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Problems in the nomenclature of North American Pleistocene camelids

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Five nominal genera of camels have been recorded from the Pleistocene of North America. No nomenclatur problems seem evident with *Palaeolama mirifica*, a southern species that ranged north to Florida and the Gulf Coast of Texas. *Palauchenia mexicana*, described from a lower jaw in 1869, is now known only from drawings prepared from photographs. The jaw is probably lost. *Titanotylopus nebrascensis* is known only from a lower jaw collected in Nebraska and described in 1934. It is possible that this name is synonym of *Palauchenia mexicana*, but this is uncertain. The many nominal species of llamas of the genus *Hemiauchenia* are, except for the Hemphillian *H. macrocephala vera*, probably synonyms of *H. macrocephala* (Cope). Some of the numerous nominal species of *Camelops* are probably valid but available materials seem to be inadequate for a generic revision.

Four or five genera of camels lived in North America in the Pleistocene epoch. The nomenclature and taxonomy of three of these are, for different reasons, confusing, and reference of fossils to species must be tentative. *Palaeolama mirifica* (Simpson) has been found in Florida and the Gulf Coast of Texas but, if there are any nomenclatorial problems with this species, they are not now evident (see Webb, 1974). Major problems involve the genera *Palauchenia*, *Titanotylopus*, *Hemiauchenia*, and *Camelops*. It seems appropriate to call attention to these problems as a first step in their solutions.

Three of the problematic genera are readily separated by characters of their lower dentitions. *Titanotylopus* has non-procumbent incisors, a canine of moderate size that is laterally compressed and recurved, and a third premolar of modest size with two roots. *Titanotylopus* was a "giant" camel. *Hemiauchenia* was a small camelid, little if any larger than the domestic llama. There are three procumbent lower incisors, a small, compressed, fang-like canine, P_1 may or may not be present (P_2 is absent in all advanced camels), P_3 is variable in occurrence and size but two-rooted when present, and P_4 small but high-crowned, becoming part of the functional occlusal surface. *Camelops* includes large to medium-sized camels with relatively hypsodont teeth. The three incisors are procumbent, the canines compressed and recurved, P_1 and P_3 absent, and P_4 a small but functional cheek tooth.

Palauchenia mexicana del Castillo, 1869

Principal synonyms:
Palauchenia mexicana del Castillo, 1869.
Palauchenia magna Owen, 1870.
Gigantocamelus magna (Owen), Maldanodo-Koerdell, 1948.
Gigantocamelus mexicana (del Castillo), Silva-Barcenas, 1969.
Camelops mexicanus (del Castillo), Dalquest, 1974.

The Mexican giant camel was described by del Castillo from a site near modern Tacabaya, Mexico City, in 1869. The description was based on a poorly preserved lower jaw with dentition that probably no longer exists. The following year Robert Owen described the same material as *Palauchenia magna*, based on photographs of the dentition furnished by del Castillo. The name was ignored by workers in the United States (see Dalquest 1974, for details). Dalquest placed the name in the synonomy of *Camelops*, as an expedient.

The fossil was discovered "in or beneath volcanic tufa" and was "associated with remains of *Elephas* and *Mastodon*" (Owen 1870). It is almost surely of Pleistocene age (Silva-Barcenas 1969) and probably from the "Becerra Formation" of Arellano & Bryan (1948). Miller & Carranza-Castaneda (1984) question the validity and utility of the "Becerra Formation."

Dalquest (1974) compared *Palauchenia mexicana* with *Gigantocamelus spatula* (Cope) but not with *Titanotylopus* because, at that time, *Titanotylopus* was considered a synonym of *Gigantocamelus*. No other specimens have been referred to *Palauchenia*. However, Dalquest probably erred in placing *Palauchenia* in *Camelops* and the genus is probably valid.

Titanotylopus nebrascensis Barbour and Schultz, 1934

Principal synonyms:
Titanotylopus nebrascensis Barbour and Schultz, 1934.
Gigantocamelus spatula (Cope), Webb, 1965.
Gigantocamelus nebrascensis (Barbour and Schultz), Breyer, 1976.
Titanotylopus nebrascensis, Barbour and Schultz, Harrison, 1985.

The nomenclature of the Nebraskan Pleistocene giant camel has involved much confusion. In 1934 Barbour & Schultz described *Titanotylopus nebrascensis*, based on a lower jaw from near Red Cloud, Webster County, Nebraska. The holotype is an almost complete right lower jaw ramus with entire symphysis, but some teeth are damaged or missing. The non-procumbent lower incisors are a unique diagnostic feature.

Five years later Barbour & Schultz (1939) named another giant camel, *Gigantocamelus fricki*, from Nebraska. Meade (1945) found that *Gigantocamelus fricki* and a giant camel, *Pliauchenia spatula* (Cope, 1893), of the Blanco local fauna of Texas, were conspecific. The Texas camel did not belong in the genus *Pliauchenia*, and therefore the proper name for the taxon was *Gigantocamelus spatulus* (Cope). Webb (1965) thought that *Titanotylopus nebrascensis* was also a synonym of *Gigantocamelus spatulus*, and his usage was followed until Breyer (1976) pointed out that *Titanotylopus nebrascensis* was specifically distinct from *Gigantocamelus spatulus*. Harrison (1985) found the two taxa to be generically distinct. The nomenclature had made a full turn. *Gigantocamelus* is considered a monotypic Blancan genus; *Titanotylopus* a monotypic Pleistocene genus.

Barbour & Schultz (1934) noted that the holotype lower jaw was found in a small pit near Red Cloud, Webster County, Nebraska, "33 feet below the surface in Pleistocene gravel of supposed Kansan age." Although no evidence of Pleistocene age is given, no subsequent worker has questioned the assigned age. The good preservation of the elongated jaw indicates that reworking from older deposits is unlikely for transportation would probably have damaged the specimen. No camelids like the holotype have been reported from earlier deposits. The relative position of the specimen, in the Pleistocene, seems unknown.

Recognition of *Titanotylopus* as a genus distinct from *Gigantocamelus* demands comparison with *Palauchenia*. The incisors of *Palauchenia mexicana* are unknown. In the holotype lower jaws of both *P. mexicana* and *T. nebrascensis* the canines are of only moderate size, and differ from the tusk-like canines of *Gigantocamelus*. *Titanotylopus* lacks the vestigial P_1, present in the *Palauchenia* jaw. This probably is not significant. The tooth varies in presence in *Hemiau-*

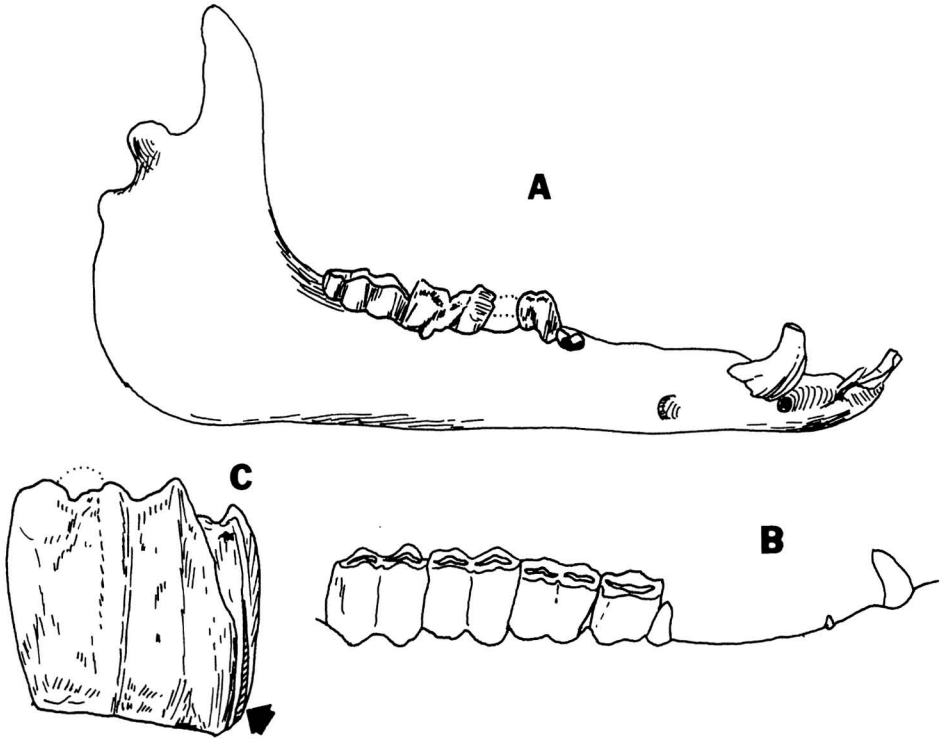

Fig. 1. — A. Holotype lower jaw of *Titanotylopus nebrascensis*, after Barbour & Schultz 1934. — B. Lower dentition of *Palauchenia mexicana* del Castillo, after Owen 1879. — C. Lower third molar of *Palauchenia mexicana*, from Owen, 1870, showing scar where third lobe has been broken away (arrow).

chenia. Both camels had P_3's of moderate size, though only the alveoli remain in the *Titanotylopus* jaw .

A major difference between the two holotypes is the relatively short M_3 and absence of the third lobe of this tooth of *Palauchenia*. Owen (1870) mentioned the short M_3 but failed to note the obvious scar on the posterior face of M_3, where a third lobe has been broken away (Fig. 1). Owen's engraving was prepared from a photograph furnished by del Castillo and Owen never saw the fossil, which is presumably now lost. The M_3 is clearly too short to be complete, scarcely larger than M_2 (length of M_3, 48 mm; the M_2 is 45 mm). Third lobes are present on all normal camel M_3's.

The *Palauchenia* jaw, and the teeth, are smaller than those of *Titanotylopus*. However, the two jaws might represent two different species of a single genus (Fig. 1). Voorhies & Corner (1986) mention that additional material representing *Titanotylopus* has been discovered. It seems best to defer further consideration of the generic status of *Titanotylopus* until this has been described.

Hemiauchenia macrocephala (Cope), 1893

Principal synonyms:
Holomeniscus macrocephalus Cope, 1893.
Camelus americanus Wortman, 1898.
Camelus vitakerianum (Cope), Wortman, 1898 (in part).
Lama stevensi Merriam and Stock, 1925.
Tanupolama stevensi (Merriam and Stock), Stock, 1928.
Prochenia americana (Wortman), Frick, 1929.
Lama (?) hollomani Hay and Cook, 1930.
Tanupolama blancoensis Meade, 1945.
Tanupolama macrocephala (Cope), Hibbard and Dalquest, 1962.
Tanupolama americana (Wortman), Hibbard and Dalquest, 1962.
Tanupolama seymourensis Hibbard and Dalquest, 1962.
Hemiauchenia macrocephala (Cope), Webb, 1974.
Hemiauchenia blancoensis (Meade), Webb, 1974.
Hemiauchenia seymourensis (Hibbard and Dalquest), Webb, 1974.

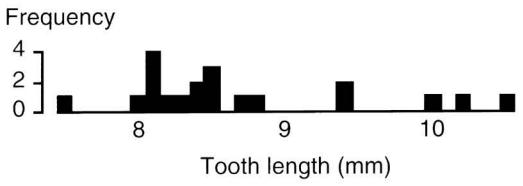

Fig. 2. Anteroposterior lengths of lower fourth premolars, measured 10 mm above base of enamel, of *Hemiauchenia* from the Broadwater local fauna, Irvingtonian Land Mammal Age, of Nebraska. Larger teeth may be of males.

Webb (1974) employed the useful term "llamas" for all of the small late Tertiary to modern camelids of North and South America. Stock (1928) proposed the generic name *Tanupolama* for the species of llamas that had previously been placed in various nominal genera. When Savage (1951) reviewed the Blancan and Pleistocene llamas of North America, ten species had been named or transferred to the genus. Hibbard & Dalquest (1962) gave a brief revision of Blancan and Pleistocene llamas; the Hemphillian *Tanupolama vera* was not included. They described a new species, *Tanupolama seymourensis*, from Knox County, Texas, and recognized as other valid species only *T. macrocephala* (Cope), *T. mirifica* Simpson, and *T. blancoensis* Meade. Webb (1974), in his revision of the North and South American llamas, found that *T. mirifica* belonged in the genus *Palaeolama* and that the name *Tanupolama* was preoccupied by *Hemiauchenia* Gervais and Ameghino, 1880. Webb recognized as valid only *H. vera* (Matthew), *H. macrocephala* (Cope), *H. blancoensis* (Meade) and *H. seymourensis* Hibbard & Dalquest. Breyer (1977) studied the lower jaws of *Hemiauchenia* from the Broadwater local fauna of Nebraska, Blancan Land Mammal Age, and reviewed the North American species of *Hemiauchenia*. He found the characters thought to separate *H. seymourensis* from *H. blancoensis* to be invalid and placed the former in the synonymy of *H. blancoensis*. Species of *Hemiauchenia* were thus reduced to *H. vera* (Hemphillian Land Mammal Age), *H. blancoensis* (Blancan and Irvingtonian Land Mammal ages), and *H. macrocephala* (Irvingtonian).

Hemiauchenia vera is distinct from Blancan and Pleistocene llamas. It is relatively small, has a slender ramus, relatively brachydont teeth, usually retains P_1 as a large, caniniform tooth, and almost always retains P_3. Even when reduced to tiny size, P_3 always has two roots.

When Breyer (1977) placed *H. seymourensis* in the synonomy of *H. blancoensis* he extended the chronological range of that species from the Blancan into the Irvingtonian Land Mammal Ages, for the holotype of *H. seymourensis* comes from an Irvingtonian local fauna. The type localities of *H. seymourensis* and *H. macrocephala* are of similar age and only 160 km apart. If *T. seymourensis* is a synonym of *H. blancoensis*, *H. blancoensis* and *H. macrocephala* were geographically sympatric in the Irvingtonian Land Mammal Age.

Breyer (1977) separated *Hemiauchenia blancoensis* from *H. macrocephala* by a relatively long mandibular diastema of the latter. Breyer used "diastema" in a narrow sense, as he explained and figured (1977: 532): the gap in the tooth row posterior to the first premolar, which might be P_1–P_3 or P_1–P_4. A more reliable measurement of the length of the symphyseal area is the C–P_4 length, measured from the anterior edge of the alveolus of P_4 to the posterior edge of the canine alveolus. I have examined, through the kindness of Dr. M. R. Voorhies, University of Nebraska State Museum, the same large collection of *Hemiauchenia* jaws from the Broadwater local fauna studied by Breyer. Nearly all of the better jaws are crushed laterally, fractured and distorted. The approximate C–P_4 length could be measured with reasonable accuracy in only eight jaws, and ranged from 59.1 to 77.5 mm (mean = 67.1 mm). The C–P_4 length in the holotype of *H. macrocephala* is 61 mm, or within the range of variation in *H. blancoensis* from Broadwater. The anterior tip of the lower jaw of the holotype of *H. blancoensis* is missing and the C–P_4 length cannot be obtained.

Thirteen jaws from Broadwater have the P_4 in place, complete, and not excessively worn. The P_4 of *Hemiauchenia* is not subject to such extreme anteroposterior shortening by wear as are the molars (as described by Breyer 1977). The lengths of the P_4's were measured 10 mm above the base of the enamel (Fig. 2). Nine teeth

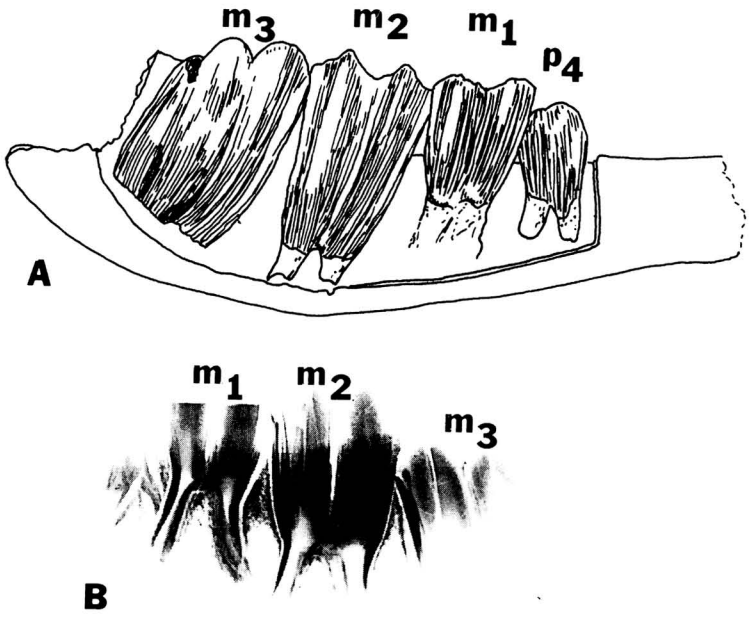

Fig. 3. — A. Lower cheek teeth of *Camelops minidokae* Hay. In this immature camel, with teeth scarcely worn, the roots on M_1 and M_2 are fully developed. Note difference in length at top and bottom of crowns and extreme height of crowns. — B. Radiograph of lower jaw of domestic llama. Deciduous premolar is still in place (not shown) and M_3 has not erupted but roots are already formed on M_1 and nearly so on M_2.

range from 7.5 to 8.8 mm (eight of these are between 8.0 and 8.8 mm). Four range from 9.4 to 10.5 mm. The measurements suggest that either two species were present or one species with marked sexual dimorphism in size. I have no measurements to show that males of the domestic llama are larger than females but observation of living animals suggests that males are slightly larger than females. Sexual dimorphism may have been greater in *Hemiauchenia*.

Two kinds of llama jaws are present in the Gilliland local fauna of the Seymour Formation, Knox County, Texas. The holotype lower jaw of *Hemiauchenia seymourensis* and the lower jaws referred to "*Tanupolama*" *blancoensis* by Hibbard and Dalquest (1962) are large, but a smaller, shorter, symphyseal region of another specimen was hesitantly referred to "*T.*" *macrocephala*.

Especially important are two specimens recently found in the Seymour Formation, at the same stratigraphic level and only 100 meters apart. One complete set of lower jaws was poorly preserved, in a bed of gray clay. The other, a lower jaw fragment with the posterior end of the symphysis and P_3–P_4, from a bed of gravel, was well-preserved. There can be no question as to contemporaneity of the two specimens. Both are of almost the same stage of tooth wear, showing only slight wear on the occlusal surface of P_4. The fragmentary specimen is large and stout; depth under P_4, 35.7 mm; breadth under P_4, 16.4 mm. Equivalent measurements for the small specimen are 29.1 and ca. 10 mm. The large jaw tapers abruptly anterior to P_3 while the small jaw tapers but slightly. The premolars, especially P_4, of the large jaw are markedly larger than those of the small jaw. The small jaw lacks P_3, a variable character in Pleistocene *Hemiauchenia*.

The cheek teeth of *Hemiauchenia*, like those of *Camelops*, are almost useless for taxonomic use, since they become shorter and broader with wear. Differences in size of lower jaws may result from sexual dimorphism and allometry, rather than sympatry of two different species. Unless material, such as skulls, and no complete skulls seem to exist in collections, becomes available, it is preferable to consider all Blancan and Pleistocene *Hemiauchenia* to belong to one variable population, *Hemiauchenia macrocephala*.

Species of *Camelops* Leidy, 1854

The genus *Camelops* has never been adequately revised, although species were briefly reviewed by Savage (1951). Webb (1965) gave a detailed

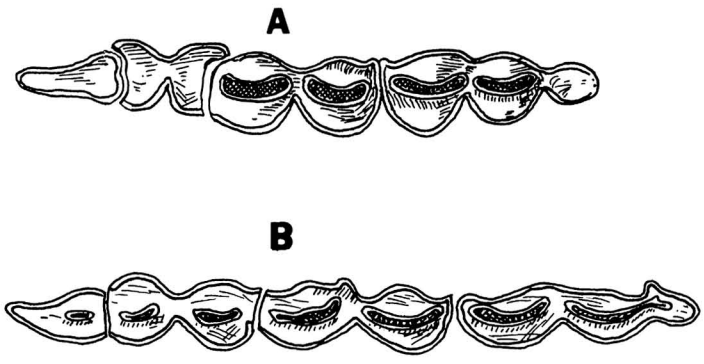

Fig. 4. Lower cheek teeth of two *Camelops* specimens that were originally of about the same length. — A. Old adult, but not senile for fossetteds remain on M_2 and M_3, anterior end of M_2 is inset into posterior end of M_1, and posterior end of P_4 is inset into anterior end of greatly shortened M_1. Tooth row has been reduced in length by approximately eight percent. — B. Young adult with teeth worn almost flat. Some destruction of enamel at ends of M_1 has already occurred as teeth float together.

account of the osteology of *Camelops hesternus* (Leidy), from the Rancho la Brea of California, that has furnished a basis for comparisons with species from elsewhere. Other workers have made helpful contributions (e.g. Lundelius 1972). Nevertheless, most specimens of *Camelops*, a genus present in almost every Pleistocene local fauna from North America with an adequate collection of large mammals (except, perhaps, from Florida and the eastern United States, Webb 1965) continue to be referred to *Camelops* sp. or only hesitantly to species.

A major problem in identification of species of *Camelops* is reliance on molar teeth for specific characters. Most species names of *Camelops* have been based on dentitions. However, cheek teeth are of limited value in specific identification.

Camelops teeth are strongly hypsodont. The height of the enamel-covered crown of a lightly worn M_2 may be twice the anteroposterior length of the tooth, and in an upper second molar height may be 20 % greater than the maximum length of the tooth. The molars of *Camelops* (and the llamas) are wedge-shaped (Fig. 3). The anteroposterior length at the top of the crown in an unworn M_2 may be almost twice the length at the base and in M^2 may be 25 % greater than the length at the base of the enamel. First molars are nearly as wedge-shaped, P_4 and M_3 less so. As cheek teeth of *Camelops* wear down, their anteroposterior length at the occlusal surface decreases drastically.

To prevent the teeth from becoming isolated from each other in the jaw as their occlusal surfaces are shortened by wear, both upper and lower teeth "floated" together, centering on first molars. In most instances the floating more than compensated for length lost to wear, and teeth became crushed and abraded on their anterior or posterior faces. Fourth premolars are rarely damaged by such wear but the anterior face of M_1 becomes much worn, the posterior part of P_4 becoming inset, sometimes to half its length, into the anterior part of the molar (Fig. 4). The posterior face of the first molar becomes greatly worn, as may the anterior part of M_2. There seems to be little wear between M_2 and M_3. By the time the teeth have been reduced to half of their original height, they have changed in length and proportions so greatly that measurements are virtually worthless unless comparisons are made with teeth in the same stage of wear (see Breyer 1977 for description of similar wear in *Hemiauchenia*).

It is possible, to some extent, to judge the relative age of *Camelops* jaws by the amount of wear exhibited on the occlusal surfaces of the lakes (selenes). Wear shows first on P_4 and M_1, followed by M_2 and then M_3. The third lobe of

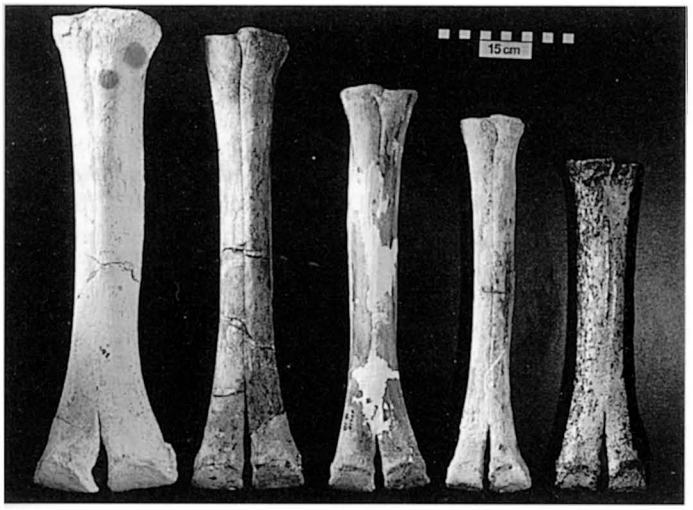

Fig. 5. Metacarpals of some North American camelids. — A. *Gigantocamelus spatula* Cope, Blanco local fauna, Texas. — B. *Titanotylopus nebrascensis* (?) Barbour and Schultz, Blanco local fauna, Texas. — C. *Camelops* cf. *huerfanensis dallasi* Lull, Hill-Shuler local fauna, Texas. — D. *Camelops* cf. *minidokae* Hay, Slaton Quarry local fauna, Texas; *Camelops traviswhitei* Mooser and Dalquest, Cedazo local fauna, Aguascalientes, Mexico.

M_3 is last to become worn. The enamel bordering the lakes does not extend to the bases of the teeth and eventually is completely worn away, the lakes progressively obliterated from M_1 backward, before a tooth is worn to its base.

Height of the enamel on a cheek tooth cannot be measured if a tooth is in place in the jaw. Unlike most artiodactyls with strongly hypsodont teeth, where development and closure of the roots is delayed while the occlusal surfaces become worn, the cheek teeth of *Camelops*, *Hemiauchenia*, and even the domestic llama (*Lama glama*) develop roots before eruption, shortly after the crowns are formed (Fig. 5). More than half of a freshly erupted tooth crown lies in the jaw beneath the alveolar surface. There is an obvious correlation of age with anteroposterior shortening of M_1 and M_2 but the relationship and individual variation cannot be determined. Most workers have used the length of the upper and lower cheek tooth rows and measurements of individual teeth as specific characters in *Camelops* when age, not size differences, were involved. Cope (1893), in the description the holotype of *Holomeniscus* (= *Camelops*) *sulcatus*, stated that it was a large species. The teeth are well worn, P_4 deeply inset into the anterior face of M_1 and the anterior face of M_2 even inset into the posterior face of M_1. The individual was not excessively old for both lakes remain on M_2. The P_4–M_3 length was reduced to 146 mm, and Savage (1951) was persuaded by the measurements that *C. sulcatus* was a small species. This was followed by Webb (1965) and Dalquest (1967). It remained for Lundelius (1972) to show that Cope was correct and *Camelops sulcatus* was a large camel. Dental characters other than size may aid in identifying species of *Camelops*. Cope (1893) thought the grooves (sulci) on the labial sides of molars to be diagnostic of some species but teeth vary widely in the development of these grooves.

Mooser & Dalquest (1975) identified *Camelops traviswhitei*, of Aguascalientes, Mexico, by open, V-shaped lakes with the enamel of the lingual sides thinner than on the labial sides. Most individual *Camelops* have lakes of bent-oval shape, enamel of uniform thickness, and filled with cementum. Dalquest (1975) found that specimens of *Camelops* from the Blanco local fauna, Blancan age, of Texas, also had large lower jaws with cheek teeth having open, V-shaped selenes with thin enamel on the lingual sides, and referred the Blanco *Camelops*, hesitantly, to *C. traviswhitei*. More recently Dr. Jon Baskin, Texas A & I University, showed me a well-preserved lower jaw from a gravel pit in the Gulf Coast area of southeastern Texas. Direct comparison showed remarkable similarity of ramus and teeth to specimens of *Camelops traviswhitei* from the Cedazo local fauna of

Aguascalientes. Chronologically, then, *C. traviswhitei* ranged from Blancan to Rancholabrean Land Mammal Ages, and geographically at least from northern Texas to Aguascalientes, central Mexico. Note however, that metacarpals from the same sediments that yielded *Camelops traviswhitei*, not found in association with skulls or lower jaws, though hesitantly referred to that species, are remarkably short and stout (Fig. 5E), while metapodials from the Blanco site are of more normal proportions. Perhaps the short, stout metacarpals belong to the camel hesitantly referred to *Camelops hesternus* (Leidy) by Mooser & Dalquest, found in the same local fauna as *Camelops traviswhitei*. It is also possible that the genus *Camelops* includes two phyletic lines, one of species with *C. traviswhitei* features and the other with those of *C. hesternus*.

Metapodials seem to be good indicators of size in *Camelops* species. Webb (1965) gives figures and measurements of metapodials of *Camelops hesternus* from the Rancho la Brea of California that may be considered typical for the genus. Metacarpals (n = 3) vary in overall length from 374 to 380 mm (mean = 376.3); midshaft breadth ranges from 51–57 mm (mean = 54.7). Metatarsals (n = 5) range in length from 357–388 mm (mean = 375.9); midshaft breadth 40–49 (mean = 45.0). The sample is small but indicates only slight variation in length and proportions. Of eight specimens, one would expect both sexes to be included, and sexual dimorphism must have been minimal.

Metapodials of the Blancan giant camel, *Gigantocamelus spatula*, must be near the maximum in length and stoutness in camelids. A metacarpal is tentatively referred to *Titanotylopus nebrascensis* (part of an almost complete forelimb from the Gilliland local fauna of Texas). Although from a young camel with the distal epiphyseal cartilage of the radius still present, the metacarpal measures 428 mm in length. This must be near the maximum for a Pleistocene camelid. Metapodials of *Camelops* species fall between the length of *Titanotylopus* (?) and *Camelops traviswhitei* Fig. 6). Too few series of metapodials have been studied to show their value as species criteria but metapodials do show the existence of definite size groups and limb proportions in *Camelops* (Fig. 5).

Skulls of *Camelops* may possess definitive species characters. Hay (1913) differentiated *Camelops huerfanensis* from *C. hesternus* by details of the cranial bones. Slaughter et al. (1962) reported cranial differences between two *Camelops* skulls from the Trinity River Pleistocene deposits near Dallas, Texas. Cranial differences between *Camelops* skulls have been reported by others as well (see Lundelius, 1972). Unfortunately, few good *Camelops* skulls exist in collections, and even fewer have been described. The range of sexual and individual variation in any species is unknown. The cranial differences noted by authors are usually confined to two skulls under study. Skulls of *Camelops* seem to have been fragile and even partially complete skulls are much less often found than, for example, those of horses. It seems probable that *Camelops* skulls will provide characters diagnostic for species but too few are available, and most of those are too incomplete, to be of value at this time.

It does appear that there were several distinct species of *Camelops* in North America during the Pleistocene. Materials suitable for a revision of the genus are lacking. Specimens from local faunas that have furnished holotypes of described species may best be referred to those species. Elsewhere, specimens are probably best referred to *Camelops* sp.

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