

P^4 is single lobed and very similar to that of *P. heterodontus*. It possesses a parastyle and a weakly developed metastyle. The paracone forms the major buccal cusp. The internal crescent consists of the protocone and weakly developed hypocone.

The molars of *P. coartatus* and *P. heterodontus* are similar. M^1 has a strong mesostyle that extends to the base. The parastyle is strong in young animals and disappears with wear. The metastyle is weakly developed.

None of the Milk Creek specimens possess the inter-columnar tubercle on M^1 that is present on the referred specimen from Fish Lake Valley (UCMP 29612). Because no other morphological differences were seen in the Fish Lake Valley specimens, we consider development of this tubercle variable and of no taxonomic significance. M^2 and M^3 both possess a strong parastyle and mesostyle; M^3 also has a small metasytle. A weak rib is present on the paracone and metacone of M^2 and M^3, and is faintly developed on the little worn M^1. In *P. heterodontus* the styles are sharper and the ribs slightly more prominent than in *P. coartatus*. M^3 of *P. coartatus* from the stratigraphically highest Milk Creek Quarry has a relatively more anteroposteriorly elongate second lobe than that of both *P. coartatus* from the stratigraphically lower Deep Spring Quarry and *P. heterodontus* from northeastern Colorado. Thus M^3 in the Milk Creek Quarry sample is larger than that in the other two samples. The other molars in the Milk Creek Quarry sample also average larger than those of the Deep Spring Quarry sample.

LOWER DENTITION: The lower incisors are spatulate. The canine of the type of *P. coartatus* is conical and pointed. Canines from the Milk Creek sample exhibit various degrees of compression, and no morphological features distinguish them from the canines of *P. heterodontus*.

P_1 in the Milk Creek sample is double rooted, with the roots closely appressed or even fused. In *P. heterodontus* the roots are widely separated. P_1 of *P. heterodontus* is anteroposteriorly elongate with a prominent, centrally located cusp (protoconid) from which anterior and posterior crests descend. In *P. coartatus* P_1 is short, and in individuals with appressed roots is peglike. In a few cases P_1 is suppressed (unerupted), or even absent. One individual from Milk Creek (F:AM 73265) has P_1 present and erupted on one side and absent on the opposite side. P_1 in *P. coartatus* is above the mental foramen, as in *P. heterodontus*.

As already noted in the literature, P_2 in *P. coartatus* is extremely small and simple. When present, P_2 is double rooted with a single central cusp. The roots are closely appressed and

sometimes fused. In contrast, P_2 of *P. hetero-dontus* is low and elongate with a central, swollen protoconid, a small posterior hypoconid, and a small anterolingually inflected paraconid. In *P. coartatus* this tooth is absent in more than half the individuals. One specimen (F:AM 73376) has P_2 present in the right ramus but absent in the left ramus. Absence of P_2 cannot be correlated with absence or suppression of P_1.

P_3 of *P. coartatus* is shorter and simpler than that of *P. heterodontus*. Measurements given by Patton (1969, p. 153) for the length of P_3 in *P. notiochorinos* indicate a very small tooth. This is, however, an approximate measurement that was taken at the alveolus of the broken tooth. Because crown length decreases toward the root, the unworn crown length of P_3 of *P. notiochorinos* is probably close to that of the type of *P. coartatus*. P_3 of *P. coartatus* consists of a large, central protoconid, a lingually inflected paraconid, and a labially swollen hypoconulid that is slightly narrower than the protoconid. A few specimens exhibit a very small entoconid that unites with the hypoconulid to form a tiny fossetid that disappears quickly with wear. In *P. heterodontus* the paraconid is larger and more strongly inflected. Furthermore, P_3 of *P. heterodontus* starts to wear early in the life of the individual, whereas in *P. coartatus* this tooth is often little worn in old individuals.

P_4 of *P. coartatus* is generally smaller than that of *P. heterodontus*. It is similar to P_3, with a central protoconid and a lingually inflected paraconid. The hypoconid and entoconid unite to form a fossettid. In *P. heterodontus* the paraconid is larger and more strongly inflected, and the lingual groove between the paraconid and protoconid is relatively deeper.

In *P. coartatus* the molars are smaller than in *P. heterodontus*. Morphologically, there is little to distinguish the molars of the two species. The type of *P. coartatus* has a pronounced parastylid on M_3, which is variably developed in the Milk Creek specimens. Some of the larger specimens from the Milk Creek and Deep Spring quarries also have a rather well-developed M_3 protostylid that unites with the parastylid to form a small anterior buttress.

The molars of *P. heterodontus* also have variably developed parastylids and rare protostylids that occasionally form buttresses.

MANDIBLE: In the Milk Creek sample the length of the mandible is variable and ranges from 270.2 mm. to 312.7 mm. The angle formed at the junction of the symphysis with the body of the horizontal ramus varies from shallow to more upright. The contour of the lower border of the symphysis is generally concave; however, in one large specimen (F:AM 73267) from Milk Creek Quarry, it is slightly convex. In most specimens the symphysis flares laterally in the region of the incisors and canines. In *P. heterodontus* the angle made at the junction of the symphysis with the horizontal body of the ramus is variable, but in most specimens the symphysis turns sharply upward. Immediately behind the symphysis in *P. heterodontus*, a pronounced concavity is present along the ventral surface of the horizontal ramus. Furthermore, the depth of the jaw at the posterior end of the symphysis in *P. heterodontus* is generally greater than in *P. coartatus*. In most *P. heterodontus* mandibles a tuberosity is present on the extreme anterior end of each ramus. These tuberosities merge anteriorly to form a rugose ridge, probably for the insertion of the digastric muscle. This rugose ridge is only weakly developed in *P. coartatus*.

The mental foramen is situated above the posterior border of the symphysis and nearer to the ventral border of the ramus in both *P. coartatus* and *P. heterodontus*. In *P. coartatus* P_1 generally erupts directly above the mental foramen; in *P. heterodontus* its position is more variable with P_1 situated behind the mental foramen in more than half of the jaws. As seen in the type of *P. coartatus* and the referred specimen (UTBEG 31132-332) from Lapara Creek, a second, small mental foramen sometimes occurs low on the body of the ramus below the posterior moiety of M_1. Immediately behind the symphysis the ventral border of the ramus is concave. Beneath P_4 the jaw straightens and becomes convex. In *P. coartatus* the depth of the jaw between P_1 and P_2 is less than in *P. heterodontus*, and the post-P_1 diastema is usually longer than in *P. heterodontus*. The dorsal border of the ramus anterior to the cheek

TABLE 4

Measurements (in Millimeters) and Statistics of the Mandibular Rami and Lower Dentitions of *Protolabis coartatus* Referred from Milk Creek, Arizona, Compared with Measurements of the Type and Referred Remains of *Protolabis coartatus* (Stirton) from Nevada and *Protolabis heterodontus* (Cope) from Colorado

	N	OR	X	S	V	UCMP 19820[a]	UTBEG 31132-332[b]	AMNH 8296[c]	AMNH 8294[c]	AMNH 9426[c]	F:AM 32881[c]
Mandible length	7	270.2-312.7	293.83	16.05	5.463	—	—	—	—	—	—
Distance mental foramen below top of ramus	14	15.1-21.0	17.26	1.685	9.764	—	—	—	—	—	—
Depth jaw between P_1 and P_2	19	23.7-31.0	26.74	2.2605	8.4529	33.4	30.0	32.9	29.4	31.1	29.9
Depth jaw at P_1	16	24.7-36.8	30.18	3.2875	10.89	—	—	—	—	—	—
Depth jaw below anterior moiety of M_3	9	40.7-63.5	50.0	8.289	16.579	49.0	50.6	—	—	64.8	—
C-P_1 diastema	17	12.9-28.5	22.17	4.289	19.349	18.5	—	12.0	19.4	20.0	23.7
P_{1-2} or P_{1-3} diastema	11	28.7-47.4	40.07	6.4949	16.208	31.0	26.2	—	21.1	28.8	28.9
Lower canine length	15	6.8-12.1	9.49	1.5777	16.619	9.4	—	11.4	9.5	9.5	10.9
P_1 length	15	5.1-7.7	6.46	0.8407	13.01	5.9	—	10.5	8.5	9.2	7.5
P_2 length	10	5.0-7.7	6.08	1.0347	17.018	7.0	—	9.4	11.0	10.0	—
P_2 width	7	3.2-4.2	3.80	0.3312	9.241	3.8	—	4.5	3.9	3.2	3.3
P_3 length	24	8.5-11.4	10.10	0.775	7.675	11.1	8.0	12.5	12.1	12.5	11.5
P_3 width	18	4.5-5.6	5.07	0.3264	6.428	5.4	—	—	4.9	4.8	4.3
P_4 length	28	10.3-13.1	11.59	0.7089	6.116	12.7	11.3	—	14.7	15.8	12.9
P_4 width	22	5.7-8.0	6.83	0.5035	7.375	7.1	5.7	—	6.9	8.5	6.4
M_1 length	26	14.2-20.2	17.18	1.576	9.169	16.9	17.2	—	19.6	21.1	18.9
M_1 width	20	10.7-13.6	11.64	0.6516	5.596	10.4	11.1	—	14.9	12.9	14.1
M_2 length	27	19.1-28.7	23.77	2.27	9.576	22.6	22.0	—	30.3	28.3	27.0
M_2 width	21	12.5-17.0	14.76	1.167	7.912	16.4	15.0	—	19.0	15.6	17.3
M_3 length	25	35.5-45.5	39.94	2.619	6.557	40.9	42.0	—	48.1	47.0	45.9
M_3 width	22	12.2-15.5	13.97	0.8886	6.359	13.6	13.0	—	17.1	14.5	17.2
P_{3-4} length	18	19.3-24.1	21.37	1.2979	6.073	24.4	20.6	—	—	—	—
M_{1-3} length	20	73.5-90.2	80.75	5.015	6.2106	82.5	84.0	—	99.3	97.7	95.3
P_2-M_3 or P_3-M_3 length	15	94.6-114.4	104.13	5.746	5.518	112.0	112.0	—	137.4	136.0	128.5

[a] UCMP 19820 is the type of *Protolabis coartatus* (Stirton, 1929)

[b] UTBEG 31132-332 is the type of *Protolabis notiochorinos* (Patton, 1969)

[c] AMNH 8296 is the type of *Protolabis heterodontus* Cope, 1874, AMNH 8294, the type of *Protolabis angustidens* (Cope, 1874) and AMNH 9426 and F:AM 32881 are referred to *Protolabis heterodontus*.
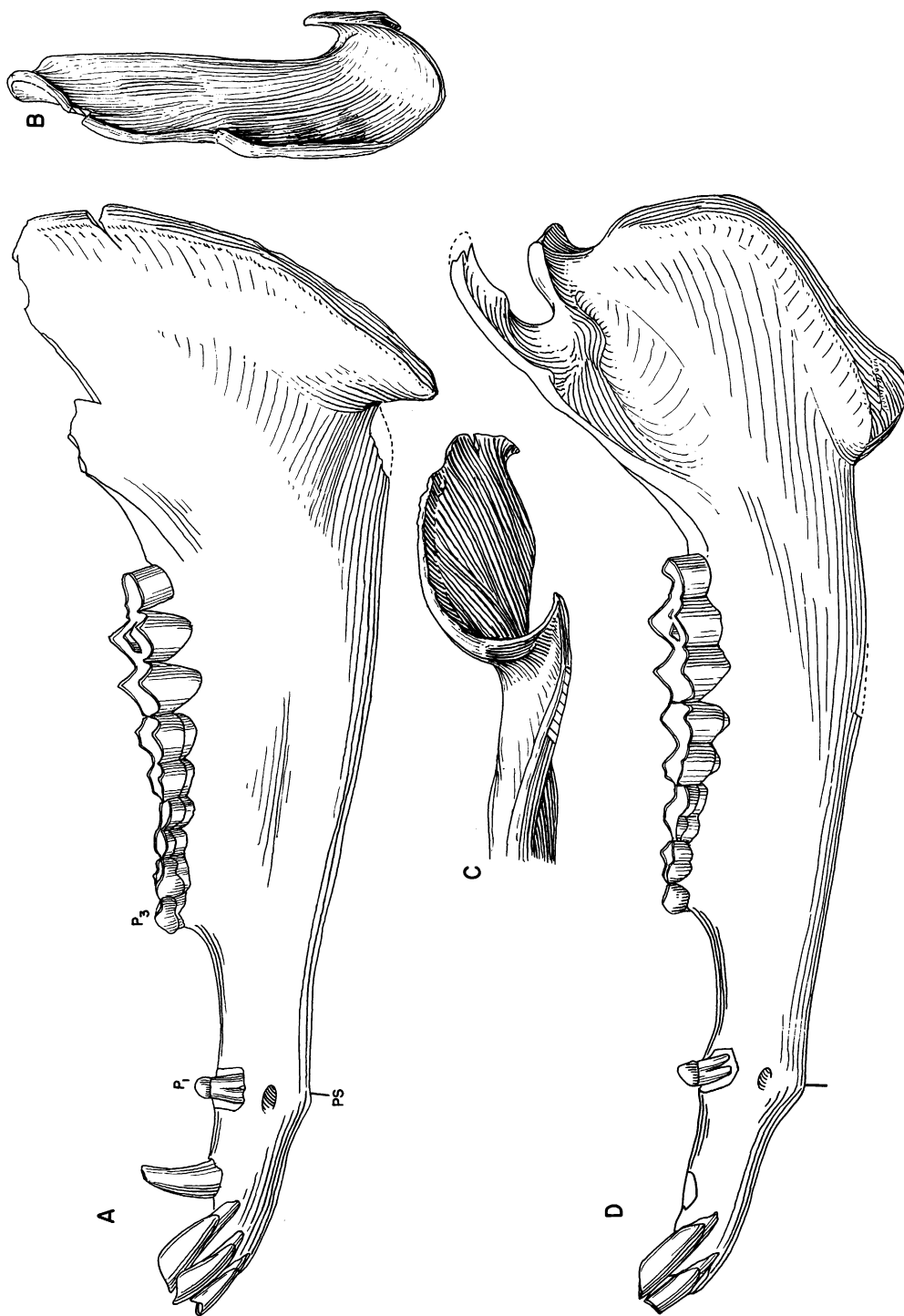
FIG. 9. A-D. *Protolabis coartatus* from Deep Spring Quarry (Clarendonian), Arizona. A-C. F:AM 73306. A. Lateral view, reversed. B. Posterior view, reversed. C. Ventral view, reversed. D. F:AM 73309, lateral view. All X½.

teeth is very thin and sharp in *P. heterodontus*, whereas in *P. coartatus* it is thicker and more rounded. Anterior to the cheek teeth, the mandible of *P. coartatus* narrows more sharply than that of *P. heterodontus*, to coincide with the extreme rostral constriction above.

The strong lateral flare of the angle (fig. 9) is the most distinctive feature of the mandibular ramus of *P. coartatus*. This flare extends upward from the posteroventral border of the angle to the relatively small angular process. The posterior rim of the angle in *P. coartatus* is rougher and thicker than that of *P. heterodontus*. See functional morphology (p. 404). A somewhat similar outward flaring of the angle is present in the type jaw of *Nothotylopus camptognathus* (Patton, 1969, p. 160, figs. 17 and 18). A slight angular flare is seen on a mandibular ramus of *P. heterodontus* (F:AM 32881), and it is also present in varying degrees in other samples of *Protolabis* in the F:AM collection. The Milk Creek sample nevertheless exhibits the most extreme development of the outward flare of the angle. The angle of the type jaw of *P. coartatus* is broken, and consequently lacks any indication of the presence of this unusual mandibular feature. Patton (1969, p. 160) considered this angular flare a distinctive feature of *P. notiochorinos*, but the flare of the Lapara Creek specimen is slightly less than that of the Milk Creek specimens. This may be due in part to the age of the individual from Lapara Creek, for the outward flare is strongest in the older individuals of *P. coartatus* from Milk Creek. One Milk Creek specimen (UALP 9005) has M_2 erupting and shows no lateral flare on the mandible.

A strongly developed mesial inflection on the posteroventral border of the horizontal ramus (fig. 9) is another characteristic feature of the mandible of *P. coartatus*. This inflection is just anterior to the lateral flare of the angle, and is associated with the pronounced development of the posteroventral shelf on the mesial surface of the horizontal ramus. This shelf runs anterodorsally for a short distance, resulting in a thickened, rugose surface for the attachment of the internal pterygoid muscle. The pterygoidal rugosity is weakly developed in *P. heterodontus*, and is variably developed in other

Protolabis specimens. Like the lateral flare, the mesial rugosity reaches its maximum shelflike development in the Milk Creek sample of *P. coartatus*.

On the lateral surface of the ascending ramus is a variably defined, shallow temporal fossa; it extends slightly forward and ventrally from the level of the condyle. The articular condyle is triangular and convex laterally and concave mesially. The coronoid process is low and extends only slightly above the level of the condyle.

DECIDUOUS DENTITION: The deciduous dentition of *P. coartatus* is well represented by many specimens from Milk Creek. The terminology employed here is that developed by Loring and Wood (1969).

In size and morphology, the deciduous upper dentition of *P. coartatus* corresponds closely to that of ?*Protolabis* (UCMP 32309) from Big Spring Canyon described by Loring and Wood (1969, p. 1204). No upper deciduous incisors or canines are recognized in the Milk Creek sample. A little worn dP^2 (F:AM 73333) consists of a short anterior crest, a central primary cusp, and a posterior cusp. The primary cusp is labially swollen, and the posterior cusp labially inflected. The two cusps join with wear. A lingual cingulum is present with prominent anterior and posterior shelves. The cingulum disappears with wear.

DP^3 is bilobed with anterior and posterior crescents (protocone and hypocone). The anterior lobe is much narrower than the posterior lobe and has a prominent anterior crest (parastyle) inflected buccally. Little worn specimens have a cingulum on the lingual side of the anterior crest, which may extend posteriorly to the lingual groove between the anterior crest and crescent. On specimens referred to *P. coartatus* a weak posterior cingulum is sometimes present on the posterior crescent. No specimens allocated to *P. coartatus* have an anterior basal cingulum on the posterior crescent. With wear the anterior and posterior crescents join and their fosettes are obliterated. The mesostyle is well developed and labial ribs are present.

DP^4 has a strong parastyle and mesostyle and a weak metastyle. The rib on the paracone

TABLE 5
Measurements (in Millimeters) and Statistics of the deciduous Dentition of *Protolabis coartatus* from Milk Creek, Arizona

	N	OR	X	S	V
dP² length	6	6.7- 8.4	7.65	7.610	0.238
dP² width	6	3.0- 4.2	3.60	0.434	12.044
dP³ length	9	12.6-16.4	15.04	1.382	9.192
dP³ posterior lobe width	9	9.4-11.9	10.71	0.807	7.533
dP³ anterior lobe width	7	7.0- 7.8	7.34	0.282	3.841
dP⁴ length	12	12.5-20.0	17.20	2.469	14.359
dP⁴ anterior lobe width	10	10.7-12.8	11.33	0.646	5.706
dP⁴ posterior lobe width	11	8.8-13.4	11.24	1.275	11.342
dP²-dP⁴ length	6	32.9-45.5	42.83	4.909	11.462
dP₂ length	5	5.0- 7.2	6.14	0.948	15.433
dP₃ length	13	7.2-11.4	9.38	1.400	14.923
dP₃ width	13	3.8- 5.4	4.37	0.405	9.268
dP₄ length	21	18.2-22.8	20.40	1.315	6.445
dP₄ width	20	7.0-10.1	8.82	0.930	10.530

is stronger than that on the metacone, and a variably developed anterior cingulum is present on the protocone. All specimens have a cingulum high on the posterior wall of the hypocone, running lingually and ventrally from the metastyle. DP⁴ is narrower in *P. coartatus* than in ?*Protolabis* from Big Spring Canyon (figured by Loring and Wood, 1969, fig. 4A).

The lower deciduous dentition of *P. coartatus* also corresponds closely with that of ?*Protolabis* (UCMP 32309) from Big Spring Canyon (Loring and Wood, 1969, fig. 4B). The deciduous incisors resemble their permanent replacements, becoming increasingly spatulate from dI_1 to dI_3. The deciduous canine is very small and blunt, with a laterally compressed crown. It is much smaller than dI_3. As in all camelids no evidence is seen for replacement of P_1 or dP_1.

DP_2 is diminutive with either a single root or two very closely appressed roots. It is somewhat shorter than the same tooth in the Big Spring Canyon specimens (UCMP 32309). A crest, ending in a small, lingually inflected stylid is anterior to a central primary cusp. Another crest with only a slight swelling is situated posterior to the primary cusp.

DP_3 has a prominent central cusp. Anteriorly, a lingually inflected anterior cusp is separated from the primary cusp by a lingual groove. Posteriorly, the tooth is wide in all specimens, due to the presence of both an entoconid and a hypoconid. In early wear a small fossettid is present between these cusps.

DP_4 is long and has a flat lingual wall. A few *P. coartatus* specimens exhibit a relatively well-developed metastylid which extends to near the base of the tooth. Both the ribs and the entostylid are only weakly developed on the lingual wall. As in the other deciduous teeth, no anterior or posterior cingula are present.

LIMBS: In size and morphology, the limbs of *P. coartatus* are indistinguishable from those of *P. heterodontus*. As in all *Protolabis*, the metapodials are short and stout (fig. 8). No associated fore and hind limbs of *P. coartatus* are known, but it is reasonable to assume that as in other *Protolabis* species, the length of the metatarsus exceeds the length of the metacarpus. This hypothesis is supported by the mean lengths of the unassociated metacarpi and metatarsi (table 6). The type of *P. coartatus* is a slightly larger individual than any in the Milk Creek collection.

DISCUSSION: The type of *Protolabis coartatus* comes from Stewart Valley, Nevada. Originally described as *Procamelus* near *gracilis* by Merriam (1916, p. 189), it was named *Procamelus coartatus* by Stirton (1929, p. 295). At that time the type material was aug-

mented by the description of a fragmentary rostrum and palate from Fish Lake Valley. Both authors commented upon the marked reduction of the anterior lower premolars and the extreme rostral constriction; the latter was considered diagnostic of the species by Stirton. In the same paper, Stirton also described a palate from Fish Lake Valley, which he allocated to *Procamelus* cf. *gracilis*, but which he later referred to *P. coartatus* (Stirton, personal commun., in Henshaw, 1940, p. 20). Stirton's reference of this material is here considered correct. Henshaw (1940, p. 20) described and allocated some material from the Avawatz Mountains to *Procamelus coartatus*. None of this material is here considered definitely referable to that species, and some of it is tentatively referred to *Michenia*. The postcranial material from Avawatz, originally assigned by Henshaw to *Procamelus coartatus* is similar in size and morphology to limbs of that species. The dental material, however, is either indeterminate or tentatively referred to *Michenia*, and is discussed further on page 407.

Patton (1969, p. 152) described *Protolabis notiochorinos* in the Lapara Creek fauna. An examination of his illustrations reveals that in size and morphology, the type is practically indistinguishable from the type of *P. coartatus*. Morphologic and morphometric differences from *P. coartatus* are considered due to preservation, and consequently *P. notiochorinos* is synonymized with *P. coartatus*. The synonymy is based on comparison with the Arizona material discussed previously.

Since 1956 a large, stratigraphically well-documented collection of *Protolabis coartatus* has been collected from Milk Creek, Arizona by the Frick Laboratory of the American Museum of Natural History. A somewhat smaller collection from the same area, initially collected under the direction of John Lance and later under the direction of Everett Lindsay, exists at the University of Arizona. Material in these two collections has added tremendously to our knowledge of *P. coartatus*, and in fact contributed significantly to the reevaluation of the genus *Protolabis*. The above description of *P. coartatus* is based on an examination of the Milk Creek specimens, and of the type and referred specimens from Nevada.

FUNCTIONAL MORPHOLOGY

Comparison with figures in Turnbull, 1970 (figs. 14-16) reveals that the lateral flare on the dentary of *P. coartatus* occurs in the insertion area of the superficial masseter in other ungulates. The origin area of the superficial masseter, the zygomatic ridge (=facial crest), is strongly developed in *P. coartatus*. The deep layer of the masseter originates on the zygomatic arch posterior to the origin of the superficial layer. As noted in the description of *P. coartatus* (p. 391), the zygomatic arch is no more robust than on *P. heterodontus*. The deep layer inserts on the dentary dorsal to the insertion of the superficial masseter. These facts suggest that the lateral flare on the dentary of *P. coartatus* is associated primarily with greater development of the superficial masseter. Similarly, the pronounced mesial flare on the dentary occurs at the insertion of the internal pterygoid muscle, and appears to be due to pronounced development of that muscle.

Because the superficial masseter and internal

TABLE 6

Measurements (in Millimeters) and Statistics of Referred Metapodials of *Protolabis coartatus* from Milk Creek, Arizona

	N	OR	X	S	V
Metacarpal length	20	191.9-242.4	224.96	12.641	5.619
Metacarpal proximal width	29	35.0- 41.1	38.19	1.749	4.580
Metacarpal narrowest transverse shaft width	15	19.9- 24.3	21.60	1.090	5.060
Metatarsal length	13	215.2-247.6	232.35	10.780	4.640
Metatarsal proximal width	11	26.9- 32.6	29.85	1.655	5.540
Metatarsal narrowest transverse shaft width	14	15.3- 19.2	17.53	1.132	6.485

pterygoid muscles are important in jaw closing and mastication, their development in *P. coartatus* is in response to selection for more force in the mastication of food. Ostrom (1964, p. 22) noted that the effective force at the dentition can be increased by "1) increasing the magnitude of the applied force [enlarging the adductors] or 2) lengthening the moment arm [of the jaw] by shifting the point of force application [insertion of the adductors] *away* from the fulcrum [glenoid condyles]". In connection with method 2) DeMar and Barghusen (1971, p. 634, fig. 13) show that as the length of the moment arm (from the condyle to the point of insertion of the adductors) is increased in an anteroventral direction, the line of force application (from the insertion to the origin of. the adductors) must be rotated anteriorly on the skull. This anterior rotation is necessary to keep the line of force perpendicular to the moment arm. The superficial masseter has the most anterior origin of the masseteric muscles, and operates with an anterodorsal line of action, thus becoming important as the moment arm lengthens (see DeMar and Barghusen, 1971, fig. 13). However, we believe that its development (and also that of the internal pterygoid) on *P. coartatus* does not reflect an increase in the length of the moment arm, for the following reasons. First, there is no increase in the depth of the angle below the glenoid condyle (corresponding to the moment arm) in *P. coartatus* relative to *P. heterodontus*. Second, as discussed on page 385, in *Protolabis* M_3^3 tend to be longer relative to M_{1-2}^{1-2} and the premolars are more reduced, than in *Procamelus*. The reduction of the anterior cheek teeth and the expansion of M_3^3 in *Protolabis* suggests that the effective force vectors in mastication were more posterior than in *Procamelus*. This is contradictory to the supposition that there was an anterior rotation of the effective force vectors on *P. coartatus*. Thus we suggest that the increase in masticating power in *P. coartatus* was accomplished only by increasing the mass of the adductors.

The small size of the cranium and coronoid process is correlated with the pronounced lateral and mesial flares (fig. 9) on the mandibular angle of *P. coartatus*. This reflects increased emphasis on the masseter and pterygoid mus-

cles in mastication, and decreased emphasis on the temporalis. Turnbull (1970, p. 256) pointed out that in ungulates the masseter is the most important muscle of mastication, generally followed by the pterygoid and last by the temporalis. He showed (1970, fig. 36) that as the size of the masseter increases, the size of the temporalis decreases. These facts are important when considering *P. coartatus* relative to *Procamelus*. In the latter, the angle of the dentary is not laterally or mesially inflected, the coronoid process is longer, and the cranium is larger, than in *P. coartatus*. Thus during the evolution of *Protolabis* there was selection for enlargement of the superficial masseter and internal pterygoid muscles relative to the temporalis. This did not occur in *Procamelus*.

We believe that the constricted rostrum posterior to the canine can best be explained by assuming a highly developed buccinator and maxillo-nasolabialis muscle. Webb (1965, p. 6) discussed the importance of the upper lips in camelids, which function both as a cropping pad and as a prehensile organ. He concluded that the lip muscles were probably highly developed in some fossil camelids. The buccinator and maxillo-naso-labialis muscles are important in manipulation of the lips and cheeks. The latter muscle originates at the junction of the lacrimal, malar, and maxillary bones. There are two divisions to this muscle. According to Webb (1965, p. 6), "The ventral division reaches the angle of the mouth and the anterior end of the diastema. The dorsal division inserts on the upper lip and, after joining fibers from the other side, on the tip of the nose." Thus a well-developed maxillo-naso-labialis muscle has an insertion in the area of the rostral constriction of *P. coartatus*. The buccinator originates on the alveolar border of the maxillary and, according to Sisson and Grossman (1975, p. 796), retracts the angle of the mouth and flattens the cheeks. The buccinator results in a distinct fossa on the alveolar border of the maxillary in certain fossil equids and the kangaroo (Gregory, 1920, fig. 1, pl. 18). The rostral constriction of *P. coartatus* is best termed a buccinator fossa, although a strong maxillo-naso-labialis muscle also probably contributed to its development.

Thus, we interpret the derived cranial fea-

tures of *P. coartatus* as a reflection of strongly developed labial, buccal, and masticatory muscles. The development of the jaw musculature and the relatively high-crowned dentition suggests that *P. coartatus* was eating tough foods, possibly grass or woody shrubs. In the Sahara, Gauthier-Pilters (1974, p. 543) noted that "camels can thrive on the hardest, driest and thorniest plants," and in fact often prefer the thorny woody-acacia. *Protolabis coartatus* may have had a similarly rigorous diet. As discussed earlier, (p. 373), Deep Springs Quarry is associated stratigraphically with aeolian dune deposits. These deposits suggest the possibility of a locally arid paleoenvironment in which tough, hardy plants thrived. Too, *P. coartatus* may have been eating grass; modern camels are known to eat grass and the high-crowned equid *Pliohippus* is occasionally found with *P. coartatus* in these sediments.

MICHENIA FRICK AND TAYLOR, 1971

Procamelus coartatus Henshaw, 1940 (in part) pp. 20-21. pl. 3, figs. 1-3, pl. 4, fig. 3.

TYPE SPECIES: *Michenia agatensis* Frick and Taylor, 1971.

INCLUDED SPECIES: *Michenia exilis* (Matthew, 1960); *Michenia agatensis* Frick and Taylor, 1971; *Michenia yavapaiensis*, new species.

KNOWN DISTRIBUTION. From late Arikareean of Texas and early Hemingfordian to Clarendonian in the western United States.

REVISED DIAGNOSIS: *Michenia* differs from *Protolabis* by smaller size; shorter braincase; weaker and more incisiform I^{1-3} in primitive species; weaker and more incisiform upper canine; smaller lower canine; less anteroposteriorly elongate $M^3_{\overline{3}}$; shallower symphysis, conspicuously unlike the deeper symphysis with more acute angle in *Protolabis*; shallower horizontal ramus; and relatively slender metapodials.

Differs from *Tanymykter* in more constricted rostrum and deeper buccinator fossa; relatively shorter braincase; weaker I^3 and C/C; shallower symphysis; and slender metapodials.

DISCUSSION: Frick and Taylor (1971, pp. 5-6) diagnosed *Michenia* on the basis of the Hemingfordian species, *M. agatensis*. As this

was the only described species of the genus, the characters of *Michenia* were necessarily those of *M. agatensis*. These authors noted, though, that *Michenia* persists through the Clarendonian.

The transfer of *coartatus* from *Procamelus* to *Protolabis* and the transfer of *exilis* from *Oxydactylus* to *Michenia* plus the description in this paper of the derived taxon, *Michenia yavapaiensis*, necessitate a revision of the original diagnosis of *Michenia*. The following points are pertinent: 1) *Michenia* was characterized by Frick and Taylor, 1971 as having a narrow muzzle, but it is not always narrower than that of *Protolabis*, as shown by the muzzle of *P. coartatus* being more constricted than that of *M. agatensis*; 2) later occurring specimens of *Michenia* sometimes have relatively smaller and simpler $P^{2-4}_{\overline{2-4}}$ than those of *Protolabis*; 3) the molars of later occurring *Michenia* specimens are taller crowned with less distinct ribs and stylids and are not always easily distinguishable from those of *Protolabis*; 4) the metapodials of *M. exilis* are unfused, in contrast with those of *M. agatensis*, upon which the original description of *Michenia* was based; and 5) the metapodials of *Michenia*, though always slenderer than those of *Protolabis*, are more solidly fused and relatively stouter in the Clarendonian than those of *M. agatensis*.

Morphological changes manifested in *Michenia* parallel those of *Protolabis*, and the character transformation from primitive to derived in both genera is in general accord with the known temporal sequence from the Hemingfordian to the Clarendonian. Derived specimens of *Michenia* and *Protolabis* have moderately hypsodont molars with weak ribs and styles. In the later occurring specimens of *Michenia* $M^3_{\overline{3}}$s lengthen to the point that they overlap the shorter $M^3_{\overline{3}}$s of *Protolabis*. Moreover, in the most derived species of both genera (*M. yavapaiensis* and *P. coartatus*) I^{1-2} are absent, $P^{2-4}_{\overline{2-4}}$ are reduced in size and simplified with the P_2 frequently lost. Furthermore, in both genera the metapodials become progressively shorter with the length of the metacarpus significantly less than that of the metatarsus. However, most of these morphological changes are not restricted to the Pro-

tolabidini but are convergent to a greater or lesser degree with other camelids.

Some of the material from the Avawatz Mountains (CIT 1989, 2316, 2318, and 2321) which Henshaw (1940) allocated to *Procamelus coartatus*, is here considered referable to *Michenia*. Specifically, Henshaw's measurements for the teeth, especially the length for P^2-M^3 of palate (CIT 1989) lie closer to the mean values of the same measurements of *Michenia yavapaiensis*. The measurement for the narrowest rostral width is less than in *Michenia yavapaiensis* and is similar to that of *P. coartatus*. Other specimens of *Michenia* in the F:AM collection, however, have rostral widths as narrow as that of CIT 1989. One symphysis (CIT 2321) with a small canine is very shallow dorsoventrally, and is inseparable from some symphysis allocated to *Michenia yavapaiensis*. It is unknown if P_1 is absent or suppressed in CIT 2321. M_3 (CIT 2318) is relatively short, falling near the mean of the M_3 length in *Michenia yavapaiensis*. Although extreme wear has undoubtedly shortened the teeth, the lengths of the extremely worn P_3-M_2 of CIT 2316 measures nearest to the mean of these teeth in *Michenia yavapaiensis*. The shallow symphysis constitutes the strongest evidence for allocating the Avawatz Mountains specimens to *Michenia*. Because rostrum (CIT 1989) is narrower than that of F:AM 73287 from Milk Creek, plus the fact that our sample is inadequate to determine the variation in rostral width in *Michenia yavapaiensis*, we refrain from allocating the Avawatz Mountain specimens to this species.

The description of the other samples of *Michenia* must await future study. The material of *Michenia yavapaiensis* described in this paper was collected by the American Museum of Natural History and the University of Arizona, and is housed at these institutions.

Michenia exilis (Matthew, 1960)
Figure 10; Tables 7, 8

Oxydactylus exilis Matthew and Macdonald, 1960, p. 2, figs. 1-4.
?*Michenia australis* Stevens, 1977, p. 48, fig. 15.

TYPE: AMNH 12997, partial skull with I^3 alveolus, C, P^1, P^{2-4}, M^{1-3}, mandible with I_3

alveolus, C, roots of P_{1-2}, P_{3-4}, M_{1-3}; partial scapula, distal end of humerus; radius; metacarpus; calcaneum; metatarsus; and proximal phalanges from near Porcupine Butte, listed by Macdonald (1963, p. 23) as "AMNH 'Rosebud' 5," Rosebud Formation (Hemingfordian), Shannon County, South Dakota.

KNOWN DISTRIBUTION: Late Arikareean of Texas and early Hemingfordian of South Dakota.

REVISED DIAGNOSIS: Differs from *Michenia agatensis* in having P^1 more elongate with more widely separated roots; molars anteroposteriorly shorter and brachyodont; upper molars with stronger buccal ribs and styles; metapodials unfused; and first phalanx shorter with distal articular surface more grooved and less anteriorly produced.

Differs from *Michenia yavapaiensis* in the above characters plus I^{1-2} present; P_{1-2} present and erupted in adults; and molar metastylids stronger.

DESCRIPTION AND COMPARISON: This species was previously described briefly, measured, and figured by Matthew and Macdonald (1960, pp. 2-6). Brief comparisons were made chiefly with *Poebrotherium*. Because we have included this species within *Michenia*, we shall supply a supplementary description of *M. exilis*, and make comparisons with *M. agatensis*, the genotypic species. We have supplied some dental measurements not provided by Matthew and Macdonald (1960, p. 5); the reader is referred to that publication for limb measurements.

SKULL: Viewed ventrally, the muzzle of *M. exilis* is long and narrow as in *M. agatensis*, and does not widen noticeably anterior to the canine. The narrowest palatal width posterior to P^1 is 14.4 mm. In *M. agatensis* the palate is slightly crushed in this area, but it was apparently similar in width. The lateral edges of the muzzle in both species form rather sharp ridges, due to the extreme lateral narrowing of the maxillaries in the area of the buccinator fossa.

Because the lateral surface of the rostrum of the type of *M. agatensis* is not preserved, a comparison is not possible. The rostrum of *M. exilis* is comparatively deep, and the nasals are comparatively shorter than in *Poebrotherium*. Consequently, the premaxillaries of *M. exilis*

are elongate and anteroposteriorly narrow, and slope posteriorly at an angle of approximately 35 degrees to the roof of the palate. The anterior edge of the ascending wing of the premaxilla is straight, becoming slightly concave near the palatal surface. Contact between the dorsal border of the premaxilla and the nasals is along a suture 25.0 mm. in length.

The bone on the lateral surfaces of the maxillaries is largely destroyed; however, the underlying matrix preserves the essential features. Posteriorly, a deep, circular maxillary fossa, approximately 28.5 mm. in diameter, crowds against the nasals. Anterior to the fossa and immediately beneath the nasals, the maxilla is laterally swollen. The buccinator fossa is beneath this swelling and forms an elongate arc extending from the canine to P^2, and is deepest above P^1. It is moderately developed as in M. *agatensis*. Posteriorly, the maxillary root of the zygomatic arc terminates above the posterior lobe of M^2, as in M. *agatensis*. Dorsally, the nasals are slender and terminate midway between C and P^1.

UPPER DENTITION: The incisors of M. *exilis* are not preserved. The canine is small, blunt, transversely flattened, and recurved posterolingually. It is approximately the same size as the canine of M. *agatensis*, but is situated more anteriorly.

P^1 is laterally compressed and elongate and contrasts markedly with that of M. *agatensis*. It consists of a central swollen paracone with elongate anterior and posterior ridges terminating in slight swelling at each end of the tooth. The roots are strong and widely flared, in contrast to the closely appressed roots of M. *agatensis*.

P^{2-4} of M. *exilis* closely resemble those of M. *agatensis*. P^2 is elongate with a central, basally swollen paraconid. A short anterior ridge connects the paracone with a prominent parastyle that is stronger than that of M. *agatensis*. A longer posterior ridge terminates in a slightly swollen metacone. The buccal sulci are relatively shallow. The lingual cingulum is more strongly developed, especially anteriorly and posteriorly, than that of M. *agatensis*. Medially, the cingulum is very weak as in M. *agatensis*.

As in M. *agatensis*, P^3 possesses a strong

central paracone, separated by a deep buccal sulcus from a buccally inflated prominent parastyle. A shallower posterior sulcus separates the metacone from the paracone. P^4 lingual cingulum is also more strongly developed on M. *exilis*, and the anterior and posterior parts are separated by a narrow groove, in contrast to the wider valley in M. *agatensis*.

P^4 of M. *exilis* differs chiefly from that of M. *agatensis* in possessing a more angular mesial crescent, consisting chiefly of the protocone. There is no trace of a metaconule, which on M. *agatensis* is relatively strong.

Although more highly worn, the molars of M. *exilis* are obviously more brachyodont and less anteroposteriorly expanded than those of M. *agatensis*. The paracone and metacone ribs on M^2 and M^3, and apparently those also of the highly worn M^1, are more strongly developed than in M. *agatensis*. The ribs, which are relatively narrow in M. *agatensis*, are slightly higher and occupy a wider area on the paracone and metacone of M. *exilis*, and the mesostyle on M^2 and M^3 is also higher and slightly wider on M. *exilis*. As in M. *agatensis*, the parastyle is prominent and the metastyle weak.

LOWER DENTITION: Matthew and Mac-

TABLE 7

Measurements (in Millimeters) of the Upper Dentition of the type (AMNH 12997) of *Michenia exilis* (Matthew)

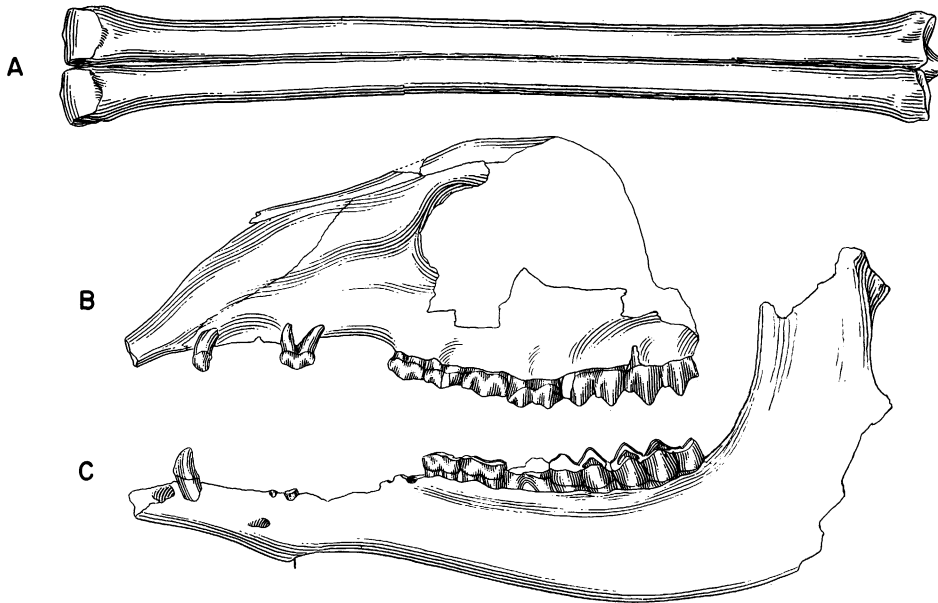|	
Palatal width between P^2	20.7
Palatal width narrowest part of rostrum	14.4
C-P^1 diastema length	18.7
P^{1-2} diastema length	20.0
Upper canine length	4.7
P^1 length	8.8
P^2 length	10.2
P^2 width	4.4
P^3 length	10.9
P^3 width	5.9
P^4 length	12.0
P^4 width	9.5
M^1 length	14.5
M^1 width	14.9
M^2 length	(16.)
M^2 width	15.6
M^3 length	17.9
M^3 width	14.7
M^{1-3} length	51.5

FIG. 10. A-C. *Michenia exilis* (Matthew), type, AMNH 12997, from the Rosebud Formation (Hemingfordian), South Dakota. A. Metatarsus, anterior view. B. Lateral view, reversed. C. Lateral view. All X½.

donald (1960, pp. 2-3) noted that the canine was moderately compressed and situated close behind the incisors. In these features and its relatively small size and lingual curvature, the canine compares favorably with that of *M. agatensis*.

Only the roots of P_1 are preserved; they are strong and separated, and more closely resemble those of the referred specimen of *M. agatensis*, (F:AM 14259), than the type. The broken P_2 is two rooted. P_3 possesses a large, central protoconid, and a strong lingually inflected paraconid. A posterolingual valley separates the buccally swollen hypoconid from the short, posterolingually directed entoconid. The entoconid is slightly more strongly developed than in *M. agatensis*. A minute tubercle is situated on the posterobuccal margin of the hypoconid. P_4 is similar to that of *M. agatensis*, having a strongly inflected paraconid, and a strong hypoconid and entoconid which unite during wear to form a small posterior fossettid.

Like the upper molars, the lower molars of *M. exilis* are brachyodont and anteroposteriorly short. In *M. exilis*, the length of the premolar row is approximately 61 percent of the length of the molar row; due to the anteroposterior expansion of the molars on *M. agatensis*, the premolar row length averages only 46.5 percent the molar row length. Extreme wear has eliminated most of the morphological details of the molars of *M. exilis*. On M_3 however, the lingual ribs are relatively stronger and wider than on *M. agatensis*.

MANDIBLE: The mandible of *M. exilis* is nearly identical with that of *M. agatensis*. As in *M. agatensis* the symphysis is dorsoventrally shallow and forms a low angle with the horizontal body of the ramus. The depth of the ramus between P_1 and P_2 is slightly less than in *M. agatensis*. The dorsal border of the ramus anterior to P_2 forms a sharp ridge, as in *M. agatensis*. Despite the more brachyodont teeth, the depth of the ramus below M_3 is the same as in *M. agatensis*. The condyle and angular process of the mandible in *M. exilis* are approximately the same height above the tooth row as in *M. agatensis*.

LIMBS: The metapodials are subequal in length, and contrast with those of *M. agatensis* in being relatively stouter and unfused. Metacarpals II and V are less strongly coossified,

and metacarpal V is slightly larger, in *M. exilis*. Metatarsals II and V are fully coossified. In contrast to *M. agatensis*, metatarsal II of *M. exilis* presents a proportionally smaller surface for articulation with the entocuneiform, and this surface slopes posteriorly at a higher angle than the nearly horizontal surface of *M. agatensis*. The shaft of the proximal phalanx is relatively stouter than that of *M. agatensis*. The dorsal surface of the shaft exhibits a slight convexity near the distal articular surface, in contrast to the straight dorsal surface in *M. agatensis*. The distal articular surface possesses a deeper groove on the anterodorsal surface, and this surface is less anterodorsally expanded, than in *M. agatensis*. Ventrally, the trochleae are more knoblike and asymetrical than in *M. agatensis*.

DISCUSSION: *Michenia exilis* was previously referred to *Oxydactylus* on the basis of brachyodont molars and uncoossified metapodials. In the discussion of the species, however, Matthew and Macdonald (1960, p. 4) expressed some uncertainty as to the validity of the generic assignment, stating, "It is questionable whether this lack of coössification may be considered as a generic character of *Oxydactylus* in spite of the fact that it is often given this distinction."

The elongate, narrow rostrum with a moderately developed buccinator fossa, incisiform up-

per canine, small, laterally compressed lower canine, and slender ramus with shallow symphysis, all clearly ally this species with *Michenia*. The brachyodont molars, unfused metapodials and the primitive features of the phalanges are merely primitive characters that were retained after the acquisition of derived features characteristic of *Michenia*. The inclusion of *exilis* in *Michenia* broadens the previous definition of this genus. It does not, however, warrant the creation of a new genus, because some specimens in the F:AM collection, although differing somewhat from *Michenia exilis* and *M. agatensis* in rostral morphology, exhibit a morphologically intermediate stage of brachyodont molars and weakly coossified metapodials.

Stevens (1977, p. 48, fig. 15) described a new species, *?Michenia australis* from the Delaho Formation in Texas and compared it with *Michenia* and *Miotylopus* but failed to compare it with *Oxydactylus exilis* Matthew. The species is based on the type mandible (40871-1) with an associated upper molar and limb fragments. Referred dentitions include two additional mandibles and an upper cheek tooth series (40693-24, fig. 15A) which she stated, "are of appropriate size for the holotypic and referred jaws." Stevens (1977, p. 49) stated that *?Michenia australis* "Differs from *Michenia agatensis* by its smaller size, more prominent molar styles and ribs, and unfused metacarpal." These are the same characters that distinguish *M. exilis* (Matthew) from *M. agatensis*. In addition, the type (40871-1) of *?Michenia australis* includes a partial phalanx that was figured by Stevens (1977, fig. 15D). The distal end of the phalanx is also morphologically similar to that of *M. exilis* and differs from that of *M. agatensis* in that the distal articular surface is more grooved and less anteriorly extended. The dentition of *?M. australis* is slightly smaller than that of *M. exilis* but judging by the size range in other samples of *Michenia* in the F:AM collection, it is within the range of a single taxon. The age of the Castolon local fauna from the Delaho Formation is considered by Stevens (1977, p. 62) to be early late Arikareean which antedates the early Hemingfordian age of *M. exilis*. Because the type and referred material of *?Michenia*

TABLE 8

Measurements (in Millimeters) of the Mandible and Lower Dentition of the type (AMNH 12997) of *Michenia exilis* (Matthew)

Depth jaw between P_1 and P_2	(12.6)
Depth jaw at P_1	16.5
Depth jaw below anterior moiety of M_3	29.7
P_{1-2} diastema	(22.7)
P_3 length	10.3
P_3 width	4.3
P_4 length	11.8
P_4 width	6.2
M_1 length	11.6
M_1 width	10.5
M_2 length	16.0
M_2 width	12.0
M_3 length	22.9
M_3 width	11.3
M_{1-3} length	52.4

australis exhibits no morphological differences to distinguish it from *M. exilis*, we are placing it in synonymy with the latter.

Michenia yavapaiensis, new species
Figures 11-12; Tables 9-12

TYPE: F:AM 73380, right partial ramus with symphysis, I_1-I_3, C erupting, P_1 unerupted, and P_3-M_3, from Milk Creek Quarry, about 103 feet above the Manzanita Quarry level, Milk Creek Formation (Clarendonian), Milk Creek area, Yavapai County, Arizona.

KNOWN DISTRIBUTION: Clarendonian of Milk Creek Formation, Milk Creek area, Yavapai County, Arizona.

REFERRED MATERIAL: From the type locality; F:AM 73283, crushed palate with P^1-M^3; F:AM 73287, partial palate with P^2 (erupting)-M^2 and M^3 broken; F:AM 73286, crushed partial skull with P^2(root)-M^3; F:AM 73289, crushed partial palate with P^2 (unerupted)-M^2 and M^3 broken; F:AM 73281, right partial maxilla with P^2-M^3; F:AM 73398, right partial maxilla with P^2-P^3 roots, P^4-M^2 and M^3 broken; F:AM 73288, right partial maxilla with P^2-M^1; F:AM 73382, right ramus with symphysis, I_1-C, P_1 unerupted and P_3(root)-M_3; F:AM 73381, left ramus with symphysis, I_1-I_3 broken, C, P_1 unerupted, P_3-P_4 and M_1-M_3 broken; F:AM 73261, left partial ramus with P_3-M_2 and M_3 broken; F:AM 73256, left partial ramus with P_3 (broken)-M_2 and M_3 broken; F:AM 73262, left partial ramus with P_3-M_2; F:AM 73271A, left partial ramus with P_4 root, M_1 alveolus and M_2-M_3; F:AM 73407, symphysis with I_1-C all broken; F:AM 99613, symphysis with I_1-I_2 alveoli and I_3-C broken; and F:AM 73262, symphysis with I_1 alveolus and I_2-C broken.

Manzanita Quarry, 10 feet below Goldie's Honeypot Quarry, Milk Creek Formation (Clarendonian), Milk Creek area, Yavapai County, Arizona: F:AM 73297, right partial maxilla with M^1-M^2; F:AM 73397, right and left partial maxillae with P^2-M^2 and M^3 broken; F:AM 73395, right partial maxilla with P^3-M^3; F:AM 73407, right detached M^2 and M^3; F:AM 73257, right partial maxilla with P^2-M^1 and M^2 broken; F:AM 73294, left partial maxilla with P^2-M^2; F:AM 73370, partial mandible with I_2

(root)-C, P_1 unerupted and P_2-M_3, incomplete metacarpus, broken calcaneum, metatarsus and first and second phalanges; F:AM 73373, mandible with I_1-C, P_1 unerupted and P_2-M_3; F:AM 73360, right partial ramus with P_1 unerupted and P_3-M_3; F:AM 73363, partial mandible with I_1 (alveolus)-I_3, C alveolus, P_1 unerupted and P_3-M_3; F:AM 73254, right partial ramus with P_3-M_3; F:AM 73372, right partial ramus with P_2-M_3 (P_3 and M_3 broken); F:AM 73362, right partial ramus with P_3-M_3; F:AM 73364, right partial ramus with P_3-M_3 (P_4, M_1 and M_3 broken); F:AM 73253, left partial ramus with P_3-M_3 broken; F:AM 73361, right partial ramus with P_3-M_3; F:AM 73371, left partial ramus with P_2-M_3 (P_3 broken); F:AM 99616, right partial ramus with P_4-M_1 and M_2-M_3 broken; F:AM 73365, right partial ramus with incomplete symphysis, I_1-C roots, P_1 unerupted, P_3-M_2 and M_3 broken; F:AM 99618, right partial ramus with P_2-M_3 all broken; F:AM 73259, right partial ramus with P_3 (root)-M_2 and M_3 broken; F:AM 73407, right partial ramus with M_1-M_3 all broken; F:AM 99614, right ramal fragment with M_2 (broken)-M_3; F:AM 73399, left immature partial maxilla with dP^4-M^2 broken germ, and possibly associated with F:AM 73399A, right metacarpus and F:AM 73399B, right tibia, astragalus, calcaneum, tarsals, right metatarsus and first to third phalanges; F:AM 73338, right immature partial ramus with dP_2 root and dP_3-dP_4 broken; F:AM 73342, left immature ramal fragment with dP_4 and M_1 broken germ; F:AM 73407, left metacarpus; F:AM 73400, right metacarpus; F:AM 73364, right metacarpus; F:AM 73408, right metacarpus; F:AM 73406, right metacarpus; F:AM 99649, left incomplete metacarpus; F:AM 73410, right metatarsus; F:AM 73411, left broken metatarsus; and F:AM 73371, distal end metatarsus.

Shields Ranch Quarry (=Stein Gallery, UALP locality 1-7), Milk Creek Formation, same horizon as Manzanita Quarry (Clarendonian), Milk Creek area, Yavapai County, Arizona: F:AM 73393, right maxilla with P^2-M^2 and M^3 broken; F:AM 73396, right partial maxilla with P^2-M^3; F:AM 73394, left partial maxilla with M^1 (broken) -M^3; F:AM 73367, left ramus with P_3-M_3; F:AM 73387, left partial ramus with C root and P_3-M_2; F:AM 73260,

left partial ramus with P_3-M_2 and M_3 broken; F:AM 99611, left partial ramus with incomplete symphysis, P_4 (erupting)-M_1 and M_2 broken; F:AM 99653, right partial ramus with symphysis, I_1-I_2 alveoli, I_3 root, C alveolus, and P_3 (root)-M_2; F:AM 99617, left partial ramus with broken symphysis, P_4-M_2 broken; F:AM 99608, immature mandible with I_1-C erupting and P_4-M_2 and M_3 erupting; F:AM 99609, right immature ramus with broken symphysis and dP_3-M_2; F:AM 73340, left immature partial ramus with dP_3 (alveolus)-M_2; F:AM 99610, left immature partial ramus with dP_4; F:AM 73340, incomplete symphysis with both I_1s erupting; F:AM 73324, right metacarpus; F:AM 73409, right metacarpus; F:AM 73325, left metatarsus; UALP 9389, right partial dentary with P_3 (roots), P_4 (broken), M_1 (broken) and M_2-M_3; UALP 5662, right maxillary with P^2-P^4 and M^1-M^3; UALP 9442, right partial ramus with P_3-P_4 (roots), M_1 (broken), M_2 and M_3 (broken); UALP 9406, left metatarsal; UALP 9407, right metatarsal; UALP 9408, left metatarsal; UALP 9409, distal metapodial; UALP 9410, distal metapodial; UALP 9412, right calcaneum, left distal humerus; UALP 9413, proximal phalanx; UALP 9414, distal metapodial; UALP 9415, right astragalus; UALP 9416, left articulated metatarsal, astragalus, calcaneum, tibia, cuboid and 2 proximal phalanges; UALP 3629, left astragalus; UALP 9417, left astragalus; UALP 9418, right cuboid and calcaneum; and UALP 9419, left proximal radius-ulna.

Trail Prospect, (same horizon as Shields Ranch Quarry), Milk Creek Formation (Clarendonian), Milk Creek area, Yavapai County, Arizona: F:AM 73279, right partial ramus with P_2-M_3, and F:AM 73405, left metatarsus.

Goldie's Honeypot Quarry (UALP locality 7498), Milk Creek Formation, 10 feet above Shields Ranch horizon, Milk Creek area, Yavapai County, Arizona: UALP 9038, left M^1 and left M_3; UALP 9037, right M^2-M^3; UALP 9039, left P^3 and left M^2; UALP 9035, palate with P^2-P^4 and M^1-M^2; UALP 9027, left partial dentary with P_3 (roots), P_4 (broken), and M_1-M_3; UALP 9036, left P^4 and left M^1-M^2; UALP 9026, right partial dentary with M_2-M_3; UALP 9031, right partial maxillary with P^4 and M^1-

M^2; UALP 9028, right partial maxillary with P^4 (broken), M^1-M^2 and M^3 (broken); UALP 9029, right partial dentary with M_2 (roots) and M_3; and UALP 9109, right metatarsal.

Deep Spring Quarry (=Johny Post, UALP locality 1-1a), about 69 feet above Manzanita Quarry and 34 feet below Milk Creek Quarry, Milk Creek Formation (Clarendonian), Milk Creek area, Yavapai County, Arizona: F:AM 99615, left premaxilla-maxilla fragment with C-P^1; and UALP 9373, left astragalus.

The stratigraphic positions of the following University of Arizona quarries are unknown.

North Fossil Ridge, UALP locality 1-6: UALP 9435, left proximal metacarpal; UALP 9436, left and right proximal radius-ulna; UALP 9437, right distal humerus; and UALP 9390, palate with P^2-P^4 and M^1-M^2.

Creek Bottom, UALP locality 1-4: UALP 9388, left partial dentary and symphysis with C (broken), P_1 (alveolus), P_3 (alveolus), P_4, M_1-M_2, M_3 (broken); UALP 9441, partial palate with M^2-M^3; UALP 9420, left metatarsal, and UALP 9421, left metacarpal.

Material from Milk Creek with no data: UALP 9439, right M_2-M_3; UALP 9124, right distal tibia; UALP 9116, right astragalus.

DIAGNOSIS: Differs from *M. exilis* in P^1 less elongate with more closely appressed roots; P^2 relatively smaller with single prominent cusp; P^{3-4} more reduced with smaller parastyles; P_1 suppressed; P_2 relatively smaller or absent; P_{3-4} smaller; molars taller crowned with weaker ribs, styles, and stylids; M_3^3 more elongate; metapodials fused with metacarpus shorter than metatarsus; and first phalanx longer with distal articular surface less grooved and more anteriorly produced.

Differs from *Michenia agatensis* in I^{1-2} frequently lost in adult; I_{1-3} higher crowned; P^2 relatively smaller with a single prominent cusp; P^{3-4} more reduced with smaller parastyles; P_1 suppressed; P_2 relatively smaller or absent; P_{3-4} smaller; molars higher crowned, with weaker ribs, styles, and stylids; M_3^3 more elongate; ramus deeper beneath cheek teeth with deeper mandibular angle; and metapodials shorter, stockier, and more strongly fused.

DESCRIPTION AND COMPARISON: Upper Dentition: No complete skulls are known and only

one rostrum of *Michenia yavapaiensis* is recognized in the Milk Creek collection. The rostrum (F:AM 73287) is long and slender, 12.4 mm. in width at the narrowest point behind P¹. In the type of *M. agatensis* the rostrum is slightly crushed and the narrowest point of the rostrum measures approximately 12.0 mm. The rostral flare between the I³s cannot be determined in the Milk Creek specimen.

An I³ alveolus is present in F:AM 73287. Anterior to the alveolus of I³ are small depressions, for the healed alveoli of I¹ and I². Thus these two teeth are occasionally present in adults. Other individuals of *Michenia* in the F:AM collection also exhibit the loss of I¹ and I². Although small, these incisors are present in *M. agatensis*. Judging by the size of alveolus, I³ of *Michenia yavapaiensis* is smaller than that of *M. agatensis*. The canine of *Michenia yavapaiensis* is small, blunt, and transversely compressed, and near the size of that of *M. agatensis*. Both the mesial and lateral surfaces are equally convex; in *M. agatensis* the lateral surface is more convex than the mesial.

A 12.0 mm. diastema separates the canine

and P¹ (F:AM 99615) in *Michenia yavapaiensis*. P¹ is single cusped and more caniniform than its double-rooted counterpart in *M. agatensis*. The length of P¹⁻² diastema ranges from 26.0 to 30.5 mm. and is longer than that (17.3 mm.) of the type of *M. agatensis*.

P²⁻⁴ are smaller than those of *M. agatensis*. P² is double rooted, though in some specimens (particularly from the Shields Ranch Quarry, F:AM 73393, 73396), the roots are very closely appressed or even fused, whereas in *M. agatensis* P² roots are more widely flaring. P² in *M. yavapaiensis* is shorter and simpler than that of *M. agatensis*. It has a buccally swollen paracone and differs from that of *M. agatensis* in lacking a parastyle. A crest runs posterobuccally from the paracone and terminates in a slight swelling (metacone). The metacone is buccally inflected and separated from the paracone by a strong buccal groove. Lingually, a weak basal cingulum extends posteriorly from the paracone to the base of the metacone.

P³ is relatively shorter than in *M. agatensis*, and consists primarily of a central paracone connected to a buccally inflected metacone.

TABLE 9

Measurements (in Millimeters) and Statistics of the Upper Dentition of *Michenia yavapaiensis*, new species from Milk Creek, Arizona

	N	OR	X	S	V
I³-C diastema length	1	13.2	—	—	—
C-P¹ diastema length	1	12.6	—	—	—
P¹-P² diastema length	1	30.2	—	—	—
Upper canine length	1	4.7	—	—	—
P¹ length	2	4.6-4.7	4.65	—	—
P² length	10	6.5-9.2	7.68	1.064	13.850
P² width	9	3.4-5.1	4.35	0.507	11.658
P³ length	15	8.3-12.1	10.48	1.003	9.569
P³ width	13	6.1-7.5	6.7	0.427	6.368
P⁴ length	16	10.0-13.9	11.38	0.908	7.977
P⁴ width	15	9.7-11.2	10.19	0.420	4.120
M¹ length	18	13.3-20.3	16.59	2.016	12.155
M¹ width	20	14.7-18.4	16.46	0.940	5.711
M² length	22	20.0-27.9	24.42	2.309	9.455
M² width	22	13.6-20.7	16.57	1.747	10.544
M³ length	12	23.2-33.4	28.56	2.778	9.725
M³ width	10	13.0-18.5	15.62	1.835	11.750
P²-P⁴ length	9	26.8-32.9	29.26	7.636	2.230
M¹-M³ length	9	60.5-82.8	71.07	6.920	9.743
P²-M³ length	5	84.4-109.2	95.74	9.509	9.932

These cusps are separated by a deep buccal groove. A crest runs anteriorly from the paracone to a vestigial parastyle which may be obliterated in early wear. The paracone is greatly swollen and confluent with the parastyle; no buccal groove separates the paracone and parastyle as in *M. agatensis*. Lingual cingula extend from the parastyle and metacone to enclose anterior and posterior fossettes in little worn teeth. The anterolingual and posterolingual cingula do not generally meet, and are less distinct and without the tiny cuspules seen on *M. agatensis*.

P^4 is only slightly shorter than in *M. agatensis*. The paracone is well developed, but the parastyle is much smaller than that of *M. agatensis*. The metastyle, when present, is only weakly expressed. The protocone is prominent, but the metaconule is represented by only a posterior elongation of the protocone or a weak posterolingual crest.

The molars of *M. yavapaiensis* are taller crowned than those of *M. agatensis*, and M^3 is especially more anteroposteriorly elongate. M^1 exhibits a strong mesostyle and weak parastyle; the metastyle is faintly indicated on only a few specimens, and a faint rib may be present on the paracone. In *M. agatensis* M^1 has ribs on both paracone and metacone, and the paracone rib is relatively stronger than in *M. yavapaiensis*. Both the parastyle and the mesostyle are usually stronger in *M. agatensis*. M^2 and M^3 of *M. yavapaiensis* possess strong parastyles and mesostyles, and M^3 also has a strong metastyle. Faint ribs are present on the paracone and metacone of both molars with the paracone rib being the stronger. Compared to *M. yavapaiensis*, *M. agatensis* has much stronger vertical ribs and styles on M^2 and M^3.

P^{2-4} length in *M. yavapaiensis* is shorter relative to M^{1-3} length than in *M. agatensis*. This is due both to the reduction in the size of the premolars and the elongation of M^3. For example, in *M. agatensis* P^{2-3} length is equal to or slightly greater than M^3 length; in contrast, P^{2-3} length in *M. yavapaiensis* is only slightly greater than one-half M^3 length.

LOWER DENTITION: The incisors of *M. yavapaiensis* are taller crowned and in early wear are more vertically oriented and less procumbent than those of *M. agatensis*. Little

worn incisors are spatulate, but with wear I_1 and I_2 become more triangular in cross section, with the transverse width equaling or exceeding the anteroposterior length. I_3 remains spatulate even in late wear.

A very short diastema separates the canine from I_3. The small, recurved canine is near the size of that of *M. agatensis*. It is transversely compressed with the buccal surface slightly more convex than the lingual surface.

P_1 of *M. yavapaiensis* is nearly always suppressed, in contrast, to that of *M. agatensis* which is fully erupted. At its maximum development P_1 approximates the size of P_1 in the type specimen of *M. agatensis*. P_1 of *M. yavapaiensis* possesses a prominent central cusp from which anterior and posterior crests extend to terminate in vestigal cuspules; P_1 is never elongate as in the referred jaw of *M. agatensis* (F:AM 14259). Many of the jaws of *M. yavapaiensis* have never been opened to expose the unerupted P_1. However, P_1s that are exposed show that the roots are fused and the tooth is oriented in any position from horizontal to upright. The suppressed P_1 is situated either directly above, or above and slightly anterior to the mental foramen.

P_2 in *M. yavapaiensis* is extremely variable; it may be erupted, suppressed, or absent. When P_2 is present, it is usually peglike, and single rooted; it is sometimes vestigial. In contrast, P_2 of *M. agatensis* is double rooted and elongate with three well-defined cusps. P_2 of *M. yavapaiensis* consists of only a protoconid; the paraconid and entoconid, which are present in *M. agatensis*, are absent. Most jaws referred to *Michenia yavapaiensis* lack an erupted P_2. Six jaws without an erupted P_2 were excavated to determine if this tooth was suppressed; in only one jaw (F:AM 73305) was P_2 found. From this small sample it appears that P_2 is more frequently absent than suppressed. Most specimens with erupted P_2s come from stratigraphically lower quarries, in which the individuals also average slightly smaller. However, within the same stratigraphic horizon, no relationship was observed between the size of the animal and eruption or noneruption of P_2.

P_3 in *M. yavapaiensis* is double rooted, but shorter and simpler than that of *M. agatensis*.

TABLE 10

Measurements (in Millimeters) and Statistics of the Lower Dentition of *Michenia yavapaiensis*, new species from Milk Creek, Arizona

	N	OR	X	S	V
Depth jaw between P_1 and P_2	23	13.3-19.1	16.64	1.142	6.863
Depth jaw at P_1	13	16.1-20.7	17.77	1.420	7.993
Lower canine length	6	4.9- 6.0	5.50	0.400	7.272
P_2 length	5	4.1- 5.7	4.82	0.691	14.328
P_2 width	4	2.8- 3.0	2.90	0.115	3.982
P_3 length	21	6.1- 9.2	8.44	0.776	9.186
P_3 width	20	2.5- 5.6	4.24	0.608	14.345
P_4 length	30	8.8-12.9	10.30	0.883	8.570
P_4 width	27	4.6- 7.0	5.95	0.563	9.457
M_1 length	29	15.6-18.9	16.13	1.429	8.866
M_1 width	23	9.7-11.9	10.76	0.704	6.542
M_2 length	31	18.5-24.8	21.39	1.495	6.989
M_2 width	26	11.6-14.5	12.68	7.861	6.190
M_3 length	24	28.7-37.3	32.86	2.260	6.879
M_3 width	21	9.9-13.8	11.85	0.962	8.114
P_3-P_4 length	18	16.2-20.5	18.28	1.129	6.173
M_1-M_3 length	17	64.7-88.8	72.78	5.939	8.159
P_2-M_3 or P_3-M_3 length	14	82.1-97.4	89.60	3.854	4.301
Postcanine diastema length	9	45.6-83.1	57.21	11.909	20.817

In early wear P_3 possesses a central protoconid that is less swollen than in *M. agatensis*. Anteriorly, a crest extends to a diminutive, lingually inflected paraconid; this cusp is much smaller and less inflected than in *M. agatensis*. A second crest from the protoconid extends posteriorly and divides to join with a small entoconid and a slightly larger hypoconid. The entoconid and hypoconid do not unite to form a fossettid as in P_4, but are separated by a lingual groove which does not quite reach the base of the tooth.

P_4 in *M. yavapaiensis* is generally shorter than that of *M. agatensis* with the paraconid strongly inflected lingually but smaller than in *M. agatensis*. The protoconid is less bulbous than in *M. agatensis*, and P_4 is widest across the entoconid and hypoconid, which unite to form a fossettid.

The molars of *M. yavapaiensis* are higher crowned and M_3 more elongate than in *M. agatensis*. Furthermore, the premolars are smaller relative to the size of the elongate molars than in *M. agatensis*. Although the smallest Milk Creek molars are no longer than those of *M. agatensis*, the crown height is always

greater than in the latter. For example, the crown height of the second lobe of M_3 (F:AM 73386) in *M. yavapaiensis* measures 34.0 mm. M_3s of *M. agatensis* (AMNH 14255 and AMNH 14259) are less worn, yet the crown heights of the second lobes measure only 24.2 and 23.8 mm., respectively. The lingual walls of the molars in *M. yavapaiensis* have small stylids and ribs, and are thus smoother than in *M. agatensis*. In early wear, M_1 and M_2 possess a small entostylid. The parastylid and metastylid are also present only as small swellings in early wear. Lingual ribs are absent or extremely faint. In *M. agatensis* the lingual ribs and stylids are usually much stronger; however the metastylid and entostylid are reduced in one referred jaw (AMNH 14259). As in *M. agatensis*, the hypoconulid broadens near the base of M_3; thus with wear the occlusal surface changes from an angular crescent to a rounded teardrop shape. Well worn M_3s of *M. yavapaiensis* have very flat lingual walls, and the molars are generally broader than those of *M. agatensis*.

MANDIBLE: The mandible of *M. yavapaiensis* resembles that of *M. agatensis*, with the symphysis slender dorsoventrally and narrow
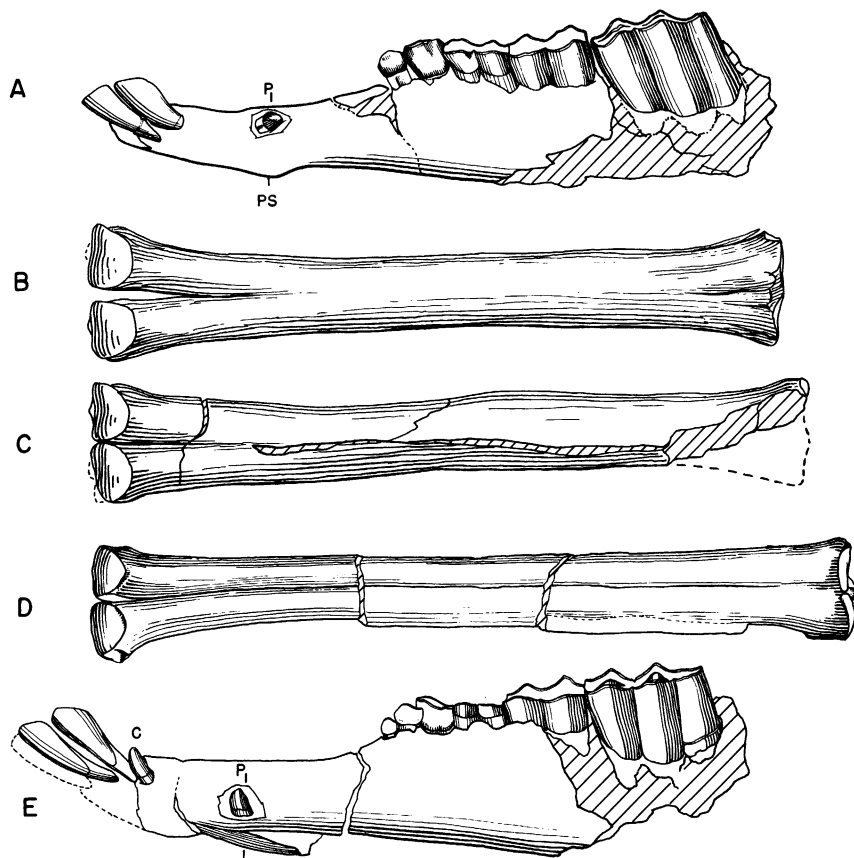
FIG. 11. A-E. *Michenia yavapaiensis* from the Clarendonian of Arizona. A. F:AM 73363, from Manzanita Quarry, lateral view, reversed. B. F:AM 73405, from Trail Prospect, metatarsus, anterior view. C-E. F:AM 73370, from Manzanita Quarry. C. Restored metacarpus, anterior view. D. Metatarsus, anterior view. E. Lateral view. All X½.

transversely, and the width narrowest between the C and P_1. As in *M. agatensis*, the symphysis is only slightly inclined from the horizontal. The posterior border of the symphysis lies between the mental foramina. Due to the suppression of P_1 and the small size of P_{2-4}, the postcanine diastema is much longer in *M. yavapaiensis*. Between the suppressed P_1 and P_3, the ramus is exceedingly slender, with the shallowest depth slightly posterior to P_1. Because of the taller crowned teeth, the depth of the horizontal ramus posterior to P_3 is greater in *M. yavapaiensis*, and the mandibular angle is also deeper.

DECIDUOUS DENTITION: The deciduous teeth of *M. agatensis* are unknown. Aside from

smaller size, there is little to distinguish the lower deciduous teeth of *M. yavapaiensis* from those of *Protolabis coartatus*. The most reliable means for separating the deciduous dentition of *M. yavapaiensis* from that of *P. coartatus* is by the smaller size of the erupting molars.

No specimens of *M. yavapaiensis* have dP_2, but on two specimens (F:AM 73338 and 73340), the alveoli indicate a small tooth with fused roots. A very worn dP_3 consists of a central primary cusp, a lingually inflected anterior crest, and a posterior cusp formed from the hypoconid and entoconid. DP_4 is shorter than that of *P. coartatus*, and has a weakly developed parastylid and entostylid on the flat lingual wall. Lingual ribs are faint.
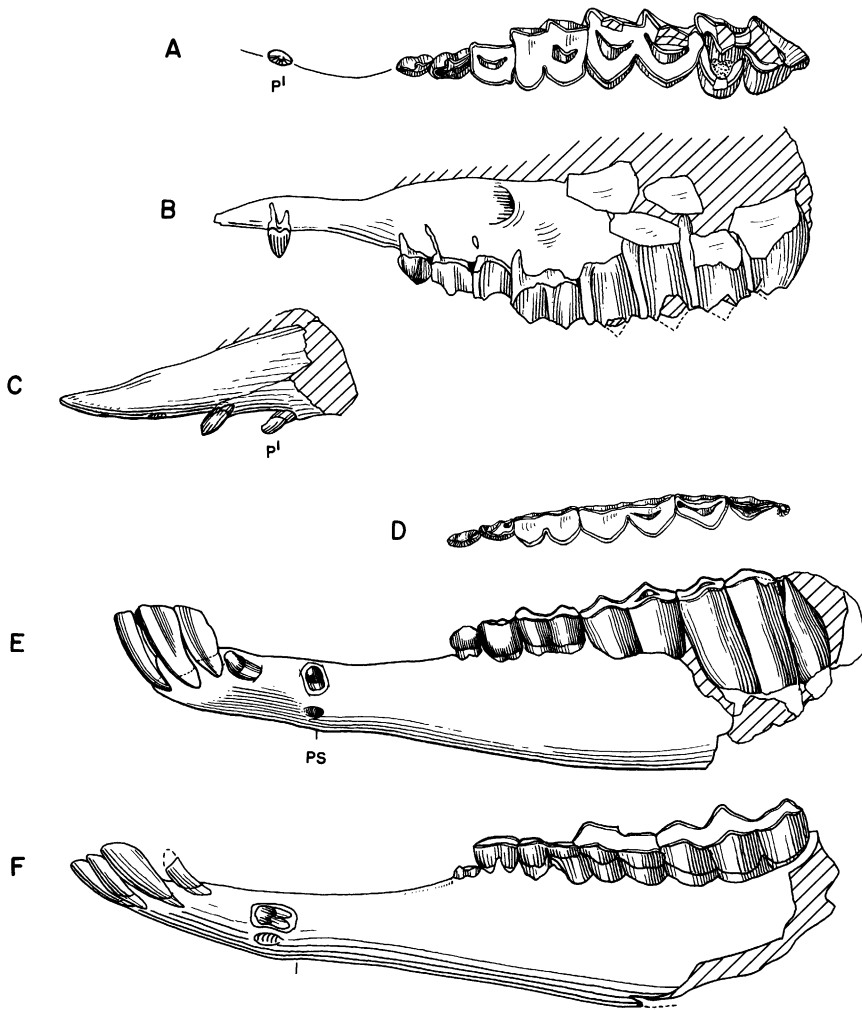
FIG. 12. A-F. *Michenia yavapaiensis* from the Clarendonian of Arizona. A-B. F:AM 73283, from Milk Creek Quarry. A. Occlusal view. B. Lateral view. C. F:AM 99615, from Deep Spring Quarry, lateral view, reversed. D-F. From Milk Creek Quarry. D-E. F:AM 73380. D. Occlusal view, reversed. E. Lateral view, reversed. F. F:AM 73382, lateral view, reversed. All X½.

POSTCRANIA: The metapodials of *M. yavapaiensis* are shorter than those of *M. agatensis*. However, there is not a corresponding slenderness in the width of the shaft, and the metapodials are stockier than those of *M. agatensis*. The metapodials are also more strongly fused in *M. yavapaiensis*, and the distal separation does not extend so far proximally as in *M. agatensis*. The other postcranial elements of *M. yavapaiensis* generally average slightly smaller than those of *M. agatensis*. Comparative measurements and statistics are given in table 11.

DISCUSSION: As noted above, the derived features of *M. yavapaiensis*, coupled with the primitive features of *M. exilis*, have necessitated a revision of the original diagnosis for *Michenia*. In view of the differences between *M. agatensis*, the genotypic species, and *M. yavapaiensis*, some question may arise as to the generic assignment of the new Clarendonian

TABLE 11

Measurements (in Millimeters) and Statistics of Referred Metapodials of *Michenia yavapaiensis*, new species from Milk Creek, Arizona

	N	OR	X	S	V
Metacarpal length	9	182.1-196.7	191.07	5.380	2.815
Metacarpal proximal width	9	27.5- 32.0	29.82	1.527	5.1206
Metacarpal shaft narrowest transverse width	10	14.2- 19.2	16.39	1.631	9.952
Metatarsal length	6	192.3-202.0	198.08	1.9097	3.782
Metatarsal proximal width	12	21.7- 28.0	24.52	1.564	6.379
Metatarsal shaft narrowest transverse width	9	11.3- 15.2	13.42	1.131	8.430

taxon to *Michenia*. But after observing the transformation of characters from *M. agatensis* to *M. yavapaiensis* in the undescribed samples in the F:AM collection, it is evident that the new species is *Michenia*. As pointed out in the description and comparison the morphological features that distinguish *M. yavapaiensis* are shared to a degree with *M. agatensis* and indicate their relationship. The derived features of *M. yavapaiensis* are an exaggeration of the character trends first seen in *M. exilis* and *M. agatensis*. The transformation of these characters from primitive to derived is in general accord with the temporal sequence of undescribed samples in the F:AM collection.

Because of the several similarities between *Michenia yavapaiensis* and *Protolabis coartatus*, it could be hypothesized that these distinct species are actually sexual variants of the same species. Thus the slender-jawed and slender-limbed *Michenia yavapaiensis* would be the females of *Protolabis coartatus*. This hypothesis is countered by the fact that based on the jaw depth the rami can be easily separated into two groups without any overlap. Correlated with this separation is the nonoverlap in the size of the lower canine between the two groups. Similarly, the metapodials are easily separated into a longer, stocky group and a shorter, slender group. In our opinion, the size and proportional differences between these groups are too great to be attributed to sexual variation. Student's t-tests were run for various dental and skeletal measurements, and the results are given in table 12. The high values of "t" for the majority of cases support the distinctness of the two samples and are considered to be of generic significance. The values of "t" for the upper dentition are somewhat smaller,

due to greater overlap between the two groups. This overlap is partially attributable to the fact that the tapering and curvature of the upper molars makes it impossible to be as rigorous in measuring the lengths and widths of these teeth. This taper and curvature also contributes to the high coefficients of variation for the upper molars in both groups.

TABLE 12

Student's t-test for Dental and Skeletal Measurements of *Protolabis coartatus* and *Michenia yavapaiensis*, new species from Milk Creek, Arizona

Variate	Degrees Freedom	t	P
P^2 length	17	3.2607	.001-.01
P^3 length	29	2.6789	.01-.02
P^4 length	33	2.5463	.01-.02
M^1 length	32	2.3329	.02-.05
M^2 length	43	2.3618	.02-.05
M^3 length	25	4.6835	<.001
P^2-P^4 length	20	1.936	.05-.1
M^1-M^3 length	21	1.8054	.05-.1
P^2-M^3 length	14	2.0451	.05-.1
Lower canine length	20	6.2712	<.001
P_2 length	13	2.4419	.02-.05
P_3 length	43	7.1562	<.001
P_4 length	56	6.108	<.001
M_1 length	53	2.6085	.01-.02
M_2 length	56	4.7524	<.001
M_3 length	47	10.113	<.001
P_3-P_4 length	34	7.608	<.001
M_1-M_3 length	35	4.4263	<.001
P_2-M_3 or P_3-M_3 length	27	7.9347	<.001
Depth jaw between P_1 and P_2	40	18.763	<.001
Depth jaw at P_1	27	12.653	<.001
Metacarpal length	27	7.66	<.001
Metatarsal length	17	7.4704	<.001

SUMMARY OF RELATIONSHIPS

In establishing the Protolabidini as a monophyletic group, we have relied upon cladistic methodology as advocated by Henning (1966). Simply put, we have searched for shared derived (synapomorphic) characters, which unite *Tanymykter*, *Protolabis*, and *Michenia*. We determine the polarity of a character (either primitive or derived) by outgroup comparison. This same comparison and the recognition of shared derived features is the evidence used here to identify the primitive sister taxon to *Protolabis* and *Michenia*, and is the basis for our hypothesis of relationships to the other camelids. We choose to present these relationships by means of a cladogram (fig. 13). We believe that a cladogram represents the most objective expression of our knowledge of these relationships, and in addition forms a testable hypothesis based upon the observed polarity of character states.

The metapodials in the Oromerycinae and Poebrotheriinae (*sensu* Wilson, 1974) are short and unfused with the length of the metacarpus less than that of the metatarsus. In addition, the molars are brachyodont and possess a mesostyle above but lack a metastylid below. Short unfused metapodials with the metacarpus shorter than the metatarsus, and brachyodont molars with mesostyles but lacking metastylids, are considered primitive characters of the Camelidae.

The Aepycamelinae and the Camelinae (point 1) share the apomorphic character of a metastylid on the lower molars. In this feature they differ fundamentally from the oromerycines, poebrotheriines, stenomylines, *Miotylopus* and *Pseudolabis* in which the metastylid is absent. The stenomylines, *Miotylopus* and *Pseudolabis* share a derived feature which is absent in the Aepycamelinae and the Camelinae, namely, a weak to absent mesostyle. The Aepycamelinae and Camelinae retain the primitive condition of a strong mesostyle on the upper molars.

The Aepycamelinae (point 2) comprise a mono-

phyletic group by sharing the following apomorphic characters:
(1) limbs elongate
(2) metapodials longer than the basal length of the skull
(3) cervical vertebrae elongate

The Camelinae (point 3) are united by the following apomorphic characters:
(1) weak buccinator fossa
(2) rostrum elongate

The Protolabidini (point 4) form a monophyletic group and possess the apomorphic characters of:
(1) rostrum narrow
(2) laterally expanded anterior nares

Tanymykter brachyodontus (point 5) is derived in having closely appressed P_1^1 roots.
Protolabis and *Michenia* (point 6) are derived with respect to *Tanymykter brachyodontus* by:
(1) the absence of elongate basioccipital tuberosities
(2) P^2 without strong, continuous lingual cingulum
(3) auditory bulla less inflated with medial plates more compressed
(4) buccinator fossa moderate to strong

Protolabis (branching point 7) possesses the apomorphic characters of:
(1) molars hypsodont
(2) M_3^3 anteroposteriorly elongate
(3) metastylid on lower molars very weak to absent
(4) ventrally produced mandibular angle with weak to strong lateral flare
(5) metapodials fused
(6) first phalanx elongate with distal articular surface anteriorly extended

Protolabis heterodontus (point 8) is primitive in all known characters relative to *Protolabis coartatus*.
Protolabis coartatus (point 9) is distinguished by:
(1) ventral rostral constriction extreme
(2) I^{1-2} usually absent

FIG. 13. Cladogram of proposed relationships within the Protolabidini and an outgroup comparison with the Aepycamelinae and the other members of the Camelinae (Camelini, Camelopini, and Lamini). Characters indicated at the numbered nodes are discussed in the body of the text.

(3) P$^{2-3}$ without parastyle
(4) upper molars with weak ribs
(5) P$_1$ small and occasionally absent
(6) P$_2$ small and usually absent
(7) mandibular angle with extreme lateral flare and mesial shelf

Michenia (point 10) is derived relative to *Protolabis* as follows:
    (1) braincase short

(2) I^3-C/weak, /C small
(3) symphysis shallow
(4) inflection of mandibular angle suppressed

Michenia exilis (point 11) is primitive in all known characters relative to other species of *Michenia*.
Michenia agatensis and *Michenia yavapaiensis*

(point 12) share the following apomorphic characters:

(1) molars anteroposteriorly elongate and hypsodont
(2) P^1 small with roots closely appressed
(3) metapodials fused
(4) first phalanx elongate with distal articular surface less grooved and more anteriorly extended
(5) metapodials slender

Michenia agatensis (point 13) is primitive relative to *M. yavapaiensis*.

Michenia yavapaiensis (point 14) is derived relative to *M. agatensis* by:

(1) I^{1-2} usually absent
(2) P_1 unerupted in adults
(3) P_2 small and generally unerupted or absent
(4) metastylid on lower molars weak to absent
(5) upper and lower molars tall crowned and anteroposteriorly elongate
(6) metapodials short and slender

Webb, (1965, p. 44) recognized the Protolabidini as a tribe of the Camelinae, and suggested that it was ancestral to the other three tribes of the Camelinae. At that time *Protolabis* was the only known member of the tribe. Later (1972, p. 107) he stated that *Protolabis* and *Michenia* "lie at the base of the radiation of the modern camelids." On the basis of our study, we shall briefly examine this hypothesis.

The weak upper and lower canines, highly constricted rostrum, slender metapodials, shallow symphysis, and short braincase are derived features which eliminate *Michenia* as the primitive sister taxon to all later camelids except the Lamini. Undescribed material in the F:AM collection shows a remarkable similarity between the skulls of some *Michenia* and some lamines, in particular those of *Lama* and *Hemiauchenia*. Features held in common between *Michenia* and some lamines include a short skull with retracted nasals, a short, rounded braincase with a weak sagittal crest, relatively large lacrimal vacuities, and rather strong, laterally produced postorbital bars. *Hemiauchenia* and *Lama* both have greater reduction in the number of premolars, a derived feature relative to

Michenia. The mandible of *Hemiauchenia* and *Lama* is relatively slender as is that of *Michenia*, and in addition *Lama* possesses relatively short metapodials, as do some *Michenia*.

There are, however, some important differences between *Michenia* and the lamines. The posterior narial notch consistently extends farther forward on the palatines in the lamines than in *Michenia*. For example, on 16 mature (M^3 in wear) *Lama* skulls examined in the AMNH (M) collection, the anterior border of the posterior narial notch is opposite the second lobe of M^2, or rarely between M^2 and M^3. On 11 mature *Hemiauchenia* palates, the anterior border of the posterior nares is nearly always opposite the posterior lobe of M^2, except in one case, where it is opposite the valley between the first and second lobes of M^3. On three *Paleolama* specimens, the anterior border is opposite the first or second lobes of M^2. In contrast, on 16 mature specimens of *Michenia* the anterior border of the posterior nares extends no farther forward than the second lobe of M^3, and often is posterior to M^3. We view the anterior extension of the posterior narial notch in the Lamini as the retention of a primitive character state, for it is similarly extended in *Poebrotherium*, *Gentilicamelus*, *Paratylopus primaevus*, *Paralabis*, *Miotylopus*, the Oromeycinae and the Protoceratidae.

Upper molars of *Lama* and *Paleolama*, and to a lesser degree those of *Hemiauchenia*, possess relatively strong ribs and styles and M_3^3 tend to be relatively short. P_4^4 of *Hemiauchenia* are large, unreduced teeth. In the above primitive characters the lamines are similar to *M. exilis* and *M. agatensis*. *Michenia yavapaiensis* and other examples of derived *Michenia* possess weaker ribs and styles on the upper molars, more elongate M_3^3, and reduced P_4^4. These same *Michenia* specimens possess a highly constricted rostrum with a strongly developed buccinator fossa. Although most camelids possess a relatively elongate rostrum showing some narrowing anterior to the cheek teeth, the great narrowing of the rostrum in *Michenia* is surely derived. *Hemiauchenia* possesses a moderately constricted rostrum with a moderately developed fossa in some specimens, whereas other specimens have the maxillary inflated above the rostrum. *Lama* and *Paleolama* show little evidence of the buccinator fossa and have more

strongly inflated maxillaries. The present evidence suggests the derived condition for the lamines is inflated maxillaries, contrasting with the strongly excavated maxillaries of *Michenia*. The lamines also possess sharp, recurved, caniniform I^3 and C/C, which contrast with the weak and generally noncaniniform I^3 and C/C of *Michenia*. A relatively large caniniform I^3 and lower canine occur in *Poebrotherium*, *Gentilicamelus*, *Paratylopus privaevus*, *Paralabis*, *Pseudolabis*, and *Miotylopus*; thus, their small size in *Michenia* is considered a derived feature. The large upper canine of the lamines would, of course, be a derived feature of this group, as would be the laterally compressed, bladelike form of the caniniform teeth. Finally, the metapodials of *Michenia* are short relative to those of *Hemiauchenia*, and those of *M. yavapaiensis* are relatively shorter than those of *M. agatensis*. Although the above differences do not entirely eliminate *Michenia* as the sister group to the Lamini, we believe the character polarities of *Michenia* do suggest that a relationship between the Lamini and derived species of *Michenia* is unlikely, because evolutionary reversals in many characters would be necessary.

Although *Protolabis* most closely resembles *Procamelus* of the later camelines, it exhibits progressive evolutionary specializations not present in *Procamelus*, which makes it highly unlikely that the two are closely related. In *Protolabis*, the subdued angular process (resulting in a small "hook") on the posterior edge of the ascending ramus is a derived feature absent in *Procamelus*. The angular process, which is slightly stronger in primitive *Protolabis* samples, is nearly absent in derived samples. The reduction of the angular process is directly correlated with the posterior and dorsal expansion of the mandibular angle, due, as hypothesized above, to the increased development of the masseteric muscle. The more pronounced angular process (stronger "hook") in *Procamelus* resembles the primitive condition seen in *Poebrotherium*.

Protolabis is also derived relative to *Procamelus*, in possessing a straight to ventrally produced lower border on the mandibular angle. This, along with the dorsal expansion of the angle, provides a greatly increased surface area for the attachment of the masseteric muscle. These changes are associated with the low, weak, coronoid process and reflect increased emphasis on the masseter, and decreased emphasis on the temporalis. These features are evident, though less pronounced, in the primitive samples of *Protolabis*. *Procamelus*, on the other hand, possesses a convex lower border on the mandible and an elongate coronoid process. The elongate coronoid process is a derived feature not exhibited by *Protolabis*, and reflects the increased emphasis placed on the temporalis, an evolutionary trend opposite to that of *Protolabis*.

Protolabis is also derived relative to *Procamelus* in possessing moderate to extreme rostral constriction. This is another progressive character which attains maximum specialization in derived samples of *Protolabis*; however, in primitive samples the width of the muzzle occasionally overlaps that of the narrowest rostra of later *Procamelus*. Interestingly, the relatively wide rostrum of *Procamelus* is also derived, and is correlated with an increase in the size of P^1 and an increase in the palatal distance between the upper canines. Thus, the specializations in each genus are again in opposite directions. The metapodials in primitive samples of *Protolabis* approximate the basal lengths of isolated skulls from the same localities; in derived samples the metapodials are much shorter and approximate the incisive border to orbital distance. Those metapodials contrast markedly with much longer, more robust metapodials of *Procamelus*. The maxillary fossa of derived species of *Protolabis* is often very shallow, and the maxillary fossa of all *Protolabis* contrasts with the more posteriorly extended, pocketlike fossa of *Procamelus*. In *Protolabis* the retention of the rectus capitus ventralis troughs separated by a narrow median ridge is a primitive character, inasmuch as this condition is also present on *Poebrotherium*. However, the derived condition in *Protolabis* is strongly depressed troughs that differ markedly from the weak troughs in *Procamelus*.

The distinguishing features discussed above convince us that a close relationship does not exist between *Procamelus* and *Protolabis*. The

most important differences between these genera involve the masticatory musculature, and the evidence for their divergent specializations is seen in even the most primitive samples of each genus. In view of these differences with *Procamelus*, we think it unlikely that *Protolabis* lies "at the base of the radiation of the modern camelids" (Webb 1972, p. 107).

Tanymykter brachyodontus is more primitive than *Protolabis* in possessing unfused metapodials, brachyodont, unelongate molars, and more inflated bullae. The primitive sister taxa to *Protolabis* and *Procamelus* would presumably possess these characters. *Tanymykter*, however, more closely resembles *Protolabis* in possessing the derived features of strong rostral constriction and lateral expansion of the anterior nares. In addition, the strongly depressed rectus capitus ventralis troughs with a narrow median ridge are features not seen in *Procamelus*. Other similarities include relatively small coronoid and angular processes on the mandible, weak, laterally situated upper incisors, and a dorsoventrally narrow rostrum. Aside from the possession of the primitive characters of unfused metapodials, brachyodont molars, and more inflated bullae, *Tanymykter brachyodontus* is nearly identical with *Pro-*

tolabis and therefore qualifies as the primitive sister taxon. Thus *Oxydactylus*, as previously considered, is a paraphyletic group, consisting of the primitive sister taxa of both the Protolabidini and the Aepycamelinae.

Our cladistic analysis highlights the parallelism so common within the Camelidae, both between closely related genera and between more distantly related groups. For example, recognition of *exilis* as a species of *Michenia* necessitates that fusion of metapodials and development of hypsodonty occurred independently in *Protolabis* and *Michenia*. These genera further paralleled each other in tooth reduction and increased rostral constriction. *Procamelus* and the three "advanced" tribes of the Camelinae (Camelopini, Lamini, and Camelini) paralleled (and of course, sometimes surpassed) the Protolabidini in reduction and loss of anterior teeth, development of digitigrade stance and fusion of metapodials. Similar changes, in various combinations, occur in more distantly related groups, such as the aepycamelines and stenomylines. Such changes occur as convergence in different monophyletic groups, and therefore do not always indicate relationship, but are characteristic of camelid evolution as a whole.

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