30 Camelidae

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INTRODUCTION

The family Camelidae, which includes the living camels, llamas, vicunas, alpacas, and guanacos, first appeared in North America in the middle Eocene (Uintan). They remained an endemic North American group until their late Miocene (late Turolian, = MN13 faunal zone) dispersal to Eurasia and probably Africa (Morales, Soria, and Aguirre, 1980; Moya-Sola and Agusti, 1989; Pickford, Morales, and Soria, 1993, 1995). In the early Pleistocene (Uquian) they spread to South America (Webb, 1974; Marshall et al., 1982). Camelids became extinct in North America during the late Pleistocene when most of that continent's megafauna vanished. Popularly, camels are associated with the deserts of Africa and Asia, but the first 36 million years or so of their fossil record is confined to North America. Restorations two fossil North American camelids are presented in Figure 30.1.

Compared to other herbivores, camelids were relatively rare in the Eocene. In late Chadronian and Orellan rocks, camelid fossils are most abundant in the White River deposits of Colorado and southeastern Wyoming, but are extremely rare in the Dakotas not many miles north, possibly suggesting some latitudinal control of their distribution. During the Miocene they lived over much of North America and are sometimes the most common large herbivore in a fossil fauna. The main radiation of the camelids occurred in the Miocene, starting in the Arikareean Land Mammal age. Their generic diversity was greatest during the Hemingfordian and Barstovian, with a minimum of thirteen genera present; during the late Barstovian, at least twenty species were present. Generic diversity decreased during the late Miocene and Pliocene, although they were still relatively common animals. The last North American camelids were *Camelops hesternus*, *Hemiauchenia macrocephala*, and *Palaeolama mirifica*, which disappeared about 11,000 years ago (Kurtén and Anderson, 1980).

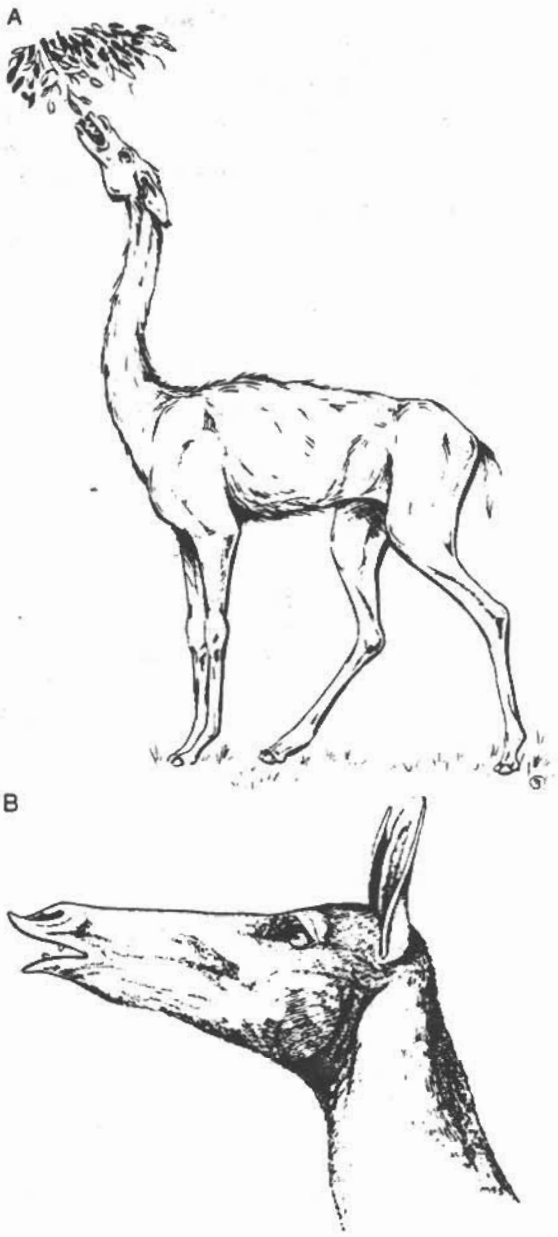

Figure 30.1. Restorations of fossil camelids. A. *Oxydactylus* (by Janet Brown and Brian Regal). B. *Floridatragulus* (by Margaret Stevens).

in Janis, C., K. M. Scott, and L.L. Jacobs (eds.) *Evolution of Tertiary Mammals of North America. Vol. I: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*. Cambridge University Press, Cambridge, 1998.

DEFINING FEATURES OF THE FAMILY CAMELIDAE

CRANIAL

Cranial armament (horns, antlers, ossicones) is lacking (Fig. 30.2). A sagittal crest is present. The rostrum is short to extremely elongate. A lacrimal vacuity is present. A maxillary fossa is usually present and is deeply pocketed in some genera, secondarily reduced in later forms. Primitively, the postorbital bar is incomplete but, except for floridatragulines, is probably complete by the early Miocene. The mastoid portion of the periotic is exposed on the posterodorsal surface of the skull between the exoccipital and squamosal. The tympanic bulla is filled with cancellous bone. The bulla consists of ventrally extended medial and lateral vertical plates that project well below the level of the basioccipital; the deep tympanohyal recess is located anteriorly between the junction of the two plates. A small to large postglenoid process is present. A distinct angular process ("hook") is present on the mandible and may be strongly inflected mesially. The mandibular symphysis is solidly fused.

DENTAL

I1–2 reduced or absent, except in stenomylines and *Miolabis*, where they are large; I3 is present and usually caniniform. The lower incisors are spatulate. The upper and lower canines are always present and usually caniniform; exceptions include some stenomylines where the lower canine is incisiform and *Michenia* where the upper canine is incisiform. The P1/p1 are retained or lost; when retained they become caniniform in derived genera. The P2/p2 and p3 are variably lost in derived genera. The p2–4 are relatively narrow transversely and usually simple, with an anteromedially inflected paraconid and a posterolingual ridge off the protoconid; usually on the p4 and sometimes on p3 the posterolingual ridge and hypoconid enclose a fossettid. Cheek teeth range from brachydont to hypsodont. The upper molars are transversely compressed with straight ectolophs and with fossettes that are closed anteriorly and posteriorly after moderate wear. The upper molars are four cusped, without paraconule and hypocone; the protocone is primitively bifurcated in some *Poebrotherium*. The mesostyle is usually present on the upper molars but may be secondarily lost. Labial ribs on the upper molars are strong to subdued. The lower molars are without a lingual notch between the metaconid and entoconid. Diastemata progressively develop in front of and behind P1/p1 in most groups. The skull and dentition of a common Miocene North American camelid, *Protolabis*, is illustrated in Figure 30.2.

POSTCRANIAL

The neck is elongate to giraffelike (*Aepycamelus*). Neural spines in the anterior cervical vertebrae are low and long. In cervicals 2 through 6, the vertebral artery passes within the pedicle of the neural arch in the anterior half of each vertebra, becoming confluent with the neural canal in the posterior half. The radius and ulna are co-ossified. The fibula is reduced to a small spine that is fused to the proximal part of the tibia, and the distal malleolus articulates with the tibia, astragalus, and calcaneum. In the carpus the trapezoid and magnum are unfused and the trapezium is usually present, although sometimes absent in Recent forms. In the tarsus the ectocuneiform is united with the mesocuneiform, but the navicular and cuboid remain unfused; a distal keel is present on the astragalus. Only metapodials III and IV are functional; II and V are extremely reduced or absent (except possibly in floridatragulids where an elongate metatarsal V splint has been identified in *Aguascalientia*). Metapodials III and IV range from completely unfused (primitive) to solidly fused except at the divergent distal ends (derived), and from extremely short to very elongate. Metatarsals III and IV have flattened dorsal surfaces. The metapodial keels are confined to the posterior surfaces of the distal trochlea. The fibular facet on the calcaneum has a proximal convexity and a dorsal concavity. Primitively, the stance was unguligrade; later genera became digitigrade. Proportions range from sheep or gazelle to giraffe height.

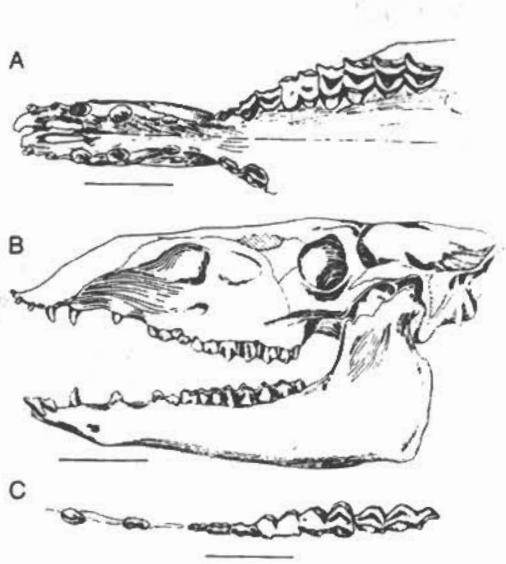

Figure 30.2. *Protolabis heterodontus*, USGS D697, from the Troublesome Formation. A. Palatal view of upper dentition. B. Side view. C. Occlusal view of c, p1–4, m1–3. Scale bar = 5 cm. (Illustration by Marge C. Leggitt.)

SYSTEMATICS

SUPRAFAMILY

Leidy (1847) described *Poebrotherium wilsoni*, the first Tertiary camelid discovered in North America. He considered *Poebrotherium* a genus of Ruminantia (which at that time included the Camelidae) intermediate between *Dorcatherium* and the "pachyderm" *Anoplotherium*. By 1869, however, Leidy had recognized the true affinities of *Poebrotherium* and included it in the Camelidae; in the intervening years *Camelops* and *Procamelus* were described and recognized as camelids by Leidy (1854, 1858). *Floridatragulus* and *Nothokemas* were originally considered hypertragulids (White, 1940, 1947).

The Old World camels and the South American lamines are the only living representatives of the suborder Tylopoda, which is included with its sister group Ruminantia in the Neoselenodontia (Webb and Taylor, 1980). In addition to numerous extinct camelids, we also include the oromerycids, protoceratids, and xiphodonts in the Tylopoda. Oromerycids were early thought to be related to camelids, based on similarities seen with *Poebrotherium* in the skull (particularly the auditory bullae), the dentition, vertebrae, and limbs (with unfused trapezoid and magnum, navicular and cuboid, and the palmar restriction of the metapodial keels). Wortman (1898) considered *Protylopus* directly ancestral to *Poebrotherium*. Matthew (1910) thought *Eotylopus* and *Protylopus* were hypertragulids broadly ancestral to the Tylopoda, although not directly ancestral to *Poebrotherium*. In his 1934 phylogenetic chart of the Artiodactyla, he showed them as basal camelids. Gazin (1955) and Golz (1976), however, viewed oromerycids and camelids as originating separately from dichobunid artiodactyls, and they considered some similarities between the two families as convergent. Most authors have included some or all oromerycids within the Tylopoda, either as members of the family Camelidae (Scott, 1940; 1945; Simpson, 1945; Wilson, 1974; Webb and Taylor, 1980) or as forming a distinct family of their own, Oromerycidae (Stirton, 1967; Patton and Taylor, 1973; Black, 1978; Prothero, 1986).

The Protoceratidae were long considered to be related to the Hypertragulidae (Matthew, 1934; Scott, 1940; Simpson, 1945). Stirton (1967) thought they were closely related to the Camelidae, perhaps with a common ancestor in the Uintan *Leptotragulus*; this hypothesized relationship was based on the retention of an unfused navicular and cuboid, a primitive feature. Patton and Taylor (1973) also listed a number of shared primitive limb features between protoceratids and camelids in support of placement of the Protoceratidae within the Tylopoda and exclusion from the Ruminantia. Webb and Taylor (1980) listed the passage of the vertebral artery through the neural arch pedicles of the cervical vertebrae as a derived feature linking the Protoceratidae and Camelidae; camelids differ, however, in that the vertebral arterial canal becomes confluent with the neural canal in the posterior half of cervicals 3 through 6. Black (1978) presented a contrary view, based almost entirely on analysis of dental characters, and allied the protoceratids with leptomerycids as the sister taxon to the combined agriochoerid-merycoidodontid group.

Xiphodonts have been classified in the Tylopoda by some authors (Matthew, 1929; Simpson, 1945; Webb and Taylor, 1980). Similarities include elongate, slender, dorsally flattened metapodials III and IV, with metapodials II and V extremely reduced; incomplete fibula; shape of mandibular condyle and basioccipital process; long, laterally compressed premolars; and inflated auditory bulla.

INFRAFAMILY

Two early approaches to the classification of North American camelids were presented by Cope (1886) and Hay (1902). Cope, on the one hand, divided genera now included within the Camelidae into three distinct families: Poebrotheriidae to include *Poebrotherium* and "*Gomphotherium*," Protolabididae to include *Protolabis* and a species later placed in *Miolabis*, and Camelidae to include members of the current Camelinae. Hay, on the other hand, included within a broader family Camelidae not only unquestioned true camels, but also *Leptotragulus*, *Hypertragalus*, and the oromerycid *Protylopus*; later (1930), however, Hay included the first two genera in the Hypertragulidae. Matthew (1904) subdivided the camels into three "series," groups of related animals that included only currently recognized true camels. With some modifications including the addition of subsequently described genera, Matthew's series were incorporated into Simpson's 1945 classification of the Camelidae, which contained five subfamilies: Poebrotheriinae (which included some oromerycids), Camelinae, Pseudolabidinae, Alticamelinae, and Stenomylinae.

Gazin (1955) established the family Oromerycidae for *Oromeryx*, and included *Protylopus*, *Camelodon*, and *Eotylopus*, genera formerly included within the Camelidae; Wilson (1974), however, regarded them as oromerycine camelids because of similarities between the molars of Chadronian *Poebrotherium* and *Protylopus*. His concept of Oromerycinae was accepted by Honey and Taylor (1978) and by Webb and Taylor (1980), who suggested that the enlarged I3 may be a shared-derived feature with camels. Wilson (1974) also established the subfamily Poebrodoninae for what he considered to be a divergent line of early camelids not ancestral to *Poebrotherium*.

The formal subfamilial divisions of the Camelidae (Fig. 30.3) adopted herein include Stenomylinae, Floridatragulinae, Protolabinae, Miolabinae, and Camelinae; the Poebrotheriinae and Alticamelinae are abandoned as paraphyletic. A cladogram showing our view of the interrelationships of camelid genera is presented in Figure 30.3.

INCLUDED NORTH AMERICAN GENERA IN THE FAMILY CAMELIDAE

The locality numbers listed for each genus refer to the list of unified localities in Appendix I. Question marks in front of the locality (e.g., ?CP101) mean the taxon is questionably known from that locality. The acronyms for museum collections are listed in Appendix III.

PRIMITIVE CAMELIDS

Poebrodon Gazin, 1955

Type species: *Poebrodon kayi* Gazin, 1955.

Type specimen: USNM 20393.

Characteristics: Presently known only from a few teeth. The teeth are characteristically camelid, having straight ectolophs and fossettes closed anteriorly and posteriorly; in addition, the teeth are more hypsodont than those of contemporary selenodont artiodactyls.

Average length of m2: 7.0 mm.

Included species: *P. kayi* (known from locality CP6B); *P. californicus* (locality CC7C).

Poebrodon sp. is also known from locality CP38C.

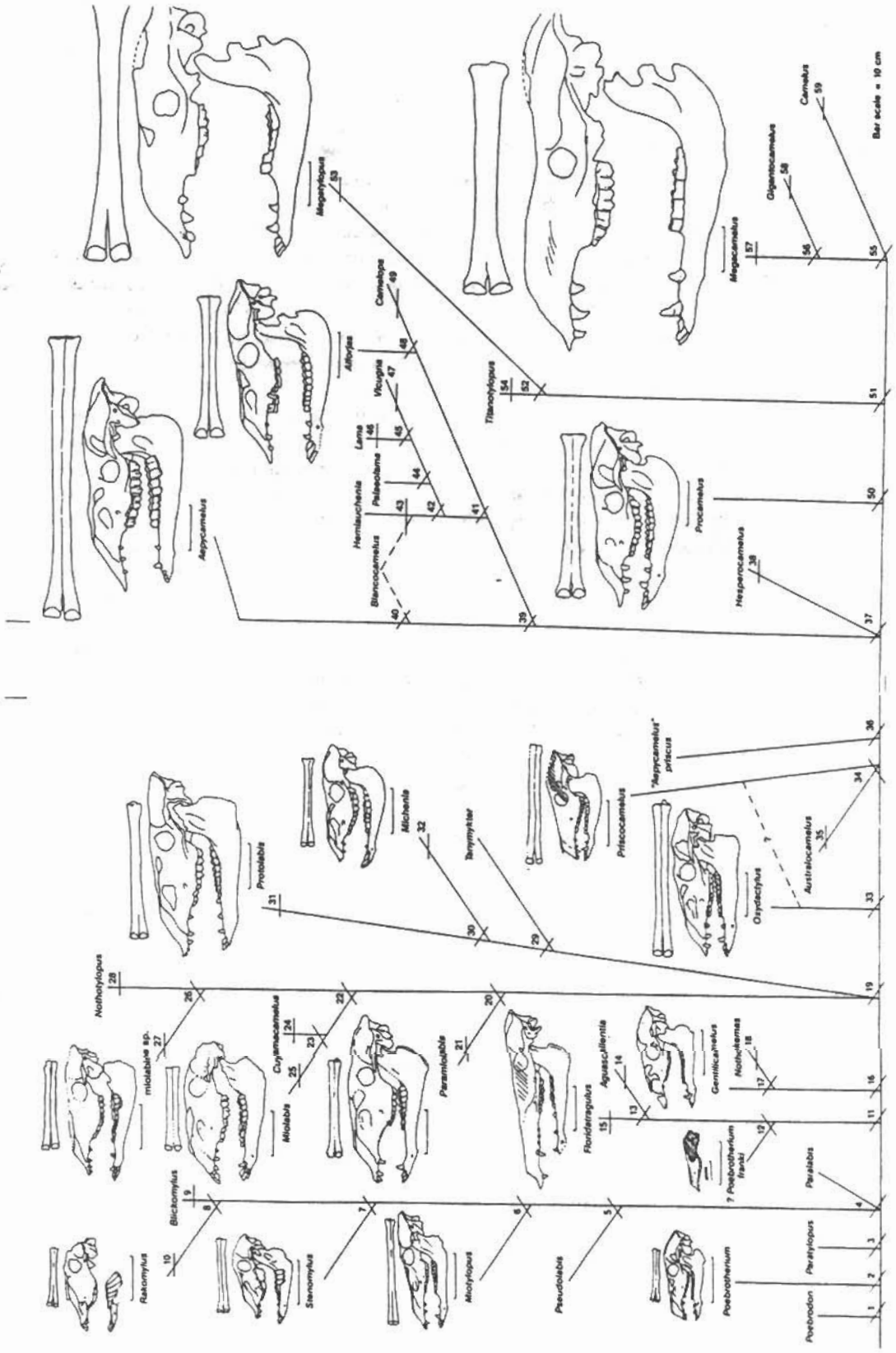
Bar scale = 10 cm
Camelus
Giganticamelus
Megacamelus
Megatylopus
Titanotylopus
Procamelus
Hesperocamelus
"Aepycamelus" priscus
Aepycamelus
Blancocamelus
Hemiauchenia
Palaeolama
Lama
Vicugna
Alticamelus
Camelops
Tanymykter
Michenia
Pritocamelus
Australocamelus
Oxydactylus
Nothotylopus
Cuyamacamelus
Miolabis
Paramiolabis
Floridatragulus
Aguascalientia
Gentilicamelus
Nothokemas
? Poebrotherium lisnikii
Poebrotherium
Miotylopus
Pseudolabis
Stanomylus
Blickomylus
miolabine sp.
Rakomylus
Protolabis
Paralabis
Paratylopus
Poebrodon

Figure 30.3. Interrelationships of camelid genera (metatarsal bones are depicted above the skulls). Key to characters at nodes: (1) Divergent distal metapodials; deep tympanohyal groove; transversely narrow, high crowned, selenodont molars; straight ectoloph on M1–3; metacarpals II and V reduced to nodules; vertebral arterial canal confluent with neural arch in posterior half of cervicals 3–6. (2) Increased hypsodonty; larger size; M2 wider posteriorly; lingual hypoconulid lobe of m3 reduced; lingual metaconid and entoconid flattened. (3) Reduced inner lobe of bulla; reduced premolars. (4) Stronger sagittal crest; smaller lacrimal vacuity; posterior extension of internal portion of bulla. (5) STENOMYLINAE: Premaxillary extended posteriorly; longer rostrum; deep, elongate maxillary fossa; elongated upper molars, which are laterally compressed and more hypsodont; weak mesostyles; partially fused metapodials; closed orbit. (6) Highly reduced P2–3. (7) Incisiform lower canine; i1–3, c, and p1 form closed row; p2–3 diastema; molars extremely hypsodont. (8) Larger incisors; P2/p2 reduced; p3 reduced; P4 reduced; molars more hypsodont; metapodials completely fused. (9) M3/m3 extremely elongated. (10) Deeper anteromaxillary fossa; P1–2 lost, p2 lost; p4 very small; metapodials very short. (11) Lower molars with metastylid present, formed by overlap of metaconid on entoconid; heavier premaxilla; large postglenoid foramen. (12) FLORIDATRAGULINAE: I1–3 lateral on premaxillary and bladelike; I3 size similar to I2; p4 equals anteroposterior diameter of p3. (13) Rostrum very elongate; p4 shorter anteroposteriorly than p3; m3 with incipient lingual selene. (14) Posterior cleft on m3 hypoconulid; larger size. (15) p2–3 diastema; m3 hypoconulid bilophed, with medial cleft; largest size. (16) Lower incisors more spatulate; P1 shortened; P3 internal cingulum stronger; orbits closed(?). (17) "NOTHOKEMATINAE": Mandibular angle enlarged; P1 roots closely appressed. (18) C larger than I3; loss of p1; p3 posterolingual stylid strong. (19) Medial plate of auditory bulla transversely compressed; rostrum lengthened; P2–3 variably reduced; molars more hypsodont; upper molars with weaker ribs. (20) MIOLABINAE: P2–3 parastyle reduced; mandibular angle enlarged; coronoid process short; cervical vertebrae short; metapodials very short. (21) P1/p1 absent; P2/p2 highly reduced or absent; lower molars with anterior buttresses; elongate, slender ramus; post-c1 diastema long and with sharp dorsal crest; rostrum inflated along nasal passage; auditory bulla with anteromedial process. (22) Maxillary fossa deepened; lateral plate of auditory bulla enlarged. (23) I2 with incipient posterior cusp; P1 reduced. (24) Skull elongate; dorsoventrally narrow rostrum. (25) I1–2 cupped; p1 absent. (26) Prominent anterior buttresses on molars; metatarsals weakly fused. (27) Lateral plate of auditory bulla flattened; bulla medially excavated. (28) p2 absent; p3–4 three lobed. (29) PROTOLABINAE: Rostrum narrow; laterally expanded anterior nares. (30) Absence of elongate basioccipital tuberosities; P2 without strong, continuous lingual cingulum; auditory bulla less inflated with medial plates more compressed; buccinator fossa moderate to strong. (31) Molars hypsodont; M3/m3 anteroposteriorly elongate; metastylids on lower molars very weak to absent; ventrally produced mandibular angle with weak to strong lateral flare; metapodials fused. (32) Braincase short; I3-C weak, c small; symphysis shallow; inflection of mandibular angle suppressed. (33) Cervical vertebrae elongate; metapodials elongate, slender, and greater than basal length of skull; metatarsus and metacarpus approximately equal in length. (34) Mandibular ramus relatively narrow, with convex lower border. (35) Lower premolars and molars laterally compressed. (36) CAMELINAE: P1/p1 caniniform; metapodials fused; metacarpus longer than metatarsus. (37) Maxillary fossa pocketed; increased hypsodonty. (38) Upper canines small, peglike; p1–2 shortened, high crowned. (39) LAMINI: Arched nasals. (40) Extremely elongate metapodials, neck. (41) I1–2 lost; P2/p2 lost; anteroexternal style present on lower molars. (42) Small P1/p1; p3 small or absent; reduced lacrimal vacuity; shortened rostrum. (43) Extremely elongate metapodials, neck. (44) P1/p1 lost; reduced maxillary fossa; moderate to strong anteroexternal style on lower molars; metapodials secondarily shortened. (45) p3 absent; metacarpal length subequal to metatarsal length; strong anteroexternal style on lower molars; greatly reduced lacrimal vacuity; extremely retracted nasals; greatly reduced p4. (46) Callosities on the inner foreleg. (47) Ever-growing lower incisors. (48) Moderately to very hypsodont molars; cheek teeth narrow in relation to length; metapodials secondarily shortened. (49) Cheek teeth very hypsodont; P1/p1 absent; p3 absent; dorsal surface of mandibular condyle transversely concave; suspensory ligament scar extends to center of proximal phalanx and has a raised center. (50) CAMELINI: I1 lost; P1/p1 single rooted; prominent sagittal and lambdoidal crests. (51) Angular process on mandible greatly enlarged; long postglenoid process on skull with correspondingly large facet on mandibular condyle; ventrally flattened auditory bulla; reduced maxillary fossa; thickened, very heavy premaxilla; diastemal crest on mandible low and rounded; C1/c1 enlarged and rounded in cross section, especially in males; strong labial styles and ribs on M1–3. (52) Reduced p1; reduced p3. (53) Reduced P3; cheek teeth higher crowned than in *Titanotylopus*. (54) p1 absent; p3 more reduced than in *Megatylopus*; larger body size than *Megatylopus*. (55) Metapodials shorter in relation to basal length of the skull; cheek teeth more hypsodont than in *Megatylopus* or *Titanotylopus*. (56) Spatulate lower incisors; splayed lower canines. (57) I3 enlarged and caniniform. (58) Short, blunt chin with a shortened ramal symphysis; larger body size than *Megacamelus*; lower incisors arrayed almost transversely; I3 absent or vestigial. (59) Reduced paroccipital process; metapodials subequal in length and shorter than the basal length of the skull; maxillary fossa reduced or absent; zygomatic arch straight in lateral view; retracted nasals; center of suspensory ligament scar raised. (Illustration by Marge C. Leggitt.)

Poebrotherium Leidy, 1847

Type species: *Poebrotherium wilsoni* Leidy, 1847.

Type specimen: ANSP 11012.

Characteristics: Complete dental formula. *Poebrotherium*, the common Oligocene camelid, is smaller, less hypsodont, and more primitive than any other except *Poebrodon*; there are no unique derived features. Differs from *Poebrodon* in its larger size, greater hypsodonty, posteriorly wider M2, reduced lingual hypoconulid lobe of m3, and flattened lingual surface of metaconid and entoconid.

Average length of m2: 11.0–13.5 mm.

Included species: *P. wilsoni* (known from localities CP40A, CP40B, CP41A, CP41B, CP68C, CP84A, CP84B, CP99A, CP99B, NP50B); *P. chadronense* (locality SB44D); *P. eximium* (localities CP40A, CP41A, CP68B, CP83C, CP84A, CP98B, CP98C, NP29C).

Poebrotherium sp. is also known from localities CP39B, CP39C, CP39F, CP39G, CP39UC, CP43, CP45A, CP84A, NP24C, NP24D, NP24E, NP34B.

Paratylopus Matthew, 1904

Type species: *Paratylopus primaevus* (Matthew, 1904) (= *Miolabis* [*Paratylopus*] *primaevus*).

Type specimen: AMNH 6520.

Characteristics: Complete dental formula. Small to medium-sized camelids with relatively brachydont teeth, reduced premolars, and large skulls relative to their tooth size. Distinguished from *Poebrotherium* by larger size and more reduced premolars; from *Paralabis* by smaller size and less reduced premolars; and from all other Whitneyan and Arikareean camelids by its brachydont teeth, which are relatively small for its skull size.

Average length of m2: 12.5–16.4 mm.

Included species: *P. primaevus* (known from localities CP41C, CP84B, CP99B); *P. labiatus* (localities CP40B, CP41B, CP68C, CP84A, CP84B, CP98C, CP99A).

Comments: "*Paratylopus*" *cameloides* from the Haystack Valley Member of the John Day Formation (locality PN6G) is more advanced than *P. primaevus*, and possibly is a primitive protolabine.

***Paralabis* Lull, 1921**

Type species: *Paralabis cedrensis* (Matthew, 1901) (= *Protomeryx cedrensis*).

Type specimen: AMNH 8969.

Characteristics: Medium-sized camelid with moderately hypsodont teeth and highly reduced premolars (ratio of lengths of P2–4/m1–3 = 0.5). Distinguished from *Poebrotherium* and *Paratylopus* by its larger size, greater hypsodonty, and more reduced premolars; distinguished from *Pseudolabis* or *Miotylopus* by lesser hypsodonty and presence of a mesostyle; otherwise very similar.

Average length of m2: 13.3–14.7 mm.

Included species: *P. cedrensis* only (known from localities CP68D, CP84B, CP99B).

STENOMYLINAE

Characteristics: Because *Pseudolabis* and *Miotylopus* share derived features with more advanced taxa such as *Stenomylus*, they are included in an expanded Stenomylinae (Matthew, 1910), which has priority as a subfamily name over Pseudolabidinae (Simpson, 1945). The expanded Stenomylinae is characterized by a long rostrum and a deep, anteroposteriorly elongate maxillary fossa. The teeth are more elongate and transversely narrower than those of *Poebrotherium*, *Paratylopus*, *Paralabis*, or *Oxydactylus*. All stenomylines lack a mesostyle and have a posteriorly extended premaxilla (posterior to the level of P1). The subfamily includes *Pseudolabis*, *Miotylopus* (including *Dyseotylopus*), and the tribe Stenomylini.

***Pseudolabis* Matthew, 1904**

Type species: *Pseudolabis dakotensis* Matthew, 1904.

Type specimen: AMNH 9807.

Characteristics: *Pseudolabis*, slightly larger than *Poebrotherium*, shows all the characteristic features of the Stenomylinae: deeply depressed maxillary fossa, posteriorly extended premaxilla, and relatively hypsodont teeth with weak mesostyles. It is also the oldest taxon of the clade to have a fully closed orbit. Unlike more derived members, it has a relatively short rostrum and unreduced premolars.

Average length of m2: 15.0–17.0 mm.

Included species: *P. dakotensis* only (known from localities CP42D, CP48, CP50, CP52, CP84B, CP85C, CP99B, CP99C, CP103).

***Miotylopus* Schlaikjer, 1935 (synonyms: *Dyseotylopus*, *Gentilicamelus*, in part)**

Type species: *Miotylopus gibbi* (Loomis, 1911).

Type specimen: YPM 10328.

Characteristics: *Miotylopus* continues the trends seen in *Pseudolabis*, but in addition has a more elongate rostrum and highly reduced premolars. Some species of *Miotylopus* are nearly identical to primitive *Stenomylus* in all features except extreme hypsodonty.

Average length of m2: 18.0–25.0 mm.

Included species: *M. gibbi* (known from localities CC9C, CC12, CP48, CP50, CP52, CP87, CP101, CP102); *M. leonardi* (localities CP47, CP48, CP50, CP52, CP101); *M. taylori* (localities CP48, CP50).

Comments: *Miotylopus* is a primitive but contemporary sister taxon to the Stenomylini. Contrary to Peterson (1908) and Frick and Taylor (1968), it is not necessary to seek a stenomyline ancestor in the Eocene. Prothero (1996) showed that *Dyseotylopus* Stock, 1935, and part of the material referred to *Gentilicamelus* by Loomis (1936) are junior synonyms of *Miotylopus*.

STENOMYLINI

***Stenomylus* Peterson, 1906**

Type species: *Stenomylus gracilis* Peterson, 1906.

Type specimen: CM 1610.

Characteristics: *Stenomylus* and the other two members of the stenomylini are extremely hypsodont and distinctive. As shown by Frick and Taylor (1968), the high-crowned teeth typically fill the entire maxilla and mandible. Also, the third molars are extremely elongated anteroposteriorly; the first and second molars are less so. The incisors, canine, and first premolar form a row of closely spaced, spatulate teeth, with a long diastema between the first and third premolars (often with an alveolus for a reduced or vestigial p2). The skull is generally short and gracile, and the animal has very gazellelike proportions. Advanced stenomylines are generally smaller than contemporary Miocene camelids.

Average length of m2: 19.5–27.0 mm.

Included species: *S. (Stenomylus) gracilis* (known from localities SB29A, CP51A, CP104B); *S. (Stenomylus) hitchcocki* (localities NB3A, CP49B, CP103, NP38B); *S. (Pegomylus) keelinensis* (locality CP52); *S. tubutamensis* (locality SB54).

Stenomylus sp. is also known from localities CC15, CC21A, SB3, SB46, SB47, CP50, CP103, CP104B, CP105.

***Blickomylus* Frick and Taylor, 1968**

Type species: *Blickomylus galushai* Frick and Taylor, 1968.

Type specimen: FAM 50840.

Characteristics: *Blickomylus* carried the hypsodonty seen in *Stenomylus* to greater extremes (see Figure 30.4). The in-

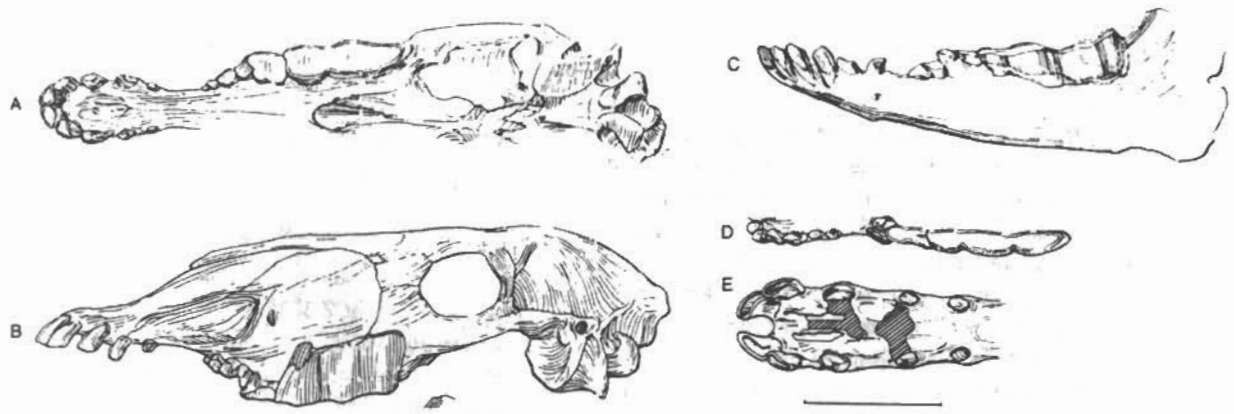

Figure 30.4. Miocene camelids. A–D. *Blickomylus galushai*. A, B, F:AM 50840 (type), palatal and side views; C, F:AM 50866, showing i1–3, c, p1–2, p4, m1–3; D, F:AM 50869, showing i1–3, c, p1–4, m1 (displaced), m2–3. E. *Miolabis longiceps*, AMNH 9108 (type), palatal view of rostrum with I1–3, C, P1. Scale bar for A–E = 5 cm. (Illustration by Brian Regal.)

cisors are enlarged, but P2/p2 and P3/p3 are greatly reduced; in some individuals one or more of these premolars is missing. Molar parastyles and parastylids are very weak or absent.

Average length of m2: 16.0–27.0 mm.

Included species: *B. galushai* only (known from localities SB29B, SB29C, SB29D, CP54B, CP73B).

Rakomylus Frick, 1937

Type species: *Rakomylus raki* Frick, 1937.

Type specimen: F:AM 30990.

Characteristics: The biostratigraphically youngest species of stenomyline is *Rakomylus*. It differs from other stenomylines in having a longer muzzle, a deeply recessed anteromaxillary fossa, and relatively short metapodials. Like *Blickomylus*, its molars are extremely hypsodont, and its premolars are highly reduced or lost. It has completely lost P1 and P2/p2. However, *Rakomylus* is not as derived as *Blickomylus* in other respects because the third molars are not as anteroposteriorly elongated.

Average length of m2: 18.4 mm.

Included species: *R. raki* only, known from locality SB32B only.

Rakomylus sp. is also known from locality SB30A.

FLORIDATRAGULINAE

Characteristics: Rostrum moderately (*?Poebrotherium franki*) to extremely (*Floridatragulus*) elongated, narrow. Skull known for *?P. franki* and *Floridatragulus*. The skull of *Floridatragulus* shows a very low profile, nasal bones nearly parallel with the palate, an open orbit posteriorly, a relatively steep occiput with prominent sagittal and lambdoidal crests, and a well-inflated auditory bulla with spongy bone and divided by a tympanohyal pit and groove (Maglio, 1966). Lower jaw of *Aquascalientia* and *Floridatragulus* with a very elongate rostrum and a very long, narrow symphysis (latter also present in *?P. franki*). Camelid mandibular "hook" demonstrated for *Floridatragulus*. Complete dental formula in all known taxa. I1–3 distinctly lateral on premaxillaries. Upper teeth anterior to P2 spaced by diastemata. Lower canine recurved in *Aguascalientia* and *Floridatragulus*. The p1 small, single rooted. The p4 equal to (*?P. franki*) or shorter than p3 (*Aquascalientia*, *Floridatragulus*). Lower canine to p1 and p1–p2 diastemata elongate in *Aguascalientia* and *Floridatragulus*; p2–p3 diastema present in *Floridatragulus*. Lower molars selenodont, brachydont, with somewhat bulbous cusps, and in *Aquascalientia* and *Floridatragulus*, with labial intercolumnar tubercles. In *Aguascalientia* and *Floridatragulus*, m3 hypoconulid with labial, and progressively developed lingual, selene. Upper molars quadrate and brachydont, with prominent styles, weak to prominent ribs, and lingual intercolumnar tubercles.

An incomplete tarsus tentatively referred to *Aquascalientia* has unfused metatarsals III and IV and an elongated metatarsal V splint (Stevens, 1977). Metapodials referred to *Floridatragulus* show unfused metacarpals III and IV, and metatarsals III and IV with some proximal fusion; metatarsal V is separate from metatarsal IV (Maglio, 1966).

The subfamily Floridatragulinae includes *?Poebrotherium franki*, *Aguascalientia*, and *Floridatragulus*.

?Poebrotherium franki (Wilson, 1974)

Type species: *Poebrotherium franki* Wilson, 1974.

Type specimen: TMM 40404-149.

Characteristics: Rostrum narrow, moderately elongated. Teeth ahead of P2 spaced by diastemata. I1–3 small, leaflike; I3 same size as I2. Upper canine very small. P1 double rooted. P2–4 relatively small. Upper molars quadrate, brachydont, with bulbous although selenodont cusps, and with prominent styles, ribs, cingula, and intercolumnar tubercles. Auditory bullae well inflated. Mandible very slender, presumably elongated. The p2–4 relatively small. The p4 as long anteroposteriorly as p3. The m1 brachydont with bulbous cusps. Symphysis ending beneath p2. Body size small.

Average length of m2: unknown. Average length of m1: 9.7 mm.

Included species: ?*P. franki* only (known from localities SB44D, SB44E).

Comments: ?*Poebrotherium franki* from the medial Chadronian Capote Mountain Tuff, Vieja Group, Trans-Pecos Texas, is an odd camelid with its small, bladelike upper incisors that are located distinctly lateral on the narrow rostrum and do not increase in size toward the posterior, p4 small and the same length as p3 instead of longer as in typical poebrotheres, long mandibular symphysis ending beneath p2, brachydont, quadrate upper molars with prominent styles, ribs, and intercolumnar tubercles, and rounded, bulbous although selenodont cusps. ?*P. franki* is associated with a typical poebrothere, *Poebrotherium chadronense* (Prothero, 1996), which shows that Camelidae were already well differentiated at this early date. Although no suitably intermediate fossils are known and considerable time separates the occurrences of ?*P. franki* and *Aguascalientia* sp., certain morphological features present in the incisors and premolars of ?*P. franki* suggests to one of us (MSS) that ?*P. franki* is possibly related to *Aguascalientia*; accordingly, ?*P. franki* is placed tentatively within the Floridatragulinae.

Aguascalientia Stevens, 1977

Type species: *Aquascalientia wilsoni* (Dalquest and Mooser, 1974) (= *Miotylopus wilsoni*).

Type specimen: TMM 41536-26.

Characteristics: Lower canine medium large, oval, caniniform. The p1 small, subcaniniform, separated from the canine by a diastema the length of m2. The p1 separated from p2 by a diastema the combined length of m1–m2. The p2–p3 small, brachydont, bulbous, with prominent, medially inflected parastylid. The p4 slightly shorter anteroposteriorly than p3 but taller crowned. Lower molars brachydont, rather broad transversely with bulbous cusps, and have an isolated metaconid crest until middle or late wear. Intercolumnar tubercles present. The m3 hypoconulid divided by two unequal selenes; labial selene well developed, lingual selene a small elongated cuspid. Body size medium to small.

Average length of m2: 13.3 mm.

Included species: *A. wilsoni* only, known from locality SB55 only.

Aquascalientia sp. is also known from locality SB46.

Comments: *Aguascalientia* has been reported only from Mexico and Trans-Pecos Texas. *A. wilsoni*, originally placed within *Miotylopus* by Dalquest and Mooser (1974), is perhaps slightly younger than the oldest *Floridatragalus*, *F. nanus*. *Aguascalientia* sp. is 50 percent smaller than *F. dolichanthereus* and 25 percent smaller than *F. nanus* and *A. wilsoni*, and may be ancestral to the last two species. Relatively small size and brachydont dentition with bulbous although selenodont cusps with distinct stylids, ribs, and intercolumnar tubercles led Stevens (1977) to suggest an origin of floridatragulines from oromerycids. However, the presumed oromerycid features seen in floridatragulines such as *Aguascalientia* are primitive features characteristic of the earliest tylopods in general.

Floridatragulus White, 1940 (synonym: *Hypermekops*)

Type species: *Floridatragulus dolichanthereus* White, 1940.

Type specimen: MCZ 3635.

Characteristics: Skull low, with notably attenuated rostrum. I1–3 large, subequal in size, caniniform, well spaced, and placed on the lateral margin of the rostrum. Canine size variable, either smaller or larger than I3, and separated from adjacent teeth by diastema. P1 (occasionally supernumerary possibly because of rostral attenuation) single rooted and separated from P2 by a long diastema. P2–4 small, with relatively simple crowns and tend to decrease in anteroposterior length toward the posterior, unusual for camelids. Upper molars brachydont, quadrate, with prominent para-, meso-, and metastyles, and distinct lingual intercolumnar tubercles. Auditory bulla well inflated, filled with cancellous bone, and divided by tympanohyal pit and groove. Occiput steep with prominent sagittal and lambdoidal crests. Postorbital bar incomplete. Lower canine relatively small, separated from p1 by diastema of m1–2 length or greater. The p1 single rooted, separated from p2 by diastema of m1–2 length or greater. The p2 longer anteroposteriorly than p4, separated from p3 by diastema variably shorter than m3. The p3–p4 small, with p4 smaller than p3. Lower molars brachydont with low, elongated intercolumnar tubercles. The m3 hypoconulid divided by lingual and labial selenes. Body size medium.

Average length of m2: 15.0–19.2 mm.

Included species: *F. dolichanthereus* (including *F. barbouri* White, 1947) (known from localities GC4B, GC4C, GC8D); *F. nanus* (locality GC3B); *F. texanus* (localities GC4B, GC4C); *F. hesperus* (locality GC4E).

Floridatragulus sp. is also known from localities GC5, GC9A, CP114B.

Comments: White (1940) thought *Floridatragalus dolichanthereus*, the first reported floridatraguline, to be a large, brachydont hypertragulid because of the spaced p2–p3, and Simpson (1945) placed it in Hypertragulidae incertae sedis. Another Thomas Farm taxon, *Hypermekops olseni* White (1942), originally placed within the Hypertragulidae, has since been transferred to *Floridatragalus* by McKenna (1966), Maglio (1966), and Patton (1966). Based in part on unpublished work by Bryan Patterson, Ray (1957) recognized *Floridatragalus* questionably as a camelid, and Olsen (1962) concluded that *Floridatragulus* was a true camel. Maglio (1966) and Patton (1966) believed *Floridatragulus* was phylogenetically well separated from the

other camelids on the basis of the greatly elongated snout, extremely long and narrow mandibular symphysis, reduced premolars (especially P4/p4), and divided m3 hypoconulid. Maglio (1966) noted that the jaw has the typical camelid "hook." *Floridatragulus* was derived from a camel more primitive than *Oxydactylus*, as indicated by the open orbit (McKenna, 1966).

Investigators have disagreed on the identifications of the teeth or alveoli anterior to P2. This disagreement arises in part because of the failure to find the premaxillary-maxillary suture on a referred skull (MCZ 3711), and the presence of supernumerary premolars on another referred specimen, F:AM 31864; in this second specimen, the rostrum is broken anterior to the upper canine. In this chapter, we follow White's (1942) interpretation that *Floridatragulus* had a complete dental formula. A restoration of the head of *Floridatragulus* is shown in Figure 30.1B.

CAMELIDAE, INCERTAE SEDIS: "NOTHOKEMATINAE"

Gentilicamelus Loomis, 1936

Type species: *Gentilicamelus sternbergi* (Cope, 1879) (= *Poebrotherium sternbergi*).

Type specimen: AMNH 7910.

Characteristics: Dental formula: I3(?)/3, C1/1, P4/4, M3/3. P1 double-rooted; p1 uncertain. P2–4 less reduced relative to M1–3 than in *Oxydactylus*. P3 internal crescent weaker than in *Oxydactylus*. Cheek teeth very brachydont (more so than in *Oxydactylus*) with large ribs and styles on upper molars. Intercolumnar tubercles present on M1–3, and at least on m3. Maxillary fossa present, but apparently shallow. Palatine notch extends as far forward as middle of M2. Auditory bulla well inflated. Metapodials slender, unfused, shorter than skull length, and with metatarsus longer than metacarpus. Proximal phalanges with distal articular surfaces unexpanded dorsally.

Length of m2: approximately 14.7 (broken). Length of M2: 12.0 mm.

Included species: *G. sternbergi* only, known from within the John Day Formation, ?locality PN6D.

Nothokemas White, 1947

Type species: *Nothokemas floridanus* (Simpson, 1932) (= *Oxydactylus floridanus*).

Type specimen: FSGS V-5247.

Characteristics: Dental formula I3(?)/3, C1/1, P4/3, M3/3. I3, C1/c1 caniniform. C1 larger than I3; c1 large, recurved. P1 with roots closely appressed or fused; p1 absent in contrast to *Gentilicamelus* and *Oxydactylus*. Long c1–p2 diastema. Cheek teeth primitively very brachydont as in *Gentilicamelus*. P2–4/p2–4 unreduced in primitive species; slight reduction in more advanced species. P2 internal cingulum weak to strong; P3 with more prominent internal cingulum. The p3–4 with strong anterolingual fold. The p3 with strong posterolingual cusp; posterolingual cusp present on p2 of some species. Intercolumnar tubercles variably present on molars, and where known, are V shaped on upper molars. Upper molars with very strong ribs and styles as in *Gentilicamelus* and primitive *Oxydactylus*. Posterior edge of m3 entoconid slightly overlaps hypoconulid. Mandible relatively deep and transversely thin as in *Oxydactylus*. Angle of mandible somewhat expanded.

Average length of m2: 10.6–20.5 mm.

Included species: *N. floridanus* (known from localities GC3B, GC8D); *N. hidalgensis* (locality GC3B); *N. waldropi* (GC8A).

Nothokemas sp. is also known from locality GC9A.

MIOLABINAE

Characteristics: I3 caniniform, equal to or larger than upper canine. P2 reduced through shortening of the anterior and posterior crests. Molars more hypsodont than in *Gentilicamelus* and *Nothokemas*, and usually more hypsodont than in *Oxydactylus*. Upper molar ribs reduced compared with those of *Gentilicamelus*. Intercolumnar tubercles variably present on molars. Orbits closed. Maximum width of rostrum occurs across the incisors. Buccinator fossa usually weak; premaxillaries and anterior maxillaries not flared strongly immediately below nasals, unlike protolabines. Maxillary fossa very shallow to deep. Mandibular angle expanded. Coronoid process short. Short cervical vertebrae. Metapodials short and unfused or only weakly fused in metatarsus. Metatarsus longer than metacarpus.

Comments: We use Hay's (1902) subfamily Miolabinae for the genera *Miolabis*, *Paramiolabis*, *Nothotylopus*, and *Cuyamacamelus*. As used by Hay (1902), Miolabinae included not only *Miolabis* sensu stricto, but also *Procamelus* (which included species once placed in *Procamelus*, *Protolabis*, *Miolabis*, and *Alticamelus* (= *Aepycamelus*)), *Camelops*, and *Pliauchenia* (including *Gigantocamelus*); as pointed out by Simpson (1945), Hay's Miolabinae was essentially synonymous with Zittel's (1893) Protolabinae. Simpson (1945) included *Miolabis* doubtfully within the Alticamelinae, following, with modifications, Matthew's (1904) association of *Miolabis* with *Paratylopus* and *Oxydactylus*. Matthew's arrangement was based on the shared-primitive characters of low-crowned molars with strong ribs and styles and simple P4s.

Species of *Miolabis* have long been known, although as shown by Frick and Taylor (1971), most were incorrectly placed in *Protolabis*. *Nothotylopus* is based on a lower jaw. Patton (1969) found precise systematic placement of *Nothotylopus* difficult because of what he termed a "strange mixture of advanced and conservative features" (p. 162), but concluded that it was probably derived from an early *Protolabis* or from an oxydactyline-*Protolabis* intermediate. Comparison of the lower jaws of *Nothotylopus* with samples of an undescribed but more completely preserved miolabine (miolabine sp.; see later) establishes that *Nothotylopus* and *Miolabis* are related, an unpublished conclusion previously reached by Beryl Taylor.

***Paramiolabis* Kelly, 1992 (synonyms: *Pliauchenia*, in part, *Miolabis*, in part, "*Merychenia*" [Frick ms. name])**

Type species: *Paramiolabis singularis* (Matthew, 1918) (= *Pliauchenia singularis*).

Type specimen: AMNH 17329.

Characteristics: Dental formula I3/3, C1/1, P2–3/2–3, M3/3. I1–2 conical, nonspatulate; I3 caniniform. All premolars reduced relative to molars, with P1/1 absent or unerupted (rare specimens show an erupted, vestigial P1), and P2/2 highly reduced and sometimes absent. The m2–3 with protostylids and parastylids forming anterior buttresses. Diastema between c1 and p2 or p3 elongate, with dorsal border of dentary having a sharp crest and commonly slightly arched upward. Ramus elongate and slender. Angle of mandible commonly expanded, flattened along the posterior edge, with a variable lateral rugosity or flaring in the area of the masseteric insertion; coronoid process short. Palate in region of C1 to P2 or P3 diastema slightly arched upward; rostrum moderately elongate and constricted, and above the C1 to P2 or P3 diastema is laterally inflated. Maxillary fossa shallow to absent. Supraorbital region slightly convex. Auditory bulla inflated, with anteromedial process present. Cervical vertebrae short. Metapodials shorter than basal length of skull, with the metacarpus unfused and the metatarsus sometimes fused proximally.

Average length of m2: 15.0–28.0 mm.

Included species: *P. singularis* (known from locality CP110); *P. tenuis* (locality CP108B); *P. taylori* (locality CC17E).

Paramiolabis sp. is also known from localities GC4B, GC4C, NB3D, NB6A, NB6B, NB6C, NB6D, SB32A, SB32B, SB32D, SB32E, CP107.

Comments: Kelly (1992) considered the type species of *Paramiolabis* to be *P. tenuis* from the Sheep Creek Formation of Nebraska, originally described by Matthew (1924) as *Miolabis tenuis*. However, in his unpublished dissertation, Barghoorn (1985) described the same genus under the Frick and Taylor manuscript name of *Merychenia* and, in agreement with their earlier conclusion, recognized the type species as *Pliauchenia singularis* Matthew (1918) from the Olcott Formation of Nebraska. Barghoorn's analysis of "*Merychenia*" was based on study of the AMNH collection of this camelid. The diagnosis of *Paramiolabis* given here relies heavily on Barghoorn's extensive diagnosis and description of "*Merychenia*," supplemented by Kelly's description of *Paramiolabis* and our own examination of the AMNH material.

***Miolabis* Hay, 1899 (in Matthew, 1899) (Synonym: *Protolabis*, in part)**

Type species: *Miolabis transmontanus* (Cope, 1879) (= *Protolabis transmontanus*).

Type specimen: AMNH 8196.

Characteristics: Dental formula I3/3, C1/1, P4/3, M3/3. I1–2 large, cupped, tending to form closed arc at front premaxillaries (Figure 30.4E). I3 caniniform, larger tha C1. P1 usually single rooted or with two fused roots; some specimens have a double-rooted P1 with flaring roots (Fig 30.4E). The p1 is absent. Premolars stouter, less laterally compressed than in *Protolabis*. P2/p2 shortened and simplified through reduction of anterior and posterior crests P3 broadened relative to *Oxydactylus*, *Gentilicamelus*, and *Paratylopus*, with a reduced parastyle and a complete internal crescent; p3 often shortened and with a high, centra protoconid. The p4 more basally swollen than in *Oxydactylus*, and with an enlarged hypoconid. Upper molars with strong parastyle and mesostyle; ribs less prominent than in *Oxydactylus* and *Gentilicamelus*. Molars lower crowned with stronger metastylids, and M3/m3 less anteroposteriorly expanded than in *Protolabis*. Intercolumnar tubercle on lower molars most common on m1. Maxillary fossa usually deeply depressed, subcircular, and deepest posteriorly and dorsally. Buccinator fossa weak to absent. Palatine notch extends anteriorly only to the posterior border of M3. Lateral plate of bulla usually projects significantly below paroccipital process and is level with or below the occlusal surface of the upper molars. Mandibular angle expanded with a lateral rugosity or ridge along the posteroinferior border; narrow internal shelf sometimes present on posteroventral margin of angle. Mandibular "hook" weak. Cervical vertebrae short. Metapodials unfused and much shorter than basal length of skull. Proximal phalanx with distal articular surface only weakly expanded dorsally.

Average length of m2: 19.0–25.0 mm.

Included species: *M. transmontanus* (known from localities PN7); *M. fissidens* (localities NB6E, CP49C, CP75C); *M. montanus* (locality NP41B); *M. longiceps* (locality CP76); *M. princetonianus* (localities CP107, CP110); *M. fricki* (localities CC17C, CC17D, CC17E). Questionably included: *M. californicus* (locality CC15).

Miolabis sp. is also known from localities CC21A, CC21B, CC21C, NB6A, NB6C, NB6D, SB32A, SB32B, SB32D, CP75B, CP108B, CP114A, ?CP114D, CP116B, ?NP10E.

Comments: Frick and Taylor (1971) have shown that most species of *Miolabis* were incorrectly placed in *Protolabis* and clarified the distinctions between the two genera. *Miolabis californicus* is herein questionably retained in *Miolabis*, with the realization that future revision may place it in another genus. *M. californicus* differs from typical *Miolabis* in having nonspatulate upper incisors.

***Cuyamacamelus* Kelly, 1992**

Type species: *Cuyamacamelus jamesi* Kelly, 1992.

Type specimen: UCMP 65339.

Characteristics: Dental formula I3/?, C1/?, P4/?, M3/?. nonspatulate, smaller than I3. I3 caniniform, larger th

C1. P1 small, single rooted. P2–3 less laterally compressed than in protolabines, and with bulbous central cusp. P2 shortened relative to P3 and P4. P3 with complete internal crescent. Molars brachydont and with strong labial ribs and styles. Skull long, with elongate, dorsoventrally narrow rostrum that is not extremely constricted laterally as it is in derived protolabines. Maxillary fossa deepest posteriorly but apparently unpocketed. Lateral plate of bulla damaged, but apparently projected below the level of the damaged paroccipital process.

Average length of m2: unknown. Average length of M2: 30.15 mm.

Included species: *C. jamesi* only, known from locality CC17D only.

Comments: Kelly (1992) compared *Cuyamacamelus* mainly with *Nothokemas*, *Floridatragulus*, and *Miolabis*, and concluded that the subfamily position of *Cuyamacamelus* was indeterminate. Although the lower jaw and postcrania of *Cuyamacamelus jamesi* are unknown, certain features present on the skull suggest a relationship with miolabines. Most important are indications that the auditory bulla extended below the paroccipital process, as in *Miolabis* and miolabine sp. (and probably also *Nothotylopus*). Also, in miolabines the P2 is reduced, with a reduced parastyle, and in *Miolabis* and miolabine sp. the P2 and P3 are commonly broad transversely with a bulbous paracone on the P3, as in *Cuyamacamelus*. In miolabines the I3 is equal in size or larger than the C1 (a primitive feature), and the P1 is often reduced. The maxillary fossa ranges from shallow to deep in miolabines, the orbit is closed, and in *Miolabis* and miolabine sp. the palatine notch is posterior to the middle of M3. Other features mentioned by Kelly (1992), such as low, flat cranium, laterally situated I2, and somewhat reduced premolars, are also found in some specimens of *Miolabis* and miolabine sp.

On *Cuyamacamelus*, the brachydont cheek teeth and (apparently) lengthened lateral plate of the auditory bulla indicate that this genus is a primitive member of the *Miolabis*-miolabine sp.-*Nothotylopus* clade. Although the I2 of *Cuyamacamelus* is not cupped, Kelly (1992) mentioned the presence on the I2 of a "small posterior incipient cusp," which may approximate the primitive condition for the cupped incisors of *Miolabis*; however, *C. jamesi* itself is too late in time to be ancestral to *Miolabis*. As in *Miolabis*, the P1 of *Cuyamacamelus* is single rooted, and the P3 has a complete internal crescent (also present in some specimens of miolabine sp.). The type specimen of *C. jamesi* is too poorly preserved to allow evaluation of its morphology relative to nodes defining the *Nothotylopus*-miolabine sp. clade; until better material is described, we place *Cuyamacamelus* near *Miolabis* based on the dental features described here.

Miolabine sp.

Rarely described but relatively common miolabines are present in localities from early Hemingfordian through late Barstovian age. Probably comprising several species, these miolabines are closely related to *Nothotylopus* and, being represented by well-preserved cranial and postcranial remains, establish the relationship between *Nothotylopus* and *Miolabis*. They differ from *Nothotylopus* mainly in the presence of the p2; whether they are species of *Nothotylopus* or belong in a new genus awaits publication of analyses of this group. The camelid described by Voorhies (1990a, p. A219) as gen. et sp. indet. may represent a species of these poorly known miolabines or their close relative, *Nothotylopus*. Characters of these miolabines include I1–2 peglike, lingually curved, and spaced; I3 conical, and equal to or larger than C1; P1/p1 double rooted, with roots often widely flared; p2–4 three lobed in labial view, with deep p4 posterolabial sulcus; lower molars with variably developed anterior buttresses and with relatively flat lingual walls (through reduction or elimination of metastylids); maxillary fossa shallow to deep, sometimes pocketed just beneath nasals; lateral plate of bulla roughly triangular and strongly compressed transversely, and extremely elongated to extend well below level of paroccipital process; medial plate of bulla strongly compressed transversely, smooth and deeply excavated on the medial side; mandibular angle greatly expanded with a posterolateral rugosity and with the ventral margin lingually inflected; coronoid process reduced; metapodials shorter than basal length of skull, with metacarpals unfused and metatarsals partly fused.

Average length of m2: 25.0–31.0 mm.

Miolabine sp. is known from localities GC4B, GC4C, SB29C, CP75B, CP75C, CP107, CP108A, CP108B, CP110, CP114C, CP114D.

***Nothotylopus* Patton, 1969**

Type species: *Nothotylopus camptognathus* Patton, 1969.

Type specimen: TMM 31081-26, formerly in the UTBEG collection.

Characteristics: Dental formula I?/3, C?/1, P?/3, M?/3. The c1 caniniform, robust. Double-rooted p1; p2 absent. Long p1–3 diastema. The p3–4 reduced relative to molars. Three-lobed p3–4, with buccal sulci anterior and posterior to the protoconid; posterior sulcus on p4 deep. The p4 parastylid generally well developed and strongly inflected lingually. Lower molars without metastylids and with pronounced protostylids and variably developed parastylids on m2–3, which form anterior buttresses. On lower jaw, masseteric insertion greatly expanded and laterally flared, angular process ("hook") prominent but not strongly inflected, and coronoid process short, weak. Referred metapodials short with metacarpals unfused and metatarsals partially fused. Differs from *Miolabis* in p1 present, p2 absent, more expanded mandibular angle, flatter walled and more strongly buttressed lower molars, and premolars smaller relative to molars. Differs from miolabine sp. in

loss of p2. Differs from *Oxydactylus* in loss of p2, buttressed lower molars, expanded masseteric insertion, and weak coronoid process.

Average length of m2: 27.0–31.0 mm.

Included species: *N. camptognathus* only, known from locality GC6B only.

Nothotylopus sp. is also known from localities SB32A, SB32B, SB32D, SP2A, CP114B, CP116B.

PROTOLABINAE

Characteristics: Dental formula: I3–1/3, C1/1, P4/4–3, M3/3. I1–2 lost in derived species. Distance between upper canines equal to or less than distance between I3s. P1/p1 double rooted (roots may be closely appressed), with low, blunt crown. The p1 may be suppressed or lost in advanced species. Shorter cranial (postorbital) length relative to facial length than in Camelini and Lamini. Tendency toward marked rostral constriction between C1 and P2, associated with progressive development of buccinator fossa. Anterior nares laterally expanded. Maxillary fossa never pocketed. Paroccipital process rarely extends below level of auditory bulla. Cervical vertebrae not elongated. Metapodials unfused or weakly fused in primitive species and fused in advanced species. Metapodials shorter and stockier in some advanced species. Length of metacarpus equal to or less than length of metatarsus.

Comments: *Protolabis* (sometimes including species later allocated to *Miolabis*) and the much later described *Michenia* have been considered ancestral to some or all later camelids (Cope, 1886; Wortman, 1898; Scott, 1937; Webb, 1965, 1972), and in this century have been classified within the Camelinae. Webb (1965, p. 44) established the tribe Protolabidini of the Camelinae as a "horizontal ancestral group" for later camelines. Honey and Taylor (1978) disputed this view, citing a number of morphological features that they felt removed the protolabidines from the ancestry of later camelids. They retained the Protolabidini within the Camelinae, however, considering that subfamily monophyletic because of the features of weak buccinator fossa and elongate rostrum. They contrasted the Camelinae with the Aepycamelinae (*Oxydactylus* and *Aepycamelus*), the latter subfamily considered monophyletic by virtue of elongate limbs and cervical vertebrae, and metapodials longer than the basal length of the skull.

Restudy of *Aepycamelus* and *Procamelus*, however, has shown a number of features indicative of close relationship (see later), and that they are more closely related to each other than either is to *Protolabis*. Retention of *Tanymykter*, *Protolabis*, and *Michenia* within the Camelinae and exclusion of *Aepycamelus* from that subfamily, as done by Honey and Taylor, results in a polyphyletic Camelinae. We therefore remove the protolabines from the Camelinae and return to the usage of Zittel's (1893) Protolabinae for this very distinctive group consisting of *Tanymykter*, *Protolabis*, and *Michenia*.

Tanymykter Honey and Taylor, 1978

Type species: *Tanymykter brachyodontus* (Peterson, 1904) (= *Oxydactylus brachyodontus*).

Type specimen: CM 664.

Characteristics: Complete dental formula. I1–2 weak, laterally compressed, concave lingually, and often more laterally situated than in *Oxydactylus*. C1 larger than I3. The p1 roots closely appressed or fused. P3 lingual cingulum unbroken. Molars lower crowned and shorter than in *Protolabis*. Rostrum generally wider than in *Protolabis* and *Michenia*, and buccinator fossa is only weakly developed. Maxillary fossa well developed. Basisphenoid with two elongate, strong, ventral tuberosities. Mandibular angle unexpanded ventrally and with weak mesial inflection. Limbs not elongated, with metapodial length less than basal length of skull. Metacarpals unfused and metatarsals weakly fused.

Average length of m2: 17.5–18.5 mm.

Included species: *T. brachyodontus* only (known from localities CC16, CP51A, CP104B, CP105).

Protolabis Cope, 1876

Type species: *Protolabis heterodontus* (Cope, 1873) (= *Procamelus heterodontus*).

Type specimen: AMNH 8296.

Characteristics: Dental formula I3–1/3, C1/1, P4/4–3, M3/3. I1–2 lost in derived species. I3, C1/c1 conical and recurved, rarely transversely compressed, and without sharp anterior and posterior edges. P1 smaller than I3. The p1 may be suppressed or absent in derived species. The p2–4 show progressive size reduction in advanced species, with p2 occasionally lost. The p3–4 with middle cusps usually equal to or wider than posterior cusps. Molar styles and ribs less prominent in advanced species. Palate narrow behind canine. Rostral constriction extreme in advanced species, and associated with pronounced development of buccinator fossa. Maxillary fossa shallow to deep, but not pocketed. Angular process of dentary ("hook") more subdued in advanced species due to posterior and dorsal expansion of insertion area for masseter, and with only slight mesial inflection. Weak (primitive) to strong (derived) lateral flare and weak (primitive) to strong (derived) mesial tuberosity on posteroventral border of mandible. Coronoid process low. Metapodials fused, equal to, or less than basal length of skull, becoming shorter in some derived species. Cranial material of *Protolabis* is illustrated in Figure 30.2.

Protolabis differs from *Tanymykter* in stronger buccinator fossa and generally narrower rostrum; basisphenoid without well-developed elongate tuberosities; P2 with weaker metastyle and parastyle and discontinuous lingual cingulum; P3 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 I1–3 in primitive species; stronger and more

caniniform C1/c1; more anteroposteriorly expanded M3/m3; deeper, more ventrally produced symphysis; deeper horizontal ramus; relatively stouter metapodials.

Average length of m2: 19.1–30.3.

Included species: *P. heterodontus* (known from localities CA9, SB32A, SP2A, CP54B, CP74B, CP75B, CP90A, CP114B, CP114D, CP116A); *P. barstowensis* (localities NB6C, NB6D, NB6E); *P. coartatus* (incl. *P. notiochorinos*) (localities GC6A, NB23C, SB6); *P. inaequidens* (= *Procamelus inaequidens*) (localities NB6E, CP114B); *P. gracilis* (*P.* cf. *gracilis*) (= *Procamelus gracilis*) (localities CP114A, CP114B).

Protolabis sp. is also known from localities CC17D, CC17G, CC17H, CC19, CC21C, NB3B, NB6B, ?NB7C, NB8, ?NB28, SB29C, SB32B, SB32C, SB32D, SB32E, SB32F, SB34A, CP73C, ?CP73D, CP75C, CP105, CP108A, CP108B, CP110, CP114A, CP114C, CP116B.

Michenia Frick and Taylor, 1971

Type species: *Michenia agatensis* Frick and Taylor, 1971.

Type specimen: AMNH 14255.

Characteristics: Dental formula I3–1/3, C1/1, P4/4–3, M3/3. I1–3 uncrowded, weak, and incisiform. I1–2 lost in derived species. C1 small, incisiform; c1 small, laterally compressed, and closely associated with incisors. The p1 suppressed in advanced species. P2–4/p2–4 progressively reduced, with p2 sometimes absent in advanced species. Molars taller crowned with weaker ribs, styles, and stylids, and M3/m3 more elongate, in advanced species. Slender horizontal ramus and shallow mandibular symphysis. Rostrum elongate and extremely narrow. Braincase short, rounded. Orbits large. Metapodials unfused (primitive) to fused (derived). Metapodials slender, becoming shorter and stockier in advanced species.

Differs from *Tanymykter* in more constricted rostrum and deeper buccinator fossa; relatively shorter braincase; weaker I3 and C1/c1; shallower symphysis; slender metapodials.

Average length of m2: 16.0–24.8 mm.

Included species: *M. agatensis* (known from localities NB3B, CP104B); *M. exilis* (including *M. australis*) (localities SB46, CP86D); *M. yavapaiensis* (localities SB6, SB33II); *M. deschutensis* (locality PN6H).

Michenia sp. is also known from localities NB6B, NB6C, NB6D, NB8, ?NB28, SB32A, SB32B, SB32C, SB32D, ?SB32E, SB32F, ?SB34A, CP51A, CP73D, ?CP74B, CP75C, ?CP104B, CP105, CP107, CP108A, CP108B, CP116A, NP10D, NP10E.

CAMELIDAE, INCERTAE SEDIS

Oxydactylus Peterson, 1904

Type species: *Oxydactylus longipes* Peterson, 1904.

Type specimen: CM 918.

Characteristics: Complete dental formula. I3, C1/c1, caniniform. I3 often as large as, or larger than, C1; distance between I3s equal to or greater than distance between C1s. P1/p1 two rooted, low crowned. P2–4/p2–4 more reduced than in *Gentilicamelus* and primitive *Nothokemas*. P3 relatively elongate and narrow, with a prominent parastyle as in *Gentilicamelus*, and with a strong internal cingulum, which is usually continuous. The p3–4 with well-developed, strongly lingually inflected paraconids; those of p3 are usually more strongly inflected than in *Miolabis*. Cheek teeth brachydont, although more hypsodont than in *Gentilicamelus*. Intercolumnar tubercles variably present on upper molars; rare on lower molars. Upper molars with strong external ribs and styles; ribs (especially on M3 metacone) weaker on later *Oxydactylus*. Paroccipital process at same level or slightly below bottom of lateral plate of auditory bulla; lateral plate at same level or above occlusal surfaces of upper molars. Auditory bulla relatively less inflated for size of skull than in *Poebrotherium*, *Paratylopus primaevus*, and *Gentilicamelus sternbergi*; bullar compression less extreme than in miolabines. Maxillary fossa shallow to deep and well defined but not pocketed; maxillaries depressed immediately beneath nasals. Palatine notch V shaped and extends as far forward as the anterior edge of the M3. Lower border of mandible relatively flat in contrast to *Aepycamelus*; slightly concave just in front of ascending ramus. Cervical vertebrae elongated; where known, elongation is greatest in third cervical. Limbs elongate, slender. Metapodials unfused, and longer than basal length of skull. Metacarpal length equal to or slightly shorter than metatarsal. Distal articular surface of proximal phalanx usually only slightly expanded dorsally, and with asymmetrical upper surface. Ungual phalanges high, narrow, and pointed. Smaller than *Aepycamelus*, with more brachydont, less massive dentition.

Average length of m2: 19.0–25.0 mm.

Included species: *O. longipes* (known from localities CC52, CP51A, CP104B, NP28B); *O. campestris* (locality CP103); *O. longirostris* (localities CP105, CP107); *O. lulli* (locality CP51A); *O. benedentatus* (localities ?CA2, GC3B); *O. wyomingensis* (locality CP52); *O. lacota* (localities CP86D, NP38B).

Oxydactylus sp. is also known from localities ?GC8C, SB4, SB28, ?CP45D, CP71, ?CP88.

Comments: *Oxydactylus* (Figure 30.1A) is a poorly understood taxon defined by elongate neck and limbs in combination with a primitive dentition; as apparent from past usage, *Oxydactylus* signifies a grade of camelid evolution and not necessarily a phylogenetically closely related group of species. *Oxydactylus* has at various times included species now referred to *Miotylopus*, *Nothokemas*, *Michenia*, and *Tanymykter*, and it is questionable whether all of the species currently referred to *Oxydactylus* actually belong there.

***Priscocamelus* Stevens, 1969 (in Stevens, Stevens, and Dawson, 1969)**

Type species: *Priscocamelus wilsoni* Stevens, 1969.

Type specimen: TMM 40849-1, formerly in UTBEG collection.

Characteristics: Complete dental formula. I3, C1/c1 caniniform. I3 larger than C1. P1/p1 double rooted, low crowned. Cheek teeth brachydont. P2–3/p2–4 long and narrow. P2 internal cingulum weak but continuous; P3 internal cingulum stronger but sometimes notched anteriorly. The p3 without posterolingual cusp seen in *Nothokemas*. Upper molars with very strong buccal ribs and styles; intercolumnar tubercles sometimes present. Lower molars less elongate, relatively wider, more brachydont, and with stronger ribs and stylids than in *Australocamelus*. Mandible shallower than in *Oxydactylus*, with downwardly convex lower border, and with less expanded masseteric insertion. Rostrum, C/c–P1/p1, and P1/p1–P2/p2 diastema shorter than in *Oxydactylus*. Palatine notch V shaped and extends as far forward as middle of M2. Cervical vertebrae shorter than in *Oxydactylus*. Metapodials unfused, longer than basal length of skull, and with metatarsus longer than metacarpus. Size smaller than in *Australocamelus*.

Average length of m2: 16.8–17.8 mm.

Included species: *P. wilsoni* only (known from localities SB46, SB47).

***Australocamelus* Patton, 1969**

Type species: *Australocamelus orarius* Patton, 1969.

Type specimen: TAMU 2466A, currently curated in TMM collections.

Characteristics: Dental formula I?/?, C?/?, P?/4, M?/3. The p1 two rooted; p2–4 unreduced, elongate, and narrow. The p1–2 diastema short. Molars subhypsodont, narrow. Mandible slender, becoming vertically constricted at p1–2 diastema. Differs from *Oxydactylus* in more shallow mandible and in laterally compressed premolars and molars (modified from Patton, 1969).

Length of m2: 21.7 mm (one specimen).

Included species: *A. orarius* only, known from locality GC3B only.

Australocamelus sp. is also known from localities SB32B, SB32D.

CAMELINAE

Characteristics: Dental formula I3–0/3, C1/1, P4–2/4–1, M3/3. I1–2 present in *Hesperocamelus* and some *Aepycamelus*. When present, P1/p1 caniniform and relatively high crowned, except where secondarily reduced. Cheek teeth relatively high crowned compared to *Oxydactylus*, with a trend of increasing hypsodonty and premolar reduction and loss. Maxillary fossa ranges from deeply pocketed to absent. Primitively, mandibular ramus convex downward along its entire lower border, rather than concave beneath ascending ramus. Metapodials fused, with metacarpus longer than metatarsus. (secondarily subequal in extant genera). On proximal phalanx, distal articular surface dorsally expanded.

Comments: In Simpson's (1945) classification, the Camelinae is a varied lot without tribal subdivision, similar to Matthew's (1904) "series B" with modifications. Webb (1965) brought some order into the subfamily when he divided it into three advanced tribes, Camelini, Camelopini, and Lamini, and an ancestral tribe, the Protolabidini. Harrison (1979) simplified this classification by discarding Camelopini, in effect showing that it is a polyphyletic tribe composed of members of the Lamini and Camelini. *Procamelus* was not assigned to the Lamini or Camelini because Harrison could find no derived features linking it to either tribe. However, both Harrison (1979) and Webb (1965, 1972) suggested a probable closer relationship of *Procamelus* with the camelines than the lamines.

Several derived features suggest that *Hesperocamelus* and *Aepycamelus* sensu lato should be included within the Camelinae (see Figure 30.3). In common with *Procamelus*, these two genera have a relatively narrow ramus with a convex lower border from front to back, a caniniform P1/p1, and fused metapodials. The metacarpus is longer than the metatarsus in *Aepycamelus* and *Procamelus*; the occurrence of this character in *Hesperocamelus* is uncertain. The earliest supposed species of *Aepycamelus*, "*A.*" *priscus* from the Sheep Creek Formation (locality CP108, early Miocene), has an unpocketed maxillary fossa, the primitive camelid condition that is also present in protolabines. A pocketed fossa on the maxillary, which in noncamelines is found in the otherwise very different stenomylines (anteromaxillary fossa) and some miolabines, appears for the first time in *Hesperocamelus*, some *Aepycamelus* from the Olcott Formation, and early *Procamelus* from the Miocene Olcott and Valentine formations (localities CP110, CP114); the latter two genera also show a distinct lateral inflation of the maxillary above the pocketed fossa and, usually, a rather broad rostrum in palatal view (note that not all later *Aepycamelus* have a pocketed maxillary fossa). *Hesperocamelus*, some later *Aepycamelus*, and *Procamelus* also show increased hypsodonty.

These similarities indicate to us that *Aepycamelus* and *Hesperocamelus* are more closely related to *Procamelus* than are the protolabines. This idea is not entirely novel: Matthew (1932) postulated that *Procamelus* was a derivative of *Alticamelus* (= *Aepycamelus*), and Frailey (1978) suggested a possible relationship between the two genera based on hypsodonty. We therefore remove the protolabines from the Camelinae and add *Aepycamelus* sensu lato and *Hesperocamelus* to that subfamily. The subfamily Aepycamelinae Webb (1965) (= Alticamelinae Simpson [1945]), which includes *Aepycamelus*, *Oxydactylus*, and various other genera depending on the author, is abandoned as paraphyletic.

Harrison (1979) raised the possibility that *Aepycamelus* and the Lamini are closely related. *Aepycamelus* shares with the dentally primitive lamine, *Hemiauchenia*, extremely elongate limbs and cervical vertebrae; some later *Aepycamelus* show the lamine features of strongly arched nasals and lower molars with anteroexternal stylids ("llama buttresses"). Moreover, *Aepycamelus* shares with the Lamini and Camelini a metacarpus that is longer than the metatarsus. For these reasons we include *Aepycamelus* within the Lamini.

"*Aepycamelus*" priscus Matthew, 1924

Type specimen: AMNH 14189

Characteristics: Dental formula I?3/3, C1/1, P4/4, M3/3. C1 laterally compressed. P1 compressed and caniniform with one root in type specimen. Maxillary fossa broad and subcircular but unpocketed. Cervical vertebrae not greatly elongated. Metapodials fused.

Average length of m2: unknown. Length of P2: 14.1 mm.

Included species: "*A.*" *priscus* only (known from localities ?CP107, CP108B).

***Hesperocamelus* Macdonald, 1949**

Type species: *Hesperocamelus stylodon* Macdonald, 1949.

Type specimen: UCMP 35382.

Characteristics: Complete dental formula. I1–3, C1, and P1 small, lingually curved, peglike, spaced, and forming more or less parallel rows on either side of rostrum, in contrast to *Aepycamelus*. I1–3 tending to wear blunt at tip. P1/p1 single or double rooted, and higher crowned than in protolabines. The c1 and p1 relatively small and flattened lingually; p1 high crowned, not recurved posteriorly, and leaf shaped. Upper cheek teeth relatively large, with premolars more massive, laterally expanded, and less reduced relative to molars, than in protolabines. Rostrum long and slender. Palate narrow, with weak buccinator fossa above P1 in contrast to most *Aepycamelus*. Maxillary fossa large, deeply pocketed posteriorly. Dentary with convex downward ventral border; angular "hook" prominent. Metapodials elongate, slender, fused, and longer than basal length of skull.

Average length of m2: 27.0–32.0 mm.

Included species: *H. stylodon* only (known from localities NB19C, NB21).

Hesperocamelus sp. is also known from localities CC21B, ?NB4, SB32B, ?CP110.

Comments: Macdonald (1949) distinguished *Hesperocamelus* from *Aepycamelus* (= *Alticamelus*) primarily on the basis of less robustness and smaller size, and included *Alticamelus alexandrae* Davidson (1923) in *Hesperocamelus*. However, "*H.*" *alexandrae* differs from *Hesperocamelus stylodon* in having robust, nonreduced I3, C1/c1, and P1/p1, a wide rostrum, and anteroposteriorly unexpanded molars; as pointed out by Macdonald (1949), it differs from *H. stylodon* also in slightly larger size and loss of I1–2. With its retention of I1–2 (primitive) and anteroposterior expansion of the molars (derived), *H. stylodon* seems to represent an evolutionary line distinct from "*H.*" *alexandrae*. The latter species shows similarities with *Aepycamelus elrodi* in the length of the cervical vertebrae, the unexpanded molars, the wide rostrum, and the robust I3, C1/c1, and P1/p1; accordingly, we have included *alexandrae* within *Aepycamelus*. Because of conflicting published data, metacarpal length versus metatarsal length in *Hesperocamelus* is uncertain, but we predict that future findings will support its position as sister taxon of the Lamini.

LAMINI

Characteristics: Dental formula I3–1/3, C1/1, P4–3/4–3, M3/3. C1/c1 recurved and laterally compressed, not extremely enlarged. P1/p1 present in *Aepycamelus*, *Alforjas*, and *Hemiauchenia*, lost in *Camelops*, *Palaeolama*, and *Lama*. The m1–3 with anteroexternal stylids ("llama buttresses") varying from weak in *Alforjas* to strong in *Lama*. Except in *Aepycamelus*, rostrum slender compared to that of Camelini. *Hemiauchenia*, *Palaeolama*, and *Lama* with facial shortening. Nasals arched in cross section. Mandibular diastemal crest sharp. Mandibular symphyseal region typically more procumbent than in Camelini. Metapodials fused; metacarpus longer than metatarsus (metacarpus and metatarsus subequal in *Lama*).

***Aepycamelus* Macdonald, 1956 (synonym: *Alticamelus*)**

Type species: *Aepycamelus giraffinus* (Matthew, 1909, in Matthew and Cook, 1909) (= *Alticamelus giraffinus*).

Type specimen: AMNH 9101.

Characteristics: Dental formula I3–1/3, C1/1, P4–3/4–3, M3/3. When present, I1–2 small, lingually curved, and peglike. Distance between I3s equal to or less than distance between C1s. I3, C1/c1, and P1/p1 caniniform, round, or laterally compressed, often heavy. P1/p1 single or double rooted. P2/p2 lost in derived species. The p3 with two roots, in contrast to most *Megatylopus*. Cheek teeth higher crowned than in *Oxydactylus*, lower crowned than in *Megatylopus*. The m1–3 with anteroexternal styles in some species. Premaxillaries form more V-shaped arc at front of palate than in *Oxydactylus*, and extend anterior to I1. Maxillary fossa often pocketed with the maxillaries inflated above the pocket. Palate typically broad, and usually with little or no constriction between C1 and P1, in contrast to protolabines. Nasals strongly arched in derived species. Angular process of dentary usually more prominent than in *Miolabis* or *Protolabis*. Dentary with convex ventral border. Neck long, with greatest elongation occurring in anterior cervical vertebrae. Limb elements slender, elongated; where known, femur and tibia elongated more than metapodials. Metapodials fused, longer than basal length of skull; metacarpus longer than metatarsus. Distal articular surfaces of proximal phalanges dorsally expanded, more symmetrical than in *Oxydactylus*. Skeleton very large and giraffelike in some species.

Average length of m2: 30.0–43.0 mm.

Included species: *A. giraffinus* (known from locality CP76); *A. proceras* (localities CP110, NP38C); *A. robustus* (localities NB23C, SP2A, CP114A, CP114B, CP114D, NP41B); *A. stocki* (localities NB23B, NP38E); *A. bradyi* (locality NB29); *A. elrodi* (locality NP41B); *A. major* (= *Megatylopus major*) (localities GC11A, GC11B, CP116A);

A. alexandrae (= *Hesperocamelus alexandrae*) (localities CC17E, CC22B, NB6E).

Aepycamelus sp. is also known from localities GC4B, GC4C, GC4E, GC6B, GC11C, GC12II, CC17B, CC17C, CC17D, CC18, NB3D, NB6B, NB6C, NB21, NB28, SB32A, SB32B, SB32D, SB32F, ?SP1A, SP1B, CP45E, CP49C, CP56, CP74B, CP75B, CP87B, CP114C, CP116B, NP38C, ?NC3B.

Blancocamelus Dalquest, 1975

Type species: *Blancocamelus meadei* Dalquest, 1975.

Type specimen: TMM 31179-20.

Characteristics: Known only from postcrania. Limbs, especially distal elements, extremely elongated and slender as in *Hemiauchenia* and *Aepycamelus giraffinus*, but more than one and a half times as long as in *Hemiauchenia*.

Included species: *B. meadei* only, known from locality SP5 only.

Blancocamelus sp. is also questionably known from locality SB50.

Hemiauchenia H. Gervais and Ameghino, 1880 (synonym: *Tanupolama*)

Type species: *Hemiauchenia paradoxa* H. Gervais and Ameghino, 1880.

Type specimen: Museo de la Plata 36.

Characteristics: Dental formula I1/3, C1/1, P3/2–3, M3/3. Less hypsodont cheek teeth than in any other lamine except *Palaeolama*. C1/c1 recurved and laterally compressed, c1 reduced. Diastemal crest on mandible sharp. Post-p1 diastema short in *H. vera*, progressively longer in *H. blancoensis* and *H. macrocephala*. The p3 present in *H. vera*, variably present with either one or two roots in later species. Lower molars with weak anteroexternal styles. Rostrum narrow and swollen above deep maxillary fossa with ridged anterodorsal border. Nasals arched and retracted, but not so far as in *Lama*. Palatine notch sharply V shaped, extending to posterior part of M2. Lacrimal vacuity not so reduced as in *Lama*. Limbs very long and slender, resembling *Blancocamelus* in proportion, but of smaller size. Metapodials fused and longer than basal length of skull. Proximal phalanx with W-shaped suspensory ligament scar not extending onto shaft.

Average length of m2: 23.0–35.0 mm.

Included species: *H. vera* (known from localities GC13B, NB10, SB9, SB34C, SB58A, SP3B, CP116D, CP116E, CP116F, CP123C, CP123D, CP126); *H. blancoensis* (localities GC14, GC17, SB14F, SB31C, SB50, SP1H, SP5, CP80, CP117B, CP128C, CP131, PN4); *H. macrocephala* (locality GC15); "*H.*" *minima* (localities GC11A, GC11B, GC11C).

Hemiauchenia sp. is also known from localities GC11B, ?GC13A, ?CC40 ("*Procamelus edensis*"), ?CC41, ?CC53, NB9, NB12B, NB13B, NB13C, NB31, NB32B, NB34, SB10, SB13, SB14B, SB15, SB16, ?SB17 ("*Procamelus longurio*"), SB18A, SB34A, SB35, SB37, SB48, SB49, SB58B, SB60, SB65, SP1B, SP1C, SP1D, SP1F, SP3A, SP4B, CP90A, CP94, CP97, CP114D, CP116B, ?CP116C, CP117A, CP118, CP121, PN3C, PN12, ?PN14, PN23A, PN23C.

Comments: As discussed by Webb (1974), *Tanupolama* is a junior synonym of *Hemiauchenia*. Webb, MacFadden, and Baskin (1981) suggested that a new generic name may be appropriate for "*Hemiauchenia*" *minima* from the Mixon Bone Bed (locality GC11B) and Love (locality GC11A) local faunas.

Palaeolama P. Gervais, 1867

Type species: *Palaeolama weddelli* (P. Gervais, 1855) (= *Auchenia weddelli*).

Type specimen: Metacarpus without published number in Muséum National d'Histoire naturelle, Paris.

Characteristics: Dental formula I1/3, C1/1, P3/2 or 3, M3/3. Cheek teeth lowest crowned among the Lamini. I3 caniniform. P3 with variable lingual crescent stronger than in *Hemiauchenia*; p3 reduced. P4 with bilobate ectoloph; p4 with complex infolding. M1–3 with strong external styles and anterior ribs; m1–3 with anteroexternal style. Limbs stocky. Metapodials shortened and robust.

Average length of m2: 19.0–23.0 mm.

Included species: *P. mirifica* (Pleistocene); *P. guanajuatensis* (known from locality SB58B). *P. weddelli* and *P. aequatorialis* are restricted to South America.

Alforjas Harrison, 1979

Type species: *Alforjas taylori* Harrison, 1979.

Type specimen: F:AM 40821.

Characteristics: Dental formula I1/3, C1/1, P3/3, M3/3. Cheek teeth more hypsodont than any lamine but *Camelops*. I3 and C1/c1 recurved and laterally compressed. The i1–3 more broadly spatulate than in *Lama* or *Hemiauchenia*. P1/p1 very small and single rooted. M1–3 with external styles not so strong as in *Palaeolama*, and with much weaker ribs. P1–P3 diastemal crest heavier and more curved as in *Camelops*. Lower molars with anteroexternal styles weak or absent. Rostrum long and slender as in *Camelops* with little facial shortening. Maxillary fossa deeper than in *Lama* or *Hemiauchenia*. Nasals strongly arched transversely. Lacrimal vacuity large. Palatine notch extends only to posterior border of M3. Mandible deeper than in *Hemiauchenia* or *Palaeolama* with long posteriorly hooked coronoid process and strongly inflected angular process. Limbs not as elongated as in *Hemiauchenia* or as heavy as in *Camelops* or *Palaeolama*. Metapodials fused and shorter than basal length of skull. Proximal phalanx with uneven W-shaped suspensory ligament scar as in *Lama* and *Hemiauchenia*, but extending farther down the shaft.

Average length of m2: 28.0–39.0 mm.

Included species: *A. taylori* only (known from localities NB32A, SP3B, CP123D).

Alforjas sp. is also known from localities SB9, SB10, SB33II, ?SB58A, SP1D, CP78, ?CP116C, CP116D.

Camelops Leidy, 1854

Type species: *Camelops kansanus* Leidy, 1854.

Type specimen: USNM 154.

Characteristics: Dental formula I1/3, C1/1, P2/1, M3/3. Cheek teeth very hypsodont. I1–2 lost. I3 recurved and caniniform, larger than C1. C1/c1 very reduced and laterally compressed. The c1–p4 diastemal crest very sharp. P1 and P2/p2 lost; p1 rarely present. P3 and p4 reduced. P4 quadrate. Molars slender in relation to length. M1–3 with reduced external styles. Lower molars with anteroexternal stylids stronger than in *Alforjas*, weaker than in *Lama*, *Palaeolama*, or *Hemiauchenia*. Premaxilla robust as in *Alforjas*, but in contrast to *Lama* and *Hemiauchenia*. Rostrum long and slender with little facial shortening. Maxillary fossa deep, but not pocketed. Lacrimal vacuity very large. Nasals very strongly arched transversely. Mandible deeper than in other lamines due to increased hypsodonty. Angular process small. Body size largest of lamines with possible exception of *Blancocamelus*. Limbs long, but stocky. Metapodials robust and somewhat shortened. Proximal phalanx with raised suspensory ligament scar extending almost to center of shaft.

Average length of m2: 31.0–44.0 mm.

Included species: *C. kansanus* (Pleistocene); *C. traviswhitei* (known from localities SB18A, SB18B, SP5); *C. sulcatus* (Pleistocene); *C. huerfanensis* (Pleistocene); *C. minidokae* (Pleistocene), *C. hesternus* (locality SB37 [possibly Irvingtonian]).

Camelops sp. is also known from localities ?CC53, NB13B, NB13C, NB36, SB13, SB14A, SB14B, SB14C, SB14D, SB14E, SB14F, SB15, SB16, SB18C, SB31C, SB37, SB50, SB65, SP1H, CP95 (*C. "vacondae"*), CP117B, CP118, CP121, CP130A, CP132B, PN4, PN23A.

Pliauchenia Cope, 1875

Type species: *Pliauchenia humphresiana* Cope, 1875.

Type specimen: USNM 2630.

Included species: *P. humphresiana* (known from locality SB32B); "*P.*" *magnifontis* (localities CP90A, CP90B, CP116B).

Comments: *Pliauchenia* was named for a fragmentary ramus containing the c1 and p1 alveoli, the p3–4 roots, a worn, broken m1, and the m2 roots, obtained from the "Santa Fe marls." Cope diagnosed *Pliauchenia* as a camel having lost the p2, thereby being intermediate between *Procamelus* with four lower premolars and the extant *Camelus* and *Lama* ("*Auchenia*") with two and one lower premolars, respectively (Cope, 1875, 1877). Since Cope's description, camelids have at various times been referred to *Pliauchenia* on the basis of lack of p2, most notably "*P.*" *magnifontis* from Big Spring Canyon (locality CP90A) (Gregory, 1942). Based on a partial skeleton, "*P.*" *magnifontis* supposedly showed for the first time associated upper and lower dentitions of *Pliauchenia*. *Pliauchenia* has also generally been thought to be in the direct line of ancestry of some later camelids, most notably the lamines.

There are problems, however, with the concept of *Pliauchenia*. The first concerns the generic diagnosis and the fragmentary nature of the type specimen, and authors have disagreed on whether or not an alveolus for a small p2 is in fact present on the type (Matthew, 1901; Matthew and Cook, 1909; Gregory, 1942). In fact, the jaw is broken in the p2 position, making it uncertain whether or not the tooth was present. Even if the p2 was proven to be absent, phylogenetic loss of p2 by itself is not a good generic criterion, as this loss occurs in several different camelid lineages (stenomylines, miolabines, protolabines, and camelines). Secondly, comparisons are usually made with the better preserved "*Pliauchenia*" *magnifontis* instead of with the type. "*P.*" *magnifontis*, however, differs from *P. humphresiana* in having a single-rooted, trenchant p1 not unlike the p1 of *Procamelus*. Although the p1 is missing in *P. humphresiana*, its alveolus indicates a double-rooted tooth. At least in some camelids (*Protolabis* and *Procamelus*), a single- versus a double-rooted p1 is of generic significance (Honey and Taylor, 1978).

It is not certain that any of the later described species of *Pliauchenia* belong to the same genus as the type specimen. Galusha and Blick (1971) considered *P. humphresiana* to be from the Skull Ridge Member of the Miocene Tesuque Formation (locality SB32B); of the camels we list from that member, *P. humphresiana* seems most closely to resemble *Protolabis*. However, detailed comparisons need to be made with all Skull Ridge camelids to prove any synonymies, if that is even possible considering the poor preservation of the type specimen of *Pliauchenia*.

CAMELINI

Characteristics: Dental formula I2–0/3, C1/1, P4–2/4–2, M3/3. Medium to giant camels more closely related to Asian *Camelus* than to New World *Lama*. The p1 lost in *Titanotylopus*. Except in *Procamelus*, molars with more strongly developed styles and ribs and more square occlusal outline than in lamines. Nasals flattened in cross section. Diastemal crest on mandible reduced and rounded. Angular process moderate in *Procamelus*, becoming large and strongly inflected in remaining Camelini. Maxillary fossa pocketed primitively (*Procamelus*), secondarily reduced in remaining genera. Lambdoidal and sagittal crests far more prominent than in other Camelinae.

Procamelus Leidy, 1858

Type species: *Procamelus occidentalis* Leidy, 1858.

Type specimen: USNM 797.

Characteristics: Dental formula I2–1/3, C1/1, P4/4, M3/3; I2 present in primitive species. I3 and C1/c1 laterally compressed and bladelike in females; large, conical, and recurved in males. P1/p1 single rooted, caniniform, often as large as I3; p1 bladelike and recurved. Cheek teeth longer and more hypsodont than in protolabines. The p2 little reduced. The p3 and p4 with posterior cusps usually wider than middle cusps. P3 internal crescent incomplete. Lower molars usually without anteroexternal stylids. Mandibular symphysis long and forms a shallow angle with horizontal body of ramus. As in *Aepycamelus* but in contrast to *Oxydactylus*, the ventral border of the ramus is smoothly convex, without a slight concavity beneath the ascending ramus. Angular process of dentary is well developed (strong "hook"), knoblike, and mesially inflected. Coronoid process long. Palate wide as in most *Aepycamelus*, and with greatest constriction beginning posteriorly to P1. Maxillary fossa usually deeply depressed and pocketlike, with maxillaries inflated above fossa. Nasals transversely flattened. Postglenoid foramen large. Paroccipital process usually projects below auditory bulla. Prominent lambdoidal and sagittal crests. Metapodials fused with metacarpals longer than metatarsals. Distal articular surfaces of proximal phalanges dorsally expanded and tend to be symmetrical.

Average length of m2: 24.0–35.0 mm.

Included species: *P. occidentalis* (known from localities GC6B, CP114A, CP114B, CP115A, NP41B); *P. leptocolon* (localities CP76, CP110); *P. grandis* (localities CA9, CA10, GC6B, GC11A, SP2A, CP56, CP90A, CP90B, CP114C, CP114D, CP116A, CP116B, PN10).

Procamelus sp. is also known from localities GC6B, ?GC11C, GC12II, CC17G, CC17H, ?NB6E, ?NB7C, NB28, ?SB7, ?SB32B, SB32D, SB33II, SP1A, SP1B, SP3A, CP87B, CP114C, CP115C, CP123A, CP126, NP11, NP42, PN11, ?PN13.

Comments: Since the naming of the genus by Leidy in 1858, numerous species have been referred to *Procamelus*. The genus was briefly reviewed by Gregory (1942) and Webb (1969), and studies by Patton (1967, 1969), Webb (1969), Honey and Taylor (1978), and Voorhies (1986) have reduced the number of nominal species of *Procamelus*. Additional species should be removed from *Procamelus*. *Procamelus inaequidens* Matthew (in Cope and Matthew, 1915, Plate CLIV), figured but never described, is here referred to *Protolabis* based on the following features: small braincase, constricted rostrum, double-rooted P1/p1, more upright mandibular symphysis, subdued angular process, and low coronoid process. *Procamelus gracilis* Leidy (1858) includes "several isolated teeth and small fragments of jaws with single teeth" (Leidy, 1869, p. 155). It is not certain whether all specimens came from the same species or individual, but at least the illustrated p2–4 (Leidy, 1869, Plate XIV, Figure 15) could have come from the same species. These premolars are smaller than in typical procamelines, lower crowned, and morphologically similar to the premolars of protolabines. In addition, the p1 referred by Leidy to *P. gracilis* is double rooted, a condition unknown in *Procamelus* but present in many protolabines. In faunal lists reporting USNM material from Nebraska Barstovian localities, including sites along the Niobrara River Valley from which the type of *P. gracilis* was collected, Voorhies (1990b) reassigned *P. gracilis* to *Protolabis*; herein we accept Voorhies's reassignment. *Procamelus leptognathus* is a small slender-jawed form from the Clarendon fauna and has never been illustrated or thoroughly described. Webb (1969) suggested a possible relation to "*Procamelus*" *gracilis* and "*Procamelus*" *coartatus* (now *Protolabis coartatus*); it also may be a small lamine. The premolar region of the lower jaw is not preserved. This species is almost certainly not *Procamelus* as that genus is now understood, and it is best considered indeterminate until more adequately described.

Megatylopus Matthew and Cook, 1909

Type species: *Megatylopus gigas* Matthew and Cook, 1909.

Type specimen: AMNH 14071.

Characteristics: Dental formula I1/3, C1/1, P3/4–3, M3/3. Cheek teeth more hypsodont than in *Titanotylopus*, but much less so than in *Megacamelus*, *Gigantocamelus*, and *Camelus*. I3 and C1/c1 large and rounded, but smaller than in other Camelini except *Procamelus*. P1/p1 present. P3/p3 reduced. Nasals flattened in cross section. Limbs long without distal shortening typical of *Gigantocamelus* and *Camelus*. Metapodials longer than basal length of skull.

Average length of m2: 39.0–50.0 mm.

Included species: *M. gigas* (known from localities CP78, CP115D, CP116C, CP116E, CP123D, CP126, NP45); *M. matthewi* (localities NB10, SB9, SB34C, SB58B, SP1D, SP3B); *M.*(?) *cochrani* (localities CP117A, CP128B, PN3C); *M.*? *primaevus* (localities GC6B, CP116B, NP38G).

Megatylopus sp. is also known from localities GC11B, ?CC17H, ?CC41, ?NB7C, NB9, ?NB23C, NB27B, ?NB31, NB36, SB10, ?SB17 ("*Procamelus coconinensis*"), SB34A, SB34B, ?SB48, ?SB57, ?SB60, SP1A, SP1B, SP1C, SP1H, SP3A, SP4B, ?CP90A, ?CP114C, CP114D, CP115B, CP115C, CP116A, CP116D, CP123D, ?NP5B, ?PN3B, PN10, PN11, PN12, PN13, PN15, PN23A.

Comments: The taxonomic status of *Megatylopus primaevus* is uncertain. Described by Patton (1969) as the most primitive species of *Megatylopus*, due to retaining a small, possibly nonfunctional p2 and having a larger and more complex p3 than other species of the genus, *M. primaevus* was considered "similar and probably closely related" (p. 167) to the slightly more advanced *Megatylopus major*.

With the reassignment of *M. major* to *Aepycamelus* (Webb, MacFadden, and Baskin, 1981; Harrison, 1985), it might be logical also to reassign *M. primaevus* to *Aepycamelus*, thus returning to a diagnosis of *Megatylopus*, which includes the loss of p2. However, in reporting the occurrence of *Megatylopus* cf. *primaevus* in Nebraska, Leite (1990) noted that *Megatylopus* has shorter limbs and more hypsodont teeth than *Aepycamelus*. Considering that the systematics of both *Megatylopus* (Voorhies and Corner, 1986) and *Aepycamelus* are not well understood, we prefer to questionably retain the species *primaevus* in *Megatylopus* until more definitive studies are made.

The relationship of *Megatylopus* to *Paracamelus*, the common Old World Pliocene camelid, is controversial, and *Megatylopus* has sometimes been considered a junior synonym of *Paracamelus* (Macdonald, 1959). Although this synonymy has generally been rejected in recent years (Webb, 1965), Voorhies and Corner (1986) suggested that further investigation of the problem is warranted.

Titanotylopus Barbour and Schultz, 1934

Type species: *Titanotylopus nebraskensis* Barbour and Schultz, 1934.

Type specimen: USNM 2606.

Characteristics: Dental formula I?/3, C?/1, P?/2, M?/3. Skull and upper dentition unknown. Cheek teeth most brachydont of tribe. The i3–c1 diastema much longer than in *Gigantocamelus*. The c1 large and rounded, but not splayed. The p1 absent; p3 double rooted and more reduced than in *Megatylopus*.

Average length of m2: broken in type. Estimated length of m3 in type: 65.0 mm.

Included species: *T. nebraskensis* only (known from localities NB13B, NB13C, SB18A, ?CP96, CP121).

Megacamelus Frick, 1929

Type species: *Megacamelus merriami* (Frick, 1921) (= *Pliauchenia merriami*).

Type specimen: UCMP 23483.

Characteristics: Dental formula I1/3, C1/1, P3/3, M3/3. Cheek teeth less hypsodont than in *Gigantocamelus*. I3 large and caniniform in contrast to *Gigantocamelus*. C1/c1 large and rounded, but only slightly splayed. The i1–3 spatulate but not transversely arrayed. The i3–c1 diastema longer than in *Gigantocamelus*, shorter than in *Titanotylopus*. P1/p1 large and caniniform. M1–3 with strong external styles. Premaxilla very robust, but not so massive as in *Gigantocamelus*. Nasals transversely flattened. Lacrimal vacuity variable. Mandibular symphysis extends beyond c1 but not so far as in *Titanotylopus*. Distal limb elements more shortened than in *Megatylopus*, less so than in *Gigantocamelus*.

Average length of m2: 48.0–55.0 mm.

Included species: *M. merriami* only (known from localities CC40, SB11, CP116F).

Gigantocamelus Barbour and Schultz, 1939

Type species: *Gigantocamelus spatula* (Cope, 1893) (= *Pliauchenia spatula*).

Type specimen: not numbered by Cope or Meade.

Characteristics: Dental formula I1–0/3, C1/1, P3/3, M3/3. Cheek teeth more hypsodont than in *Megacamelus* or *Megatylopus*. I3 vestigial or lost. C1/c1 rounded and extremely large. The i1–3 spatulate and transversely arrayed. Mandibular symphysis barely extends beyond widely splayed c1. Chin blunt in contrast to *Titanotylopus*. The i3–c1 diastema very short. P1/p1 present, but variable in female rami. M1–3 with very strong external styles. Premaxilla heavy and robust. Nasals transversely flattened. Lacrimal vacuity reduced or absent. Maxillary fossa reduced. Distal limb elements shortened as in *Camelus*. Metapodials shorter than basal length of skull. Proximal phalanx very short and stocky.

Average length of m2: 44.0–60.0 mm.

Included species: *G. spatula* only (known from localities SP5, CP97, CP117A, CP117B, CP118, CP121, CP128B).

Gigantocamelus sp. is also known from localities SB38, SB49, CP80, CP94, CP131, PN23C.

INDETERMINATE CAMELIDS

Fragmentary remains ascribed to camelids are also known from localities WM21A, WM21B, GC9C, GC27, GC28, CC9B2, CC23, CC25A, CC25B, CC26B, CC32A, CC35A, CC36, CC38, CC39B, NB7D, NB11, NB18, NB27A, SB12, SB19, SB59, SB63, SB64, CP123E, CP130B, NP5A, NP25C, NP32B, NP34B, NP34D, NP40A, PN6F, PN8B, PN9B. Undoubtedly, indeterminate camelid fossils occur at many more localities than mentioned herein.

BIOLOGY AND EVOLUTIONARY PATTERNS

Camelids were a highly successful group in North America in the Cenozoic; in this chapter we record 95 species distributed among 36 genera. Although future study will likely demonstrate synonymies, we expect that the total number of genera and species of camelids will increase through the description of new forms.

In the broad view, there were four camelid radiations in North America (Figures 30.5 and 30.6). The first was the Chadronian through earliest Arikareean (late Eocene through mid-Oligocene) evolution of the archaic camelids *Poebrotherium* and *Paratylopus*. The second was the Whitneyan through Arikareean (late Oligocene to early Miocene) radiation of the stenomylines; during the early Arikareean stenomylines were dominant, and nonstenomylines (*Gentilicamelus*, *Poebrotherium*) were rare. Although *Blickomylus* (Fig. 30.4) and *Rakomylus* evolved later, the stenomylines never again achieved the success of the early Arikareean, and they went extinct in the early Barstovian (middle Miocene).

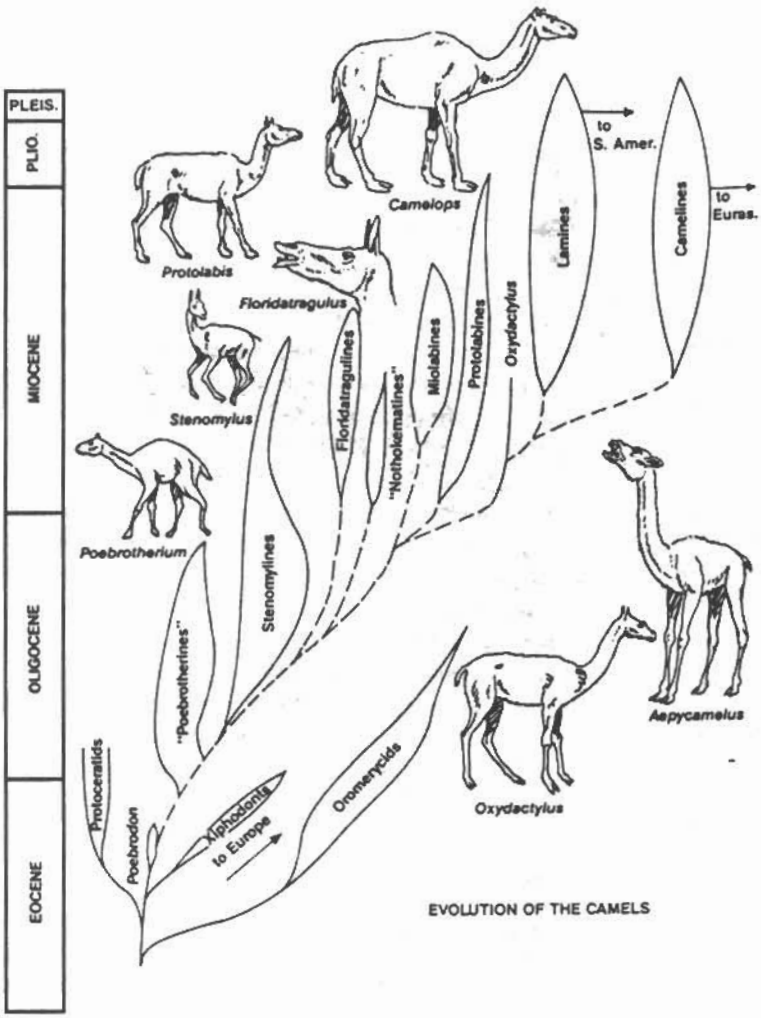

Figure 30.5. Evolution of the camels (Illustration by Clifford R. Prothero.)

Probably the most striking event in camelid history is the appearance of "higher camelids" (those with metastylids on the lower molars) in the late Oligocene and early Miocene (early and late Arikareean), marking the third major radiation. In the late Arikareean the number of camelid genera more than doubled. The Arikareean appearance of higher camelids, however, was not a single event. *Gentilicamelus*, from the John Day Formation, was probably found in the Arikareean Turtle Cove Member (locality PN6D). In Nebraska the earliest higher camelid, *Oxydactylus* (Fig. 30.1A), is found in the late Arikareean Harrison Formation (locality CP103, Miocene); but *Tanymykter* and *Michenia* do not occur until the overlying Marsland Formation (locality CP104B, Miocene); cf. *Protolabis* also does not occur until late late Arikareean. *Gentilicamelus sternbergi* would appear to be a fairly good structural ancestor for *Priscocamelus*, *Oxydactylus*, and *Tanymykter*. *Gentilicamelus* was not derived from the stenomylines with their reduced mesostyles, but may have come from *Paratylopus*.

A fourth major radiation of camelids began in the late Hemingfordian and early Barstovian (late early to early middle Miocene) with the evolution of the Camelinae. *Aepycamelus* sensu lato may have been the ancestral taxon for both the Lamini and Camelini: early *Procamelus* shows a striking resemblance to *Aepycamelus*, and later *Aepycamelus* acquire certain lamine characteristics. By the latest Barstovian at the youngest, and possibly earlier in the Barstovian, the camel-llama split had occurred. With the diversification of the Camelinae in the Barstovian and later, the more archaic groups such as the protolabines and miolabines decline to their late Miocene extinction in the later Hemphillian (based on the occurrence of an undescribed protolabine genus in the Wickieup local fauna [locality SB9] [MacFadden, Johnson, and Opdyke, 1979]), although they were apparently last abundant only in the Clarendonian (late Miocene). Total known generic diversity in the late Blancan (late Pliocene) was 5 genera (questionably 6), down from highs of 11 to 13 genera in the Hemingfordian and Barstovian. Only 3 genera survived into the Rancholabrean (late Pleistocene).

The appearance of camelids in the late Eocene to early Oligocene coincided with a drying trend that produced the first areas of true savanna in North America (Webb, 1977). The limb morphology of *Poebrotherium* suggests that camelids were adapted to a cursorial existence in more open habitat by the early Oligocene; *Poebrotherium*

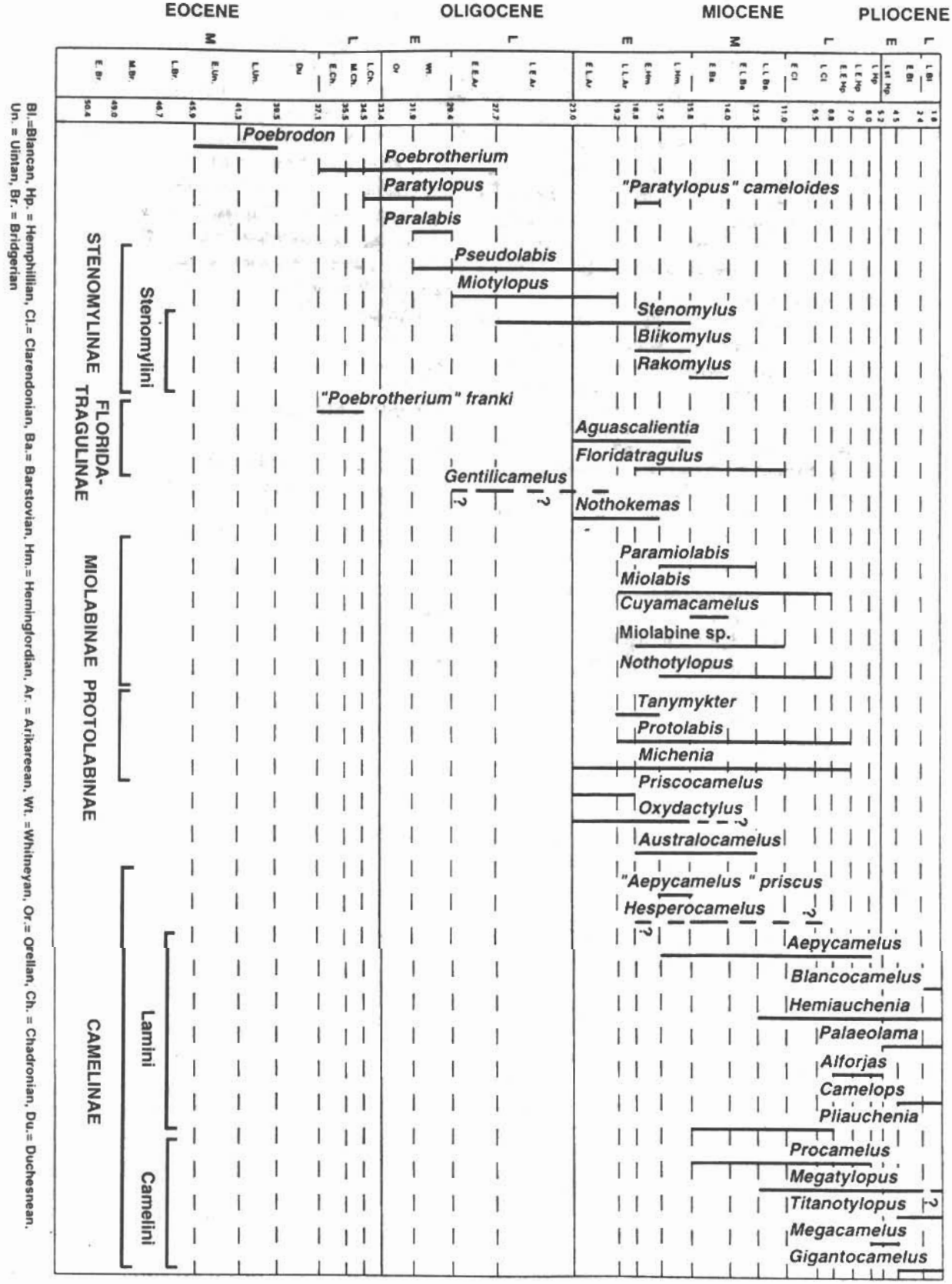

Figure 30.6. Temporal ranges of North American camelid genera.

has very elongate axial metapodials, reduced lateral metapodials, and sharp ungual phalanges. Unlike the living camelids, which are digitigrade and have padded feet, *Poebrotherium* was unguligrade and its ungual phalanges probably bore deerlike hooves (Webb, 1972). The padded feet and digitigrade stance of living camelids is a secondary condition probably associated with the development of a pacing mode of locomotion; correlative changes include fused metapodials and fore- and hindlimbs more equal in length (Webb, 1972). The phalanx morphology of the earliest camelines, *Procamelus* and *Aepycamelus*, and that of the protolabines *Protolabis* and *Michenia*, indicate that these camelids were digitigrade; a transitional morphology is shown by *Oxydactylus* and *Tanymykter*. It is possible that this transition from unguligrade to digitigrade stance occurred more than once within the Camelidae.

Miocene and later camelids evolved very different adaptations. Early and middle Miocene stenomylines were the most hypsodont of all camelids. Late Arikareean *Stenomylus*, which is found nearly everywhere except Florida, had gazellelike proportions and an unguligrade stance, suggested by its slender, pointed ungual phalanges (Scott, 1937) and its proximal phalanges showing only incipient proximodorsal expansion of the distal articular surface; *Stenomylus* probably occupied open habitats. The later stenomylines were more restricted in distribution (Wyoming, Colorado, New Mexico, Mexico), and in the United States may have been adapted to more arid habitats (Webb, 1977; Munthe, 1979). The "giraffe-camel" *Aepycamelus*, as evidenced by its extremely long limbs and cervical vertebrae, and only moderately high crowned teeth, was presumably a high-level savanna browser. *Aepycamelus* probably was the New World ecomorph of the Old World giraffe. *Aepycamelus* disappeared in the Hemphillian (late late Miocene), probably as a result of the restriction of woodland savanna and spread of steppe (Webb, 1977). Its likely predecessor, *Oxydactylus* (Fig. 30.1A), shows the beginnings of these limb and vertebral specializations; a gerenuklike habit of standing on its hind legs to reach the highest browse has been suggested for *Oxydactylus* (Janis, 1982). A study that included specimens of the camelids *Hemiauchenia*, *Alforjas*, *Palaeolama*, *Camelops*, *Procamelus*, and *Megatylopus* indicated that they also were browsers or at most intermediate feeders; none were grazers (Dompierre and Churcher, 1996).

At the opposite extreme from the "giraffe-camels" are the short-legged miolabines and derived protolabines. The short legs (seen particularly in the metapodials) is a secondary, derived condition of later protolabines and probably also of the miolabines; in protolabines, for example, the metapodials became progressively shorter and relatively more stocky over time. Janis (1982) suggested that the protolabines were ground-level feeders. The extremely constricted rostrum of derived *Protolabis* was thought to indicate highly developed labial and buccal musculature (Honey and Taylor, 1978). In conjunction with the relatively short metapodials, the constricted rostrum may also indicate a feeding behavior pattern of selective low-level browsing and grazing.

Floridatragulines (Fig. 30.1B) are reported primarily from relatively low latitudes. Their most primitive and/or earliest occurrences appear to have been in and adjacent to Mexico (Trans-Pecos Texas), but during the Hemingfordian the group spread eastward along the Gulf Coastal Plain. Floridatraguline habitats have been interpreted as savanna or open woodland, where the floridatragulines were probably selective browsers as evidenced by their brachydont, selenodont dentitions and greatly elongated, slender rostra. The association of *Heloderma*, the gila monster, with floridatragulines (Stevens, 1977; but also see Estes, 1963) certainly suggests that their environment was subtropical, but such environments then also existed elsewhere (Dorf, 1959; Webb, 1977). In a faunal list, Voorhies (1990b) reported *Floridatragulus* sp. from the late Barstovian Valentine Railway Quarries of Nebraska; this is the only reported occurrence of a floridatraguline north of Texas. Why floridatragulines rarely ventured northward into other subtropical savanna parklands of North America is unresolved. The distribution of floridatragulines may have been determined by a subtle environmental factor difficult to detect from the fossil record, such as the distribution of one or more sensitive plant food species.

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