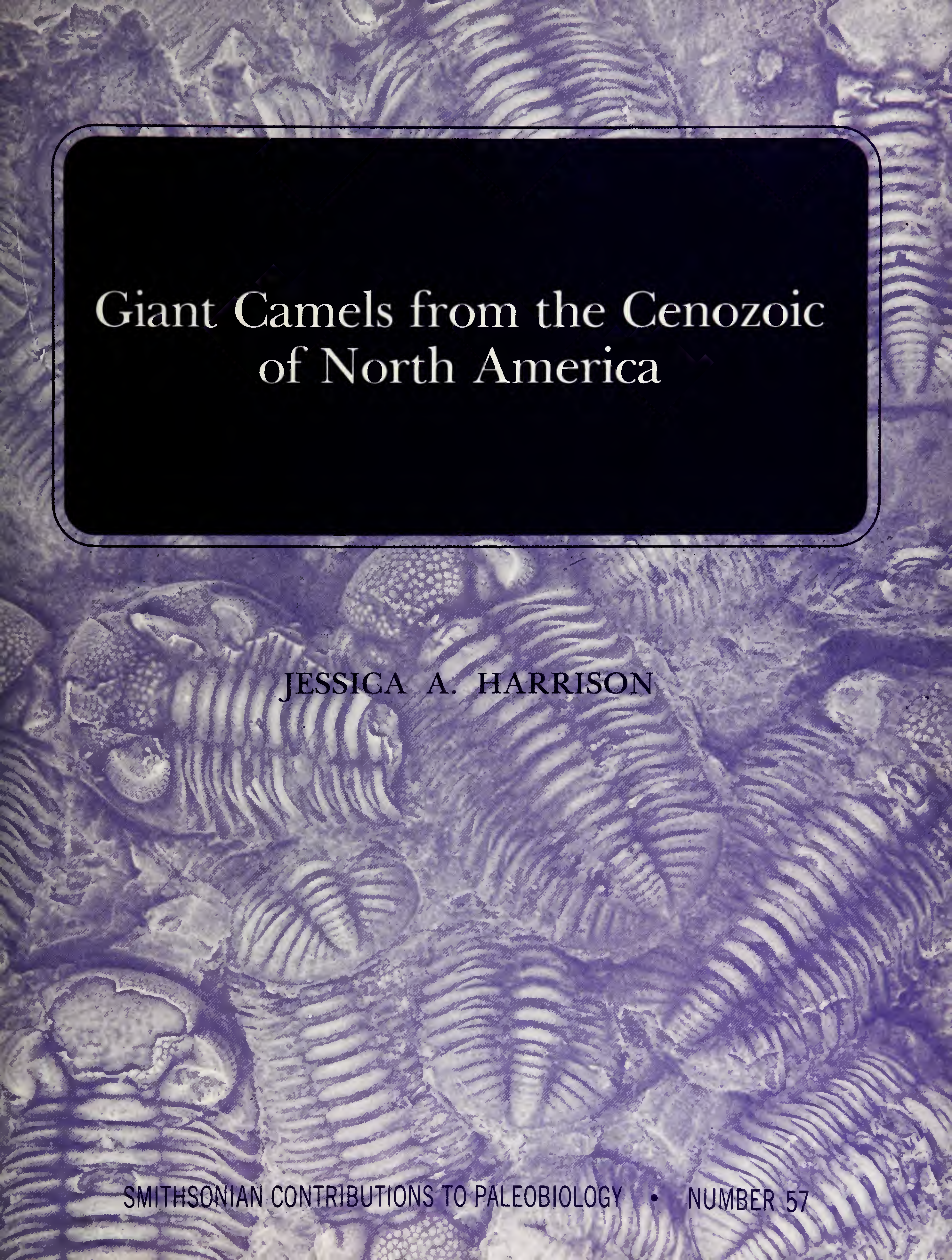

Giant Camels from the Cenozoic of North America

JESSICA A. HARRISON

SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 57

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Jessica A. Harrison

SMITHSONIAN INSTITUTION PRESS
City of Washington
1985

ABSTRACT

Harrison, Jessica A. Giant Camels from the Cenozoic of North America. *Smithsonian Contributions to Paleobiology*, number 57, 29 pages, 17 figures, 1985.—Seven genera of giant camels occurred in North America during the interval from the late Clarendonian to the early Holocene. *Aepycamelus* was the first camel to achieve giant size and is the only one not in the subfamily Camelinae. *Blancocamelus* and *Camelops* are in the tribe Lamini, and the remaining giant camels *Megatylopus, Titanotylopus, Megacamelus, Gigantocamelus,* and *Camelus* are in the tribe Camelini. *Megacamelus* is a late Hemphillian giant camel most closely related to *Gigantocamelus*. *Titanotylopus* is reserved for the brachyodont form from the Irvingtonian of Nebraska, and *Gigantocamelus* is reinstated for the broad-chinned, Blancan form.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The trilobite *Phacops rana* Green.

Library of Congress Cataloging in Publication Data
Harrison, Jessica A.
Giant camels from the Cenozoic of North America.
(Smithsonian contributions to paleobiology ; no. 57)
Bibliography: p.
Supt. of Docs. no.: SI 1.30:57
1. Camels, Fossil. 2. Paleontology—Cenozoic. 3. Paleontology—North America. I. Title. II. Series.
QE701.S56 no. 57 [QE882.U3] 560s [599.73'6] 84-600303

Contents

Page

Introduction 1

Acknowledgments 1

Phylogenetic Relationships 1

Aepycamelus 4

Megatylopus 5

Titanotylopus 7

Gigantocamelus 8

Megacamelus 10

Megacamelus merriami, new combination 11

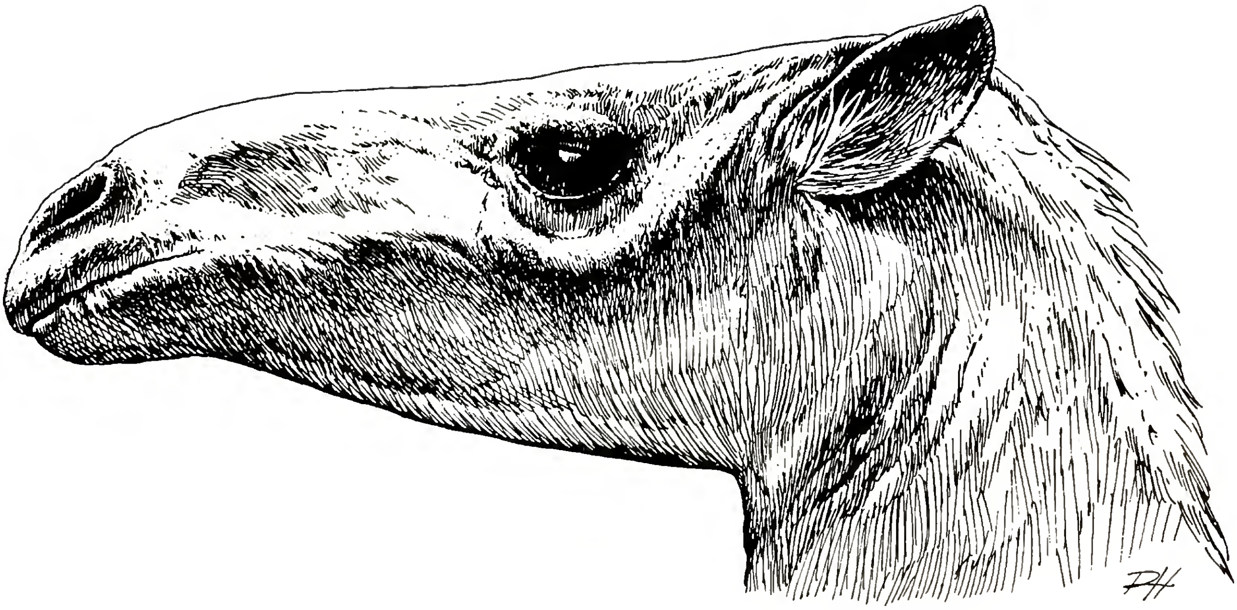
Camelus 21

Blancocamelus 23

Camelops 24

Summary 24

Literature Cited 26



FRONTISPIECE.—Reconstruction of the head of *Megacamelus merriami*.

Giant Camels from the Cenozoic of North America

Jessica A. Harrison

Introduction

Throughout the later Cenozoic, camels often figure as an abundant and diverse element of any fauna in which they occur. Until the late Pleistocene, when the group fell on hard times, the Camelidae must be accounted one of the more successful ungulate families. As in many other herbivore families, the earliest members of the Camelidae were of small body size. However, a trend toward gigantism can be observed throughout the later Cenozoic, from the Clarendonian into the Holocene.

Descriptions of very large camels are almost as abundant in the literature as their remains in late Cenozoic faunas. The confusing taxonomic history of the giant camels is such that, for every specific identification, there are many more referrals to "camelid, large, gen. et sp. indet." The purpose of this paper is to provide a temporal, geographic, and systematic framework for the large, late Cenozoic camels.

ACKNOWLEDGMENTS.—I am grateful for the use of specimens from the Frick Collection, Department of Vertebrate Paleontology, American Museum of Natural History (F:AM), the University of California Museum of Paleontology (UCMP), the University of Nebraska State Museum (UNSM), and the University of Kansas Museum of Natural History (KUVP). I very much appreciate careful and constructive reviews by George Corner, Michael Voorhies, John Breyer, and Robert Emry. Drs. Corner and Voorhies were particularly generous in sharing with me their new information on *Titanotylopus.* The frontispiece was done by Robert Hynes.

Phylogenetic Relationships

The cladogram in Figure 1 summarizes relationships within the Camelinae. It is interesting to note that the trend toward gigantism is far more apparent in the Camelini than in the Lamini. All of the genera comprising the Camelini can be called giants, but only two of the Lamini, *Camelops* and *Blancocamelus*, achieve a formidable body size. *Aepycamelus*, the only noncameline genus, represents the camels' earliest experimentation with gigantism.

The characters appearing at nodes 1 through 35 in the cladogram are listed below. The composition and apomorphies of the Protolabidini are from Honey and Taylor (1978:419–420), whereas those of the Lamini and Camelini appeared in part in Harrison (1979:3–8). More detailed discussion of the characters may also be found in those papers.

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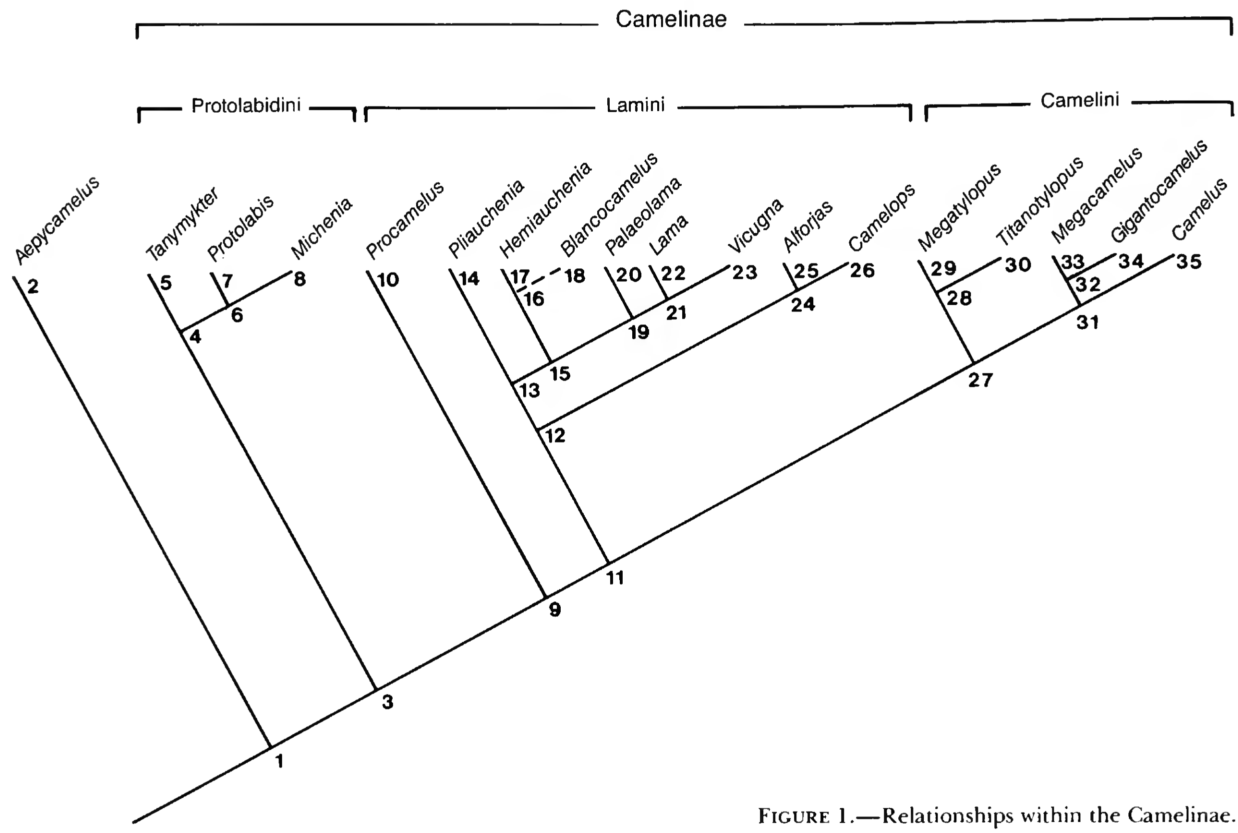


FIGURE 1.—Relationships within the Camelinae.

Node 1. *Aepycamelus* shares with the Camelinae
 a. metastylid present on the lower molars

Node 2. *Aepycamelus* is distinguished by
 a. extremely elongate limbs
 b. extremely elongate cervical vertebrae
 c. metapodials longer than the basal length of the skull

Node 3. The Camelinae are united by
 a. weak buccinator fossa
 b. elongate rostrum

Node 4. The Protolabidini are united by
 a. narrow rostrum
 b. laterally expanded anterior nares

Node 5. *Tanymykter* is distinguished by
 a. closely appressed P^1_1 roots

Node 6. *Protolabis* and *Michenia* are derived relative to *Tanymykter* by
 a. the absence of elongate basioccipital tuberosities
 b. P^2 without strong, continuous lingual cingulum
 c. auditory bulla less inflated with medial plates more compressed
 d. moderate to strong buccinator fossa

Node 7. *Protolabis* is distinguished by
 a. hypsodont molars
 b. anteroposteriorly elongate M^3_3
 c. very weak to absent metastylid on lower molars
 d. ventrally produced mandibular angle with weak to strong lateral flare
 e. fused metapodials
 f. elongate proximal phalanx with distal articular surface anteriorly extended

Node 8. *Michenia* is derived relative to *Protolabis* in having
 a. short braincase
 b. weak I^3-C^1, small C_1
 c. shallow symphysis
 d. inflection of mandibular angle suppressed

Node 9. The Camelinae exclusive of the Protolabidini are united by
 a. metacarpal length exceeds metatarsal length
 b. metapodials completely fused
 c. I^1 absent

Node 10. *Procamelus* is the sister taxon to the remaining camelines.
 It retains several primitive characters but has almost completed the loss of I^2

Node 11. The Lamini share with the Camelini
- a. I^2 absent
- b. P^2_2 absent
- c. raised posterolateral edges on the proximal end of the proximal phalanx

Node 12. The Lamini are united by
- a. in cross section the anterior end of the nasals form a high, bilobed arch (Harrison, 1979, fig. 3)
- b. anteroexternal style (= llama buttress) present on lower molars

Node 13. *Pliauchenia*, *Hemiauchenia*, (?)*Blancocamelus*, *Palaeolama*, *Lama*, and *Vicugna* share
- a. reduced lacrimal vacuity
- b. shortened rostrum

Node 14. *Pliauchenia* is primitive in all known characters to the remaining Lamini.

Node 15. *Hemiauchenia*, (?)*Blancocamelus*, *Palaeolama*, *Lama*, and *Vicugna* are united by
- a. small P^1_1
- b. small or absent P_3

Node 16. *Hemiauchenia* and *Blancocamelus* share
- a. extremely elongated metapodials

Node 17. *Hemiauchenia* is distinguished by
- a. extremely elongated cervical vertebrae

Node 18. *Blancocamelus* is distinguished by
- a. great size

Node 19. *Palaeolama*, *Lama*, and *Vicugna* share
- a. P^1_1 absent
- b. reduced maxillary fossa
- c. moderate to strong anteroexternal style on lower molars

Node 21. *Lama* and *Vicugna* are derived relative to *Palaeolama* in having
- a. P_3 absent
- b. metacarpal length subequal to metatarsal length
- c. strong anteroexternal style on lower molars
- d. greatly reduced lacrimal vacuity
- e. extremely retracted nasals
- f. greatly reduced P_4

Node 22. *Lama* is distinguished by
- a. callosities on the inner foreleg

Node 23. *Vicugna* is distinguished by
- a. hypsodont lower incisors

Node 24. *Alforjas* and *Camelops* are derived relative to other lamines in having
- a. moderately hypsodont to very hypsodont molars
- b. cheek teeth narrow in relation to length

Node 25. *Alforjas* is primitive in all known characters relative to *Camelops*

Node 26. *Camelops* is derived relative to *Alforjas* in having
- a. cheek teeth much more hypsodont
- b. P^1_1 absent
- c. P_3 absent
- d. dorsal surface of the mandibular condyle transversely concave
- e. suspensory ligament scar extends to center of proximal phalanx and has a raised center

Node 27. The Camelini are united by
- a. angular process on mandible enlarged and strongly inflected
- b. large postglenoid foramen
- c. long postglenoid process on skull with correspondingly large facet on mandibular condyle
- d. C^1_1 enlarged and rounded in cross section, especially in males
- e. ventrally flattened auditory bulla
- f. diastemal crest on mandible low and rounded
- g. reduced maxillary fossa
- h. thickened, heavy premaxilla

Node 28. *Megatylopus* and *Titanotylopus* share
- a. reduced P_1
- b. reduced P_3

Node 29. *Megatylopus* is distinguished by
- a. reduced P^3
- b. cheek teeth higher crowned than *Titanotylopus*

Node 30. *Titanotylopus* is derived relative to *Megatylopus* in having
- a. P_1 absent
- b. P_3 more reduced than in *Megatylopus*
- c. larger body size than *Megatylopus*

Node 31. *Megacamelus*, *Gigantocamelus*, and *Camelus* share
- a. metapodials shorter in relation to basal length of the skull
- b. cheek teeth more hypsodont than *Megatylopus* or *Titanotylopus*

Node 32. *Megacamelus* and *Gigantocamelus* share
- a. spatulate lower incisors
- b. splayed C_1

Node 33. *Megacamelus* is primitive in all characters relative to *Gigantocamelus* except for
- a. I^3 enlarged and caniniform

Node 34. *Gigantocamelus* is distinguished by
- a. short, blunt chin with a shortened ramal symphysis
- b. greater size than *Megacamelus*
- c. lower incisors arrayed almost transversely
- d. I^3 absent or vestigial

Node 35. *Camelus* is distinguished by
- a. reduced paroccipital process
- b. metapodials subequal in length and shorter than the basal length of skull
- c. maxillary fossa reduced or absent
- d. zygomatic arch straight in lateral view
- e. retracted nasals
- f. center of suspensory ligament scar raised

Aepycamelus Macdonald, 1956

TYPE-SPECIES.—*Aepycamelus giraffinus* Macdonald, 1956:198 (= *Alticamelus giraffinus* Matthew in Matthew and Cook, 1909:402).

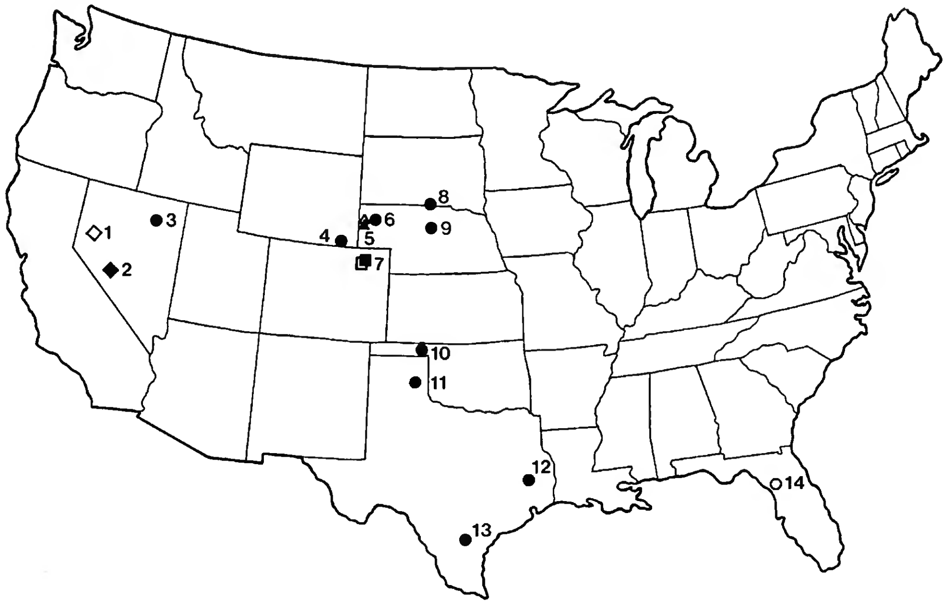
Aepycamelus is the geologically oldest of the giant camels, ranging from the Barstovian through the early Hemphillian and occurring through the southern and western United States (Figure 2). When Marsh (1894:274) described *Procamelus altus* from Oregon, he based it solely upon an isolated calcaneum. Cope (1894:869) took almost instant exception to the designation of such an undiagnostic element as a type specimen. Matthew (1901:429), under the impression that the type of *P. altus* was more extensive, described *Alticamelus* from northeastern Colorado and named *A. altus* the genotypic species. When he became aware of the indeterminate nature of the type of *A. altus*, Matthew renamed the Colorado material *A. giraffinus* (Matthew and Cook, 1909:402). Macdonald (1956:198) maintained that *Alticamelus* was a nomen vanum and proposed *Aepycamelus* as a replacement name, with *A. giraffinus* as the new genotypic species.

All of the species of *Aepycamelus* are noted for extremely elongate, slender limbs and cervical vertebrae. The teeth are quite brachyodont, and the dental formula is $I_3^{1-3}C_1^1P_4^4M_3^3$. When present, $I^{1.2}$ are reduced to stumps as in the type of *A. giraffinus*. P_2^2 is always present and less reduced than in *Procamelus*.

Matthew and Cook (1909:402) described *Alticamelus procerus* from the Snake Creek beds of Nebraska, and later Matthew (1924:187) described a second species, *Alticamelus priscus*, from the Sheep Creek beds. Matthew (1924:187) also referred material from Snake Creek to *Alticamelus leptocolon* described by him from the Pawnee Creek area of Colorado. Davidson (1923:399) described *Alticamelus alexandrae* from Barstow, California, but Macdonald (1949:190) referred this form to *Hesperocamelus*. Henshaw (1942:153) named a species from Tonopah, Nevada, *Alticamelus? stocki*. Macdonald (1956:199) described *Aepycamelus bradyi* from the Nightingale Road fauna, Truckee Formation, Nevada. Leidy (1886:12) described *Auchenia major* from Mixson, Florida; Leidy and Lucas (1896:53) later changed the name to *Procamelus major*. Although Simpson (1930:196) referred this material to *Megatylopus major*, it is more likely an advanced species of *Aepycamelus* (pers. comm., Beryl E. Taylor, 1973).

Aepycamelus bradyi is the largest of the species, followed by *A. giraffinus*. *Aepycamelus procerus* is smaller than *A. giraffinus* and has completely lost $I^{1,2}$. *Aepycamelus stocki* is smaller than *A. procerus* but larger than *A. leptocolon* and retains $I^{1,2}$. *Aepycamelus priscus* is the smallest of the lot. In *A. bradyi* and *A. stocki* the premolars are a bit more reduced than in the other species of *Aepycamelus* but are not so reduced as in *Procamelus*. *Aepycamelus bradyi* has as well an almost complete internal crescent on P^3. Although such a project is not within the scope of this paper, it may be seen that the genus *Aepycamelus*, often difficult to distinguish from *Procamelus*, would benefit considerably from a revision.

A number of specimens have been referred simply to *Aepycamelus*. Hesse (1936:66) referred two partial jaws from Beaver Quarry, Oklahoma, to *?Alticamelus*. Savage (1941:701) referred a series of metapodials and phalanges from the Optima fauna of Oklahoma, but the dimensions of these specimens are more characteristic of *Hemiauchenia*. Macdonald (1966:12) described an associated partial skeleton and jaws from the Camp Creek fauna of Nevada. Skinner, Skinner, and Gooris (1968:432) reported a partial radius-ulna of *Aepycamelus* from Turtle Butte, South Dakota. Webb (1969:147) referred two partial metapodials from Burge Quarry, Nebraska, to *Aepycamelus* sp. Patton (1969:149) referred limb elements from the Cold Spring fauna and the Lapara Creek fauna of Texas to *Aepycamelus* sp. Forsten (1970:48) referred an astragalus and some teeth from the Trail Creek fauna of Wyoming to *?Alticamelus*; Cassiliano (1980:55) changed the reference to *Aepycamelus* sp. Galusha (1975:54) listed *Aepycamelus* cf. *A. priscus* in a preliminary faunal list from the Box Butte Formation of Nebraska.



Key

◇	*A. bradyi*	5	Sheep Creek/Snake Creek, Nebraska
◆	*A. stocki*		
□	*A. leptocolon*	6	Box Butte, Nebraska
■	*A. giraffinus*	7	Pawnee Creek, Colorado
△	*A. procerus*	8	Turtle Butte, South Dakota
▲	*A. priscus*	9	Burge, Nebraska
○	*A. major*	10	Beaver Quarry, Oklahoma
●	*A.* sp.	11	Clarendon, Texas
1	Nightingale Road, Nevada	12	Cold Spring, Texas
2	Tonopah, Nevada	13	Lapara Creek, Texas
3	Camp Creek, Nevada	14	Mixson, Florida
4	Trail Creek, Wyoming		

FIGURE 2.—Geographic distribution of *Aepycamelus*.

Megatylopus Matthew and Cook, 1909

TYPE-SPECIES.—*Pliauchenia gigas* Matthew and Cook, 1909:396.

Megatylopus is the geologically oldest of the giant Camelini. It ranges from the late Clarendonian into early Blancan throughout the western United States (Figure 3). *Megatylopus* was originally proposed as a subgenus of *Pliauchenia* and was later elevated to generic rank. The type provenience of *M. gigas*, the genotypic species, is the late Hemphillian ZX Bar fauna, Snake Creek Formation, Nebraska (Skinner, Skinner, and Gooris, 1977:360). *Megatylopus* shares with *Titanotylopus* a tendency to reduce the third and fourth premolars. Its teeth are higher crowned than those of *Titanotylopus*, but both genera are more brachyodont than *Megacamelus*, *Gigantocamelus*, and *Camelus*. The limbs of *Megatylopus*, particularly the metapodials, are not shortened in relation to the basal length of the skull.

Additional species of *Megatylopus* are *M. cochrani* (Hibbard and Riggs, 1949:854) from Keefe Canyon, Kansas, and *M. matthewi* (Webb,

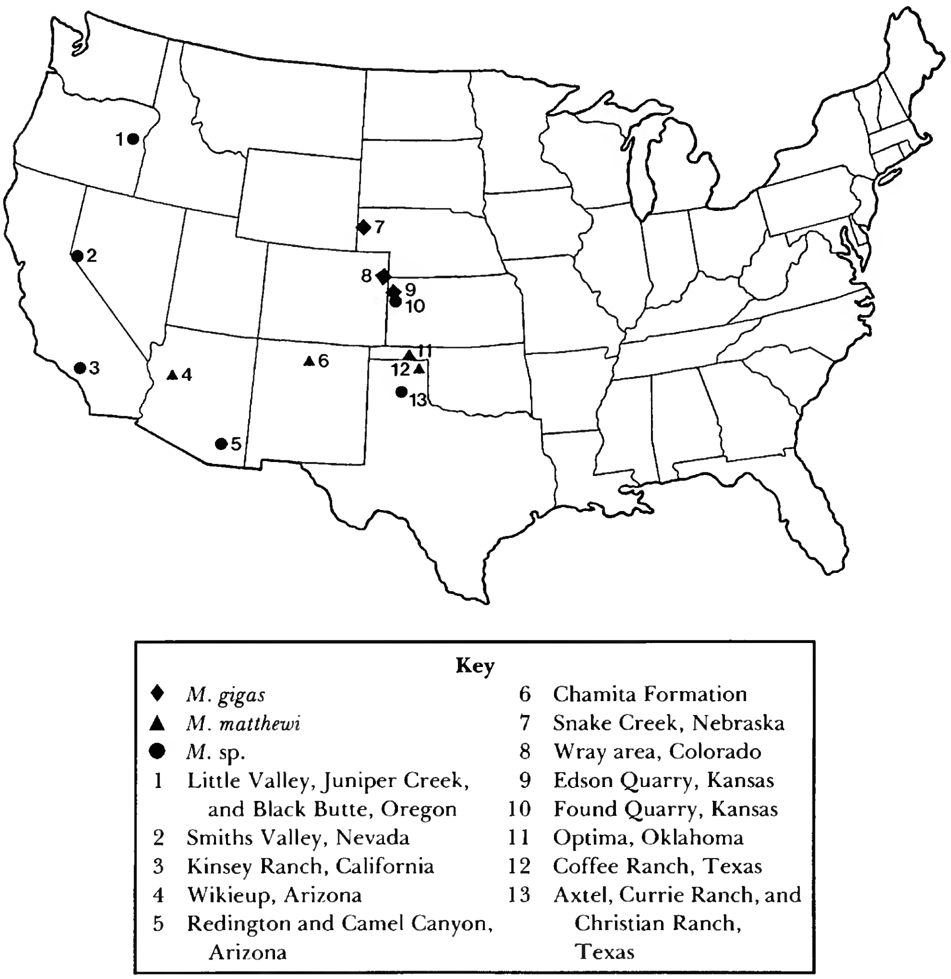


FIGURE 3.—Geographic distribution of *Megatylopus*.

1965:42) from the Coffee Ranch fauna of Texas. *Megatylopus cochrani* was originally described as *Pliauchenia cochrani* but was transferred to *Megatylopus* by Webb (1965:42). Although these workers have commented on the similarity of *M. cochrani* to *Camelops*, Corner and Voorhies (pers. comm., 1984) believe that *M. cochrani* may be more closely related to *Titanotylopus*. *Megatylopus matthewi* is distinguished from *M. gigas* by the complete internal crescent on P^3, the greater reduction of P_3, and a deeper maxillary fossa. In addition to other specimens of *M. matthewi*, Dalquest (1980:110) described five thoracic vertebrae preserved in articulation. Based on their structure, he proposed a large dorsal hump, pyramidal in profile rather than rounded. Table 1 lists additional occurrences of *Megatylopus*.

A fourth species of *Megatylopus*, *M. major*, was originally described by Leidy (1886:12) as *Auchenia major* and based upon an isolated astragalus from Mixson, Florida. Leidy and Lucas (1896:53) transferred the species to *Procamelus* and assigned to it a composite dentition, also from Mixson, which they believed had come from a single individual. Simpson (1930:196) changed the identification to *?Megatylopus major*, noting that the species was nearly as large as *M. gigas*. He also distinguished *M. major* as having broader cheek teeth than *M. gigas* and a complete internal crescent on P^3. Subsequent excavation

TABLE 1.—Additional occurrences of *Megatylopus*.

Species	Locality	Reference
M. gigas	Wray area, Colorado	Cook, 1922:11
	Edson Quarry, Kansas	Harrison, 1983:8
M. matthewi	Chamita Formation, New Mexico	MacFadden, 1977:791
	Optima, Oklahoma	Schultz, 1977:75
	Wikieup, Arizona	MacFadden, Johnson, and Opdyke, 1979:357
	Ocote, Mexico	Dalquest and Mooser, 1980:18
M. cochrani	White Bluffs, Washington	Gustafson, 1978:48
M. sp. or ?*M.*	Smiths Valley, Nevada	Macdonald, 1959:885
	Little Valley, Oregon	Shotwell, 1970:98
	Juniper Creek, Oregon	Shotwell, 1970:98
	Black Butte, Oregon	Shotwell, 1970:96
	Kinsey Ranch, California	Miller and Downs, 1974:11
	Axtel, Texas	Schultz, 1977:89
	Currie Ranch, Texas	Schultz, 1977:89
	Christian Ranch, Texas	Schultz, 1977:89
	Redington, Arizona	Lindsay, 1978:270
	Camel Canyon, Arizona	Lindsay, 1978:270
	Found Quarry, Kansas	Bennett, 1979:12

of the Mixson bone bed produced a much larger sample of this camel, currently housed in the Frick Collection of the Department of Vertebrate Paleontology, American Museum of Natural History. Skulls and mandibles bearing complete dentitions as well as diagnostically elongate metapodials and cervical vertebrae indicate that *M. major* should be transferred to *Aepycamelus major* (pers. comm., Beryl E. Taylor, 1973).

Titanotylopus Barbour and Schultz, 1934

TYPE-SPECIES.—*Titanotylopus nebraskensis* Barbour and Schultz, 1934:291.

Barbour and Schultz (1934:291) described *Titanotylopus nebraskensis* based on a single mandible from a Pleistocene gravel pit near Red Cloud, Nebraska (Figure 4). Other than a proximal phalanx from another Pleistocene gravel pit, no more specimens have been referred to *T. nebraskensis*. Based upon this material, Webb (1965) and Breyer (1976) felt that the differences between *Gigantocamelus* and *Titanotylopus* warranted distinction only at the specific level. Corner and Voorhies (pers. comm., 1984) have since identified additional material, which is referrable to *T. nebraskensis* and which they believe validates the generic independence of these two taxa. I agree with Corner and Voorhies that the name *Titanotylopus* should be applied to a single species, *T. nebraskensis*, as yet known only from early Irvingtonian localities in Nebraska.

The type mandible of *Titanotylopus* is very large, 662 mm long, with a dental formula of $I_3C_1P_2M_3$. The mandibular symphysis is long and extends well beyond the large canines. The nonspatulate incisors are arrayed in an arc. There is no indication of P_1. P_3 is broken, but its position is indicated by alveoli for its two roots. P_4, like the molars, has sustained some breakage. All of the cheek teeth are quite brachyodont.

In their study of *Gigantocamelus spatulus* from Keefe Canyon, Hibbard and Riggs (1949) classified as female those jaws with small C_1 and no P_1, whereas jaws classified as male had large C_1, and P_1 was present. Webb (1965:36) felt that the type of *T. nebraskensis* fell within the range of variation assigned to females and hence attached

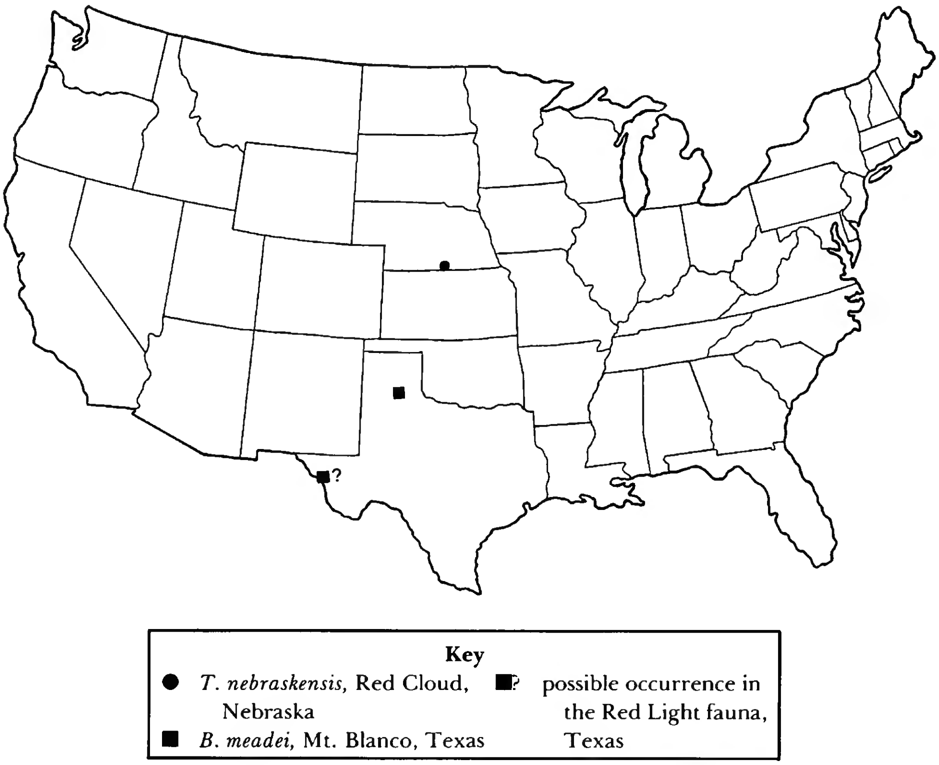


FIGURE 4.—Type-localities of *Titanotylopus nebraskansis* and *Blancocamelus meadei.*

little significance to the missing P_1. His synonymy of *Titanotylopus* and *Gigantocamelus* has been followed by most authors except Hibbard (Skinner et al., 1972:114). Considerations of P_1 aside, the highly derived chin and greater degree of hypsodonty in *G. spatulus* as well as the much shorter distance between C_1 and P_3 in *T. nebraskensis* must weigh heavily against the congenerity of these two species.

Gigantocamelus Barbour and Schultz, 1939

TYPE-SPECIES.—*Gigantocamelus fricki* Barbour and Schultz, 1939:17 (= *Pliauchenia spatula* Cope, 1893:70; = *Gigantocamelus spatulus* Meade, 1945:531; = *Titanotylopus spatulus* (Meade) fide Webb, 1965:36).

Gigantocamelus is known from Blancan localities throughout the central and western United States (Figure 5). The giant camel from the Blanco beds of Texas was first described as *Pliauchenia spatula* by Cope (1893:70). Barbour and Schultz (1939:17) subsequently described a large sample of giant camel from Lisco, Nebraska, as *Gigantocamelus fricki.* Meade (1945:531) recognized these camels as the same species and united them under the name *Gigantocamelus spatulus.* Hibbard and Riggs (1949:844) followed Meade when they described a third large sample of this giant camel from Keefe Canyon, Kansas.

Gigantocamelus is a much more hypsodont camel than *Titanotylopus.* Its chin is blunt with the ramal symphysis extending only a few centimeters beyond the large, splayed canines. The spatulate lower incisors are arrayed almost transversely. In *Titanotylopus* the chin is long, C_1 is large but not greatly splayed, and the nonspatulate incisors are arrayed in an arc. P_1 is present in *Gigantocamelus* and absent in *Titanotylopus.* As indicated in the preceding section, many workers have followed Webb (1965) and Breyer (1976)

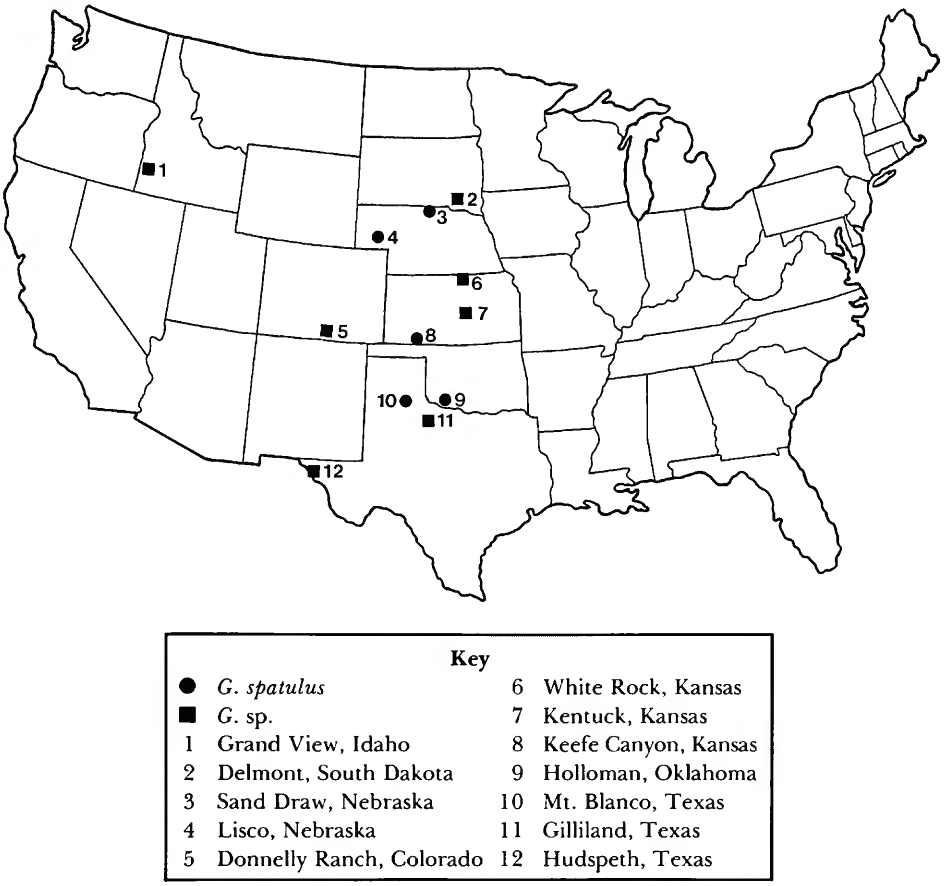


FIGURE 5.—Geographic distribution of *Gigantocamelus*.

in synonymizing *Gigantocamelus* and *Titanotylopus*. I believe that the above characters, in addition to the new data from Corner and Voorhies, support the generic validity of *Gigantocamelus*.

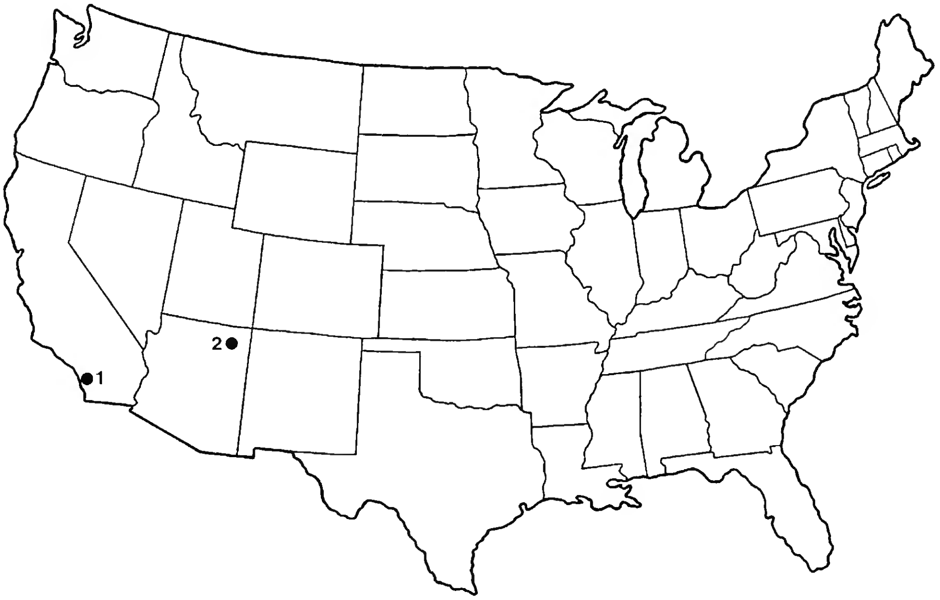
Several other workers have made reference to *Gigantocamelus* in one or more of its previous taxonomic incarnations. Dumble (1894:559), Wortman (1898:128), Gidley (1903:627), Matthew (1901:423; 1909:120), and Merriam (1917:435) noted the presence of *Pliauchenia spatula* at Mt. Blanco. Matthew (1899:75) listed material from Goodnight, Texas, as *P. spatula*, but this is more likely *Megatylopus*. From the Saw Rock fauna of Kansas, Hibbard (1953:407) referred a toe bone to *Gigantocamelus* cf. *G. spatulus*. Although I have not seen this specimen, the measurements fall within the range of *Megacamelus*. If indeed the toe can be identified as *Gigantocamelus*, it would be the earliest occurrence of this genus. From the Gilliland fauna of Texas, Hibbard and Dalquest (1962:86) referred a distal radius, some distal metapodials, an astragalus, and three phalanges to ?*Gigantocamelus*, and later added a cervical vertebra and changed the identification to ?*Titanotylopus*, reflecting Webb's synonymy. Strain (1966:50) referred two distal metapodials from the Hudspeth fauna of Texas to *Gigantocamelus* sp. Semken (1966:164) referred a partial calcaneum from the Kentuck fauna of Kansas to *Gigantocamelus* sp. A number of foot and limb bones from the Grand View fauna of Idaho were referred to *Titanotylopus* sp. by Shotwell (1970:96). Hibbard (Skinner et al., 1972:114) referred some material from the Sand

Draw fauna of Nebraska to *G. spatulus*. Martin and Harksen (1974:14) referred a partial mandible from the Delmont fauna of South Dakota to *Titanotylopus*. Dalquest (1975:42) described additional specimens of *T. spatulus* from Mt. Blanco. Eshelman (1975:47) referred a proximal ulna from the White Rock fauna of Kansas to *Gigantocamelus* sp. Hager (1975:14) referred some tooth fragments and foot bones from the Donnelly Ranch fauna of Colorado to *Gigantocamelus* sp. Dalquest (1977:260) described a radius of *T. spatulus* from the Holloman fauna of Oklahoma. Corner and Voorhies (pers. comm., 1984) regard the specimens from the Gilliland and Holloman faunas as generically indeterminate between *Gigantocamelus* and *Titanotylopus*. Ferrusquia-Villafranca (1978:255) listed *Gigantocamelus mexicanus* and *G. magnus* from the Mexican faunal assemblage. Dalquest (1974:196–197) noted that these two species were based upon the same type material, *G. mexicanus* being the senior synonym, and identified them as *Camelops*.

Megacamelus Frick, 1929

TYPE-SPECIES.—*Pliauchenia merriami* Frick, 1921:358 (= *Megacamelus merriami*, new combination).

Megacamelus is presently known only from the late Hemphillian of the southwestern United States (Figure 6). Frick (1921:358) described *Pliauchenia merriami* from Mt. Eden, California, and later (1929:107) named *Megacamelus blicki* from Keams Canyon, Arizona. Study indicates that these camels are conspecific. The Mt. Eden camel is clearly not *Pliauchenia* and although Webb (1965:36) referred it to *Titanotylopus*, it does not belong to that genus for reasons discussed below. Therefore, a new taxonomic com-



Key

- ● *M. merriami*, new combination
- 1 Mt. Eden, California
- 2 Keams Canyon, Arizona

FIGURE 6.—Geographic distribution of *Megacamelus*.

bination, *Megacamelus merriami*, is proposed for the giant camels from Mt. Eden and Keams Canyon.

Megacamelus merriami (Frick, 1921), new combination

FIGURES 7–16

Pliauchenia merriami Frick, 1921:358.
Megacamelus blicki Frick, 1929:107.

HOLOTYPE.—UCMP 23483, anterior portion of the upper jaws bearing right and left I^3, C^1, P^1; anterior portion of the lower jaws bearing right $I_{2,3}$, C_1, P_1, partial P_3 and left $I_{2,3}$, C_1, P_1; distal humerus, proximal radius-ulna, distal radius-ulna, scaphoid, lunar, cuneiform, pisiform, distal tibia, astragalus, calcaneum, navicular, cuboid, ectocuneiform, proximal metatarsus, 2 distal metapodials, 6 proximal phalanges, 5 medial phalanges, 7 distal phalanges, and 8 sesamoids.

REFERRED SPECIMENS.—From Mt. Eden, California: UCMP 23416, left P^3; UCMP 23433, right partial upper molar; UCMP 23783, left I_2; UCMP 23790, right I_3; UCMP 23791, left I_3; UCMP 23435, left $M_{2(?)}$; UCMP 23789, left $M_{1(?)}$.

From Keams Canyon, Arizona (all of the following are F:AM numbers): skulls, 23201, 23202, 23202A, 23203, 23207; partial skulls, 23203A, 23203B, 23203C, 23204, 23205, 23205A, 23208, 23209, 104395; partial maxillae, 23206, 23210; mandibles, 23216, 23218, 23220, 23230, 23231, 23232, 23233, 23235, 23239A; rami, 23217A, 23217B, 23219, 23221, 23222, 23223A, 23223B, 23225, 23226, 23227, 23228, 23229, 23233A, 23234, 23240B; partial rami, 23224, 23317, 23320, 104274; incisors, 104329, 104330, 104333, 104334, 104335; canine, 104383; associated postcrania, 23312 (astragalus, calcaneum, tarsal fragments, and metatarsus); atlas, 104291, 104292, 104293, 104294, 104295; axis, 104284, 104299; cervical vertebrae, 104281, 104282, 104283, 104285, 104286, 104287, 104288, 104289, 104290, 104297, 104298; thoracic vertebrae, 104286, 104296, 104305; lumbar vertebrae, 104277, 104300, 104301, 104304; sacra, 104280, 104302; scapulae, 23245, 23246, 23247, 23248, 23249, 23250, 23251, 23275, 23276, 104278, 104279, 104408, 104607; humeri, 23254, 23255, 23256, 23257, 23258, 104405, 104406, 104407; radius-ulnae, 23260, 23261, 23261A, 23262, 23263, 23264, 23265, 23266, 23267, 23268, 23269, 23270, 104400, 104600; scaphoids, 104311, 104351, 104352, 104376, 104377, 104603; lunars, 104309, 104323, 104324, 104349, 104350, 104361; cuneiforms, 104325, 104332, 104389, 104605; pisiforms, 104312, 104345, 104356, 104370, 104371, 104372; trapezoids, 104316, 104341, 104359; magna, 104339, 104360, 104390; unciforms, 104307, 104308, 104342, 104343, 104344, 104346, 104364; metacarpi, 23277, 23278, 23279, 23280, 23281, 23282, 23283, 23284, 23285, 23301, 104401; pelves, 104303, 104396; femora, 23290, 23291, 23292, 23293, 23294, 23295, 104403, 104404; patellae, 104358, 104394; tibiae, 23271, 23296, 23297, 104399; distal fibula, 104347, 104375; astragali, 104229, 104230, 104231, 104232, 104233, 104234, 104235, 104236,104272, 104273, 104602; calcanea, 104237, 104238, 104239, 104240, 104601; naviculars, 104310, 104331, 104373, 104374; cuboids, 104306, 104336, 104353, 104354, 104355, 104362, 104363; ectocuneiforms, 104313, 104322, 104378, 104379, 104380, 104381, 104382, 104384, 104385, 104386, 104392, 104393; metatarsi, 23302, 23303, 23304, 23305, 23306, 23307, 23308, 23313; partial metapodials, 23314, 23316, 104326, 104327, 104328, 104397, 104398, 104402; sesamoids, 104315, 104317, 104318, 104319, 104320, 104321, 104337, 104338, 104348, 104357, 104365, 104366, 104367, 104368, 104369, 104387, 104388, 104606; proximal phalanges, 104241, 104242, 104243, 104244, 104245, 104246, 104247, 104248, 104249, 104250, 104251, 104252, 104253, 104254, 104255, 104256, 104257, 104258, 104259, 104260, 104261, 104262, 104263, 104265, 104266, 104267, 104268, 104269; medial phalanges, 104210, 104211, 104212, 104213, 104214, 104215, 104216, 104217,

TABLE 2.—Measurements (cm) of the skull and upper dentition of *Megacamelus merriami*, new combination, from Keams Canyon (O.R. = observed range, $\bar{X}$ = sample mean, s.d. = standard deviation).

Element		No.	O.R.	$\bar{X}$	s.d.
Length from premaxilla to occipital crest		3	69.30-82.05	73.65	
Length from premaxilla to occipital condyles		3	61.67-71.35	65.54	
Width of muzzle across I^3		3	6.68-8.25	7.68	
Width of muzzle across C^1		3	7.69-8.59	8.16	
Minimum width at postorbital constriction		4	6.71-9.65	8.45	
Maximum width across zygomatic arches		2	26.40-27.34	26.87	
Width of occipital condyles		7	9.25-11.55	10.14	0.76
Diastema I^3-C^1		2	2.10-2.30	2.20	
Diastema C^1-P^1		2	3.08-3.27	3.17	
Diastema P^1-P^3		3	7.10-8.83	7.81	
I^3	length	2	2.20-3.19	2.69	
	width	2	1.22-1.73	1.47	
C^1	length	3	2.88-3.46	3.15	
	width	3	1.82-2.33	2.11	
P^1	length	4	1.94-2.52	2.20	
	width	4	1.38-1.74	1.54	
P^3	length	6	1.84-3.05	2.62	0.44
	width	7	1.88-2.03	1.95	0.06
P^4	length	7	2.85-3.25	3.03	0.18
	width	6	2.75-3.31	3.04	0.22
M^1	length	6	4.30-4.75	4.54	0.15
	width	6	3.80-4.45	4.11	0.27
M^2	length	8	4.89-5.66	5.42	0.35
	width	6	3.82-4.75	4.46	0.34
M^3	length	7	5.40-6.13	5.69	0.28
	width	6	3.86-4.39	4.20	0.19
I^3-M^3	length	3	37.77-41.10	39.06	
P^3-M^3	length	5	18.96-20.03	19.41	
dP^2	length	2	1.39-1.50	1.44	
	width	2	0.42-0.82	0.62	
dP^3	length	3	3.29-3.60	3.43	
	width	3	2.45-2.65	2.55	
dP^4	length	3	3.72-4.15	3.86	
	width	3	3.00-3.20	3.07	
dP^2-M^2	length	1	16.00		
dP^3-M^2	length	2	14.88-15.96	15.42	

104218, 104219, 104220, 104221, 104222, 104223, 104224, 104225, 104270, 104604; distal phalanges, 104226, 104227, 104228, 104271, 104314, 104340, 104391.

TABLE 3.—Measurements (cm) of the mandible and lower dentition of *Megacamelus merriami*, new combination, from Keams Canyon (O.R. = observed range, $\bar{X}$ = sample mean, s.d. = standard deviation).

Element		No.	O.R.	$\bar{X}$	s.d.
Maximum length of ramal symphysis		5	12.81-17.10	14.89	
width of manidbular condyle		8	4.35-5.93	5.36	0.51
Diastema I_3-C_1		4	0.63-1.06	0.88	
Diastema C_1-P_1		5	3.36-4.38	3.90	
Diastema P_1-P_3		6	7.26-8.23	7.55	0.41
C_1	length	6	3.19-3.88	3.48	0.25
	width	6	2.19-3.17	2.58	0.41
P_1	length	6	2.23-2.63	2.36	0.18
	width	6	1.23-1.89	1.49	0.29
P_3	length	8	1.87-2.38	2.08	0.16
	width	7	1.16-1.35	1.24	0.06
P_4	length	10	2.72-3.26	2.96	0.18
	width	9	1.72-2.07	1.88	0.12
M_1	length	12	4.05-5.05	4.41	0.33
	width	12	2.32-2.90	2.64	0.19
M_2	length	12	4.86-5.44	5.09	0.28
	width	14	2.27-3.53	2.96	0.38
M_3	length	11	5.98-6.84	6.49	0.26
	width	9	2.61-3.43	3.04	0.29
C_1-M_3	length	5	36.05-39.41	38.09	
P_3-M_3	length	6	20.34-21.74	20.71	0.51
dP_2	length	3	1.06-1.31	1.18	
	width	3	0.12-0.13	0.13	
dP_3	length	3	2.05-2.29	2.18	
	width	3	1.20-1.27	1.23	
dP_4	length	2	4.21-5.30	4.75	
	width at posterior cusp	2	2.06-2.16	2.11	

DESCRIPTION.—The extensive sample from Keams Canyon contains several fine skulls and mandibles as well as a wealth of postcrania (Figures 7–11). With one exception (F:AM 23312), none of the material is associated. The Keams Canyon camel compares well with that described by Frick (1921) from Mt. Eden. Both exhibit very large, caniniform I^3, C^1, and P^1, a massive premaxilla, and heavy anterior ramus with large C_1 and large, caniniform P_1. The size and proportions of the postcrania from both localities are comparable.

The skull of *M. merriami* is long with a flattened dorsal profile and a deep, massive rostrum. The occipital crest is a broad fan that extends

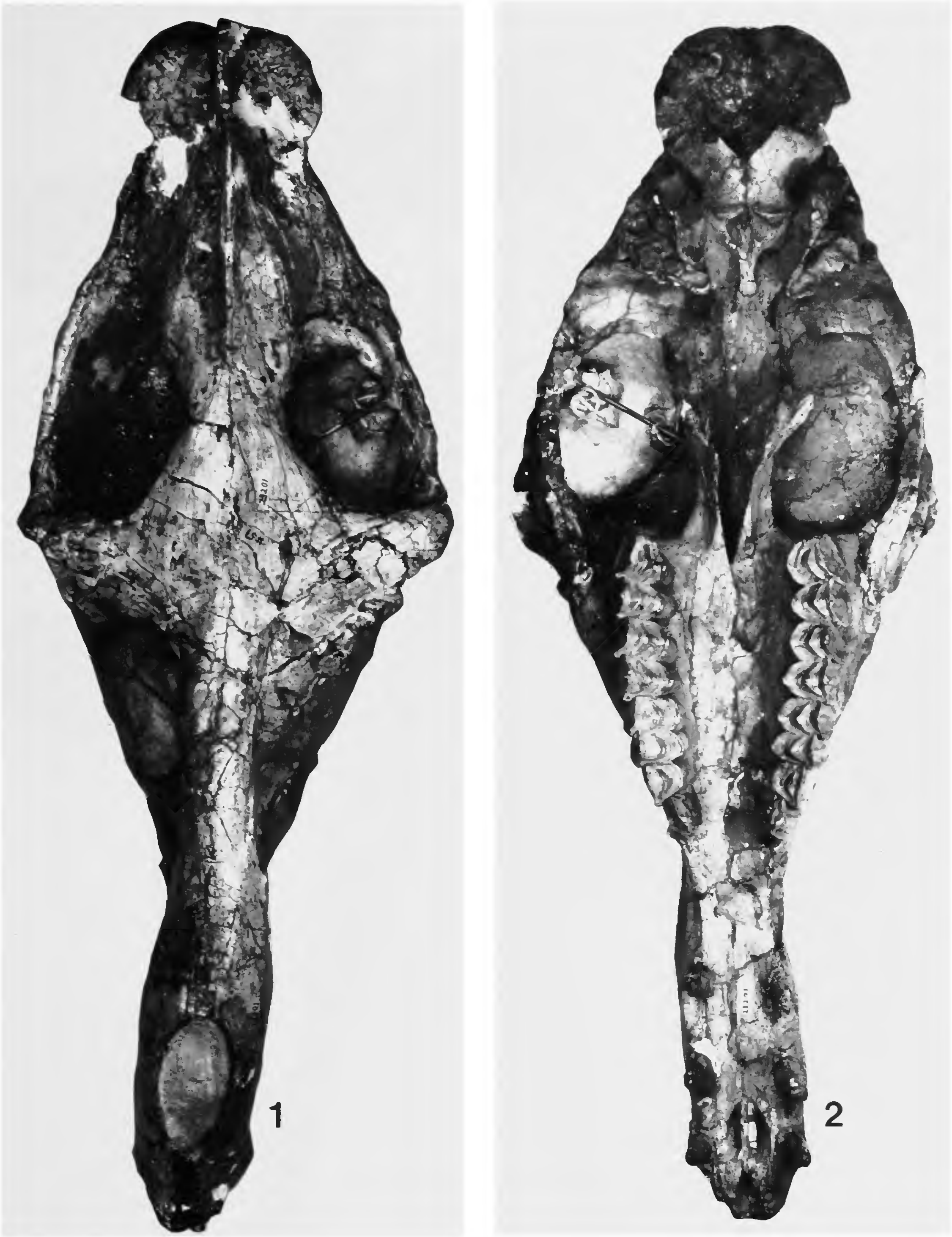


FIGURE 7.—*Megacamelus merriami*, new combination, from Keams Canyon, Arizona, F:AM 23201, skull: *1*, dorsal view; *2*, occlusal view. (× ¼.)

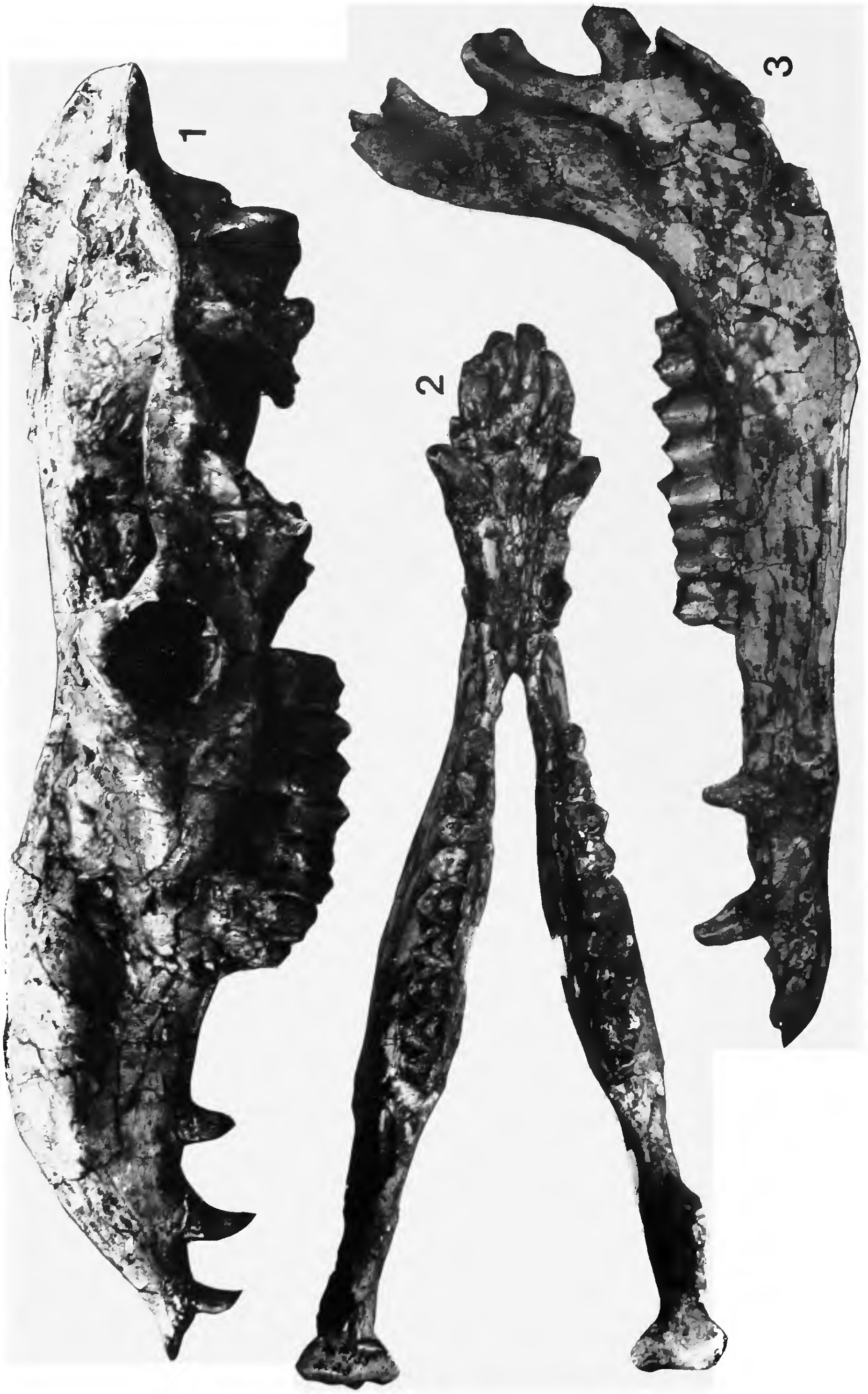


FIGURE 8.—*Megacamelus merriami*, new combination, from Keams Canyon, Arizona: *1*, F:AM 23201, skull, lateral view; *2*, *3*, F:AM 23232, mandible, occlusal and lateral views. (× ¼.)

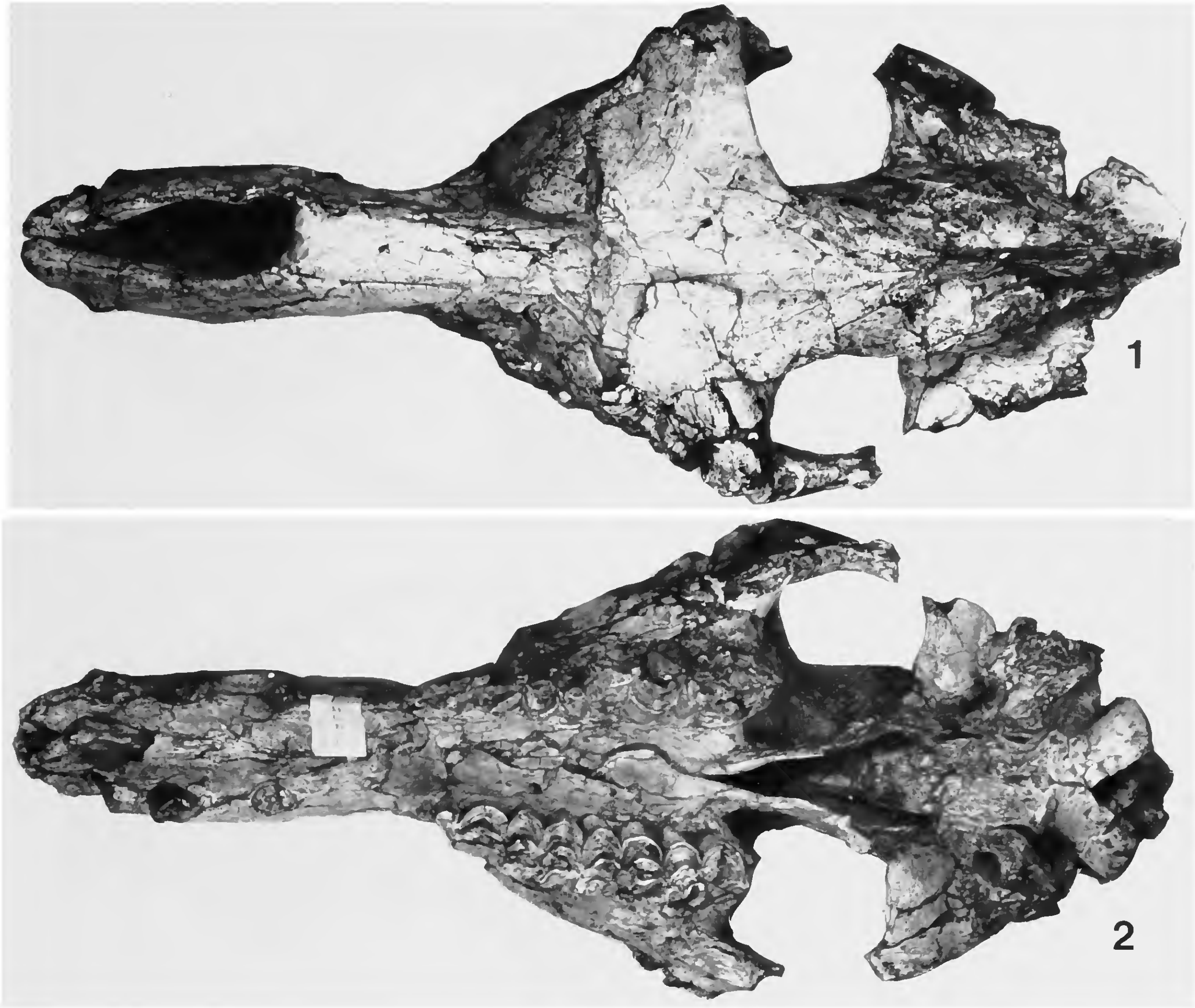


FIGURE 9.—*Megacamelus merriami,* new combination, from Keams Canyon, Arizona, F:AM 23202, skull: *1,* dorsal view; *2,* occlusal view. (× ¼.)

well posterior to the occipital condyles. The sagittal crest is likewise well developed. The orbit is circular in outline followed by a strong postorbital bar. A triangular lacrimal vacuity is present in most of the Keams Canyon *M. merriami*, but it is a highly variable feature. In one specimen. F:AM 23202, it is present on the left side of the skull, but reduced to a slit on the right side (Figure 9). Another skull, F:AM 23202A, bears well-developed lacrimal vacuities on both sides (Figure 10). Although Meade (1945:531) reported the presence of a lacrimal vacuity in *M. spatulus* from Mt. Blanco, Hibbard and Riggs (1949:846) reported its absence and, moreover, suggested that the opening in the Mt. Blanco skulls could represent an artifact of preservation.

The upper dentition consists of I^3, C^1, $P^{1,3,4}$, M^{1-3}. I^3 is always present and, as mentioned above, is large and caniniform. C^1 is large and deviates slightly from a vertical orientation. Presumably, when Barbour and Schultz (1939:24) stated that the canines of the Keams Canyon

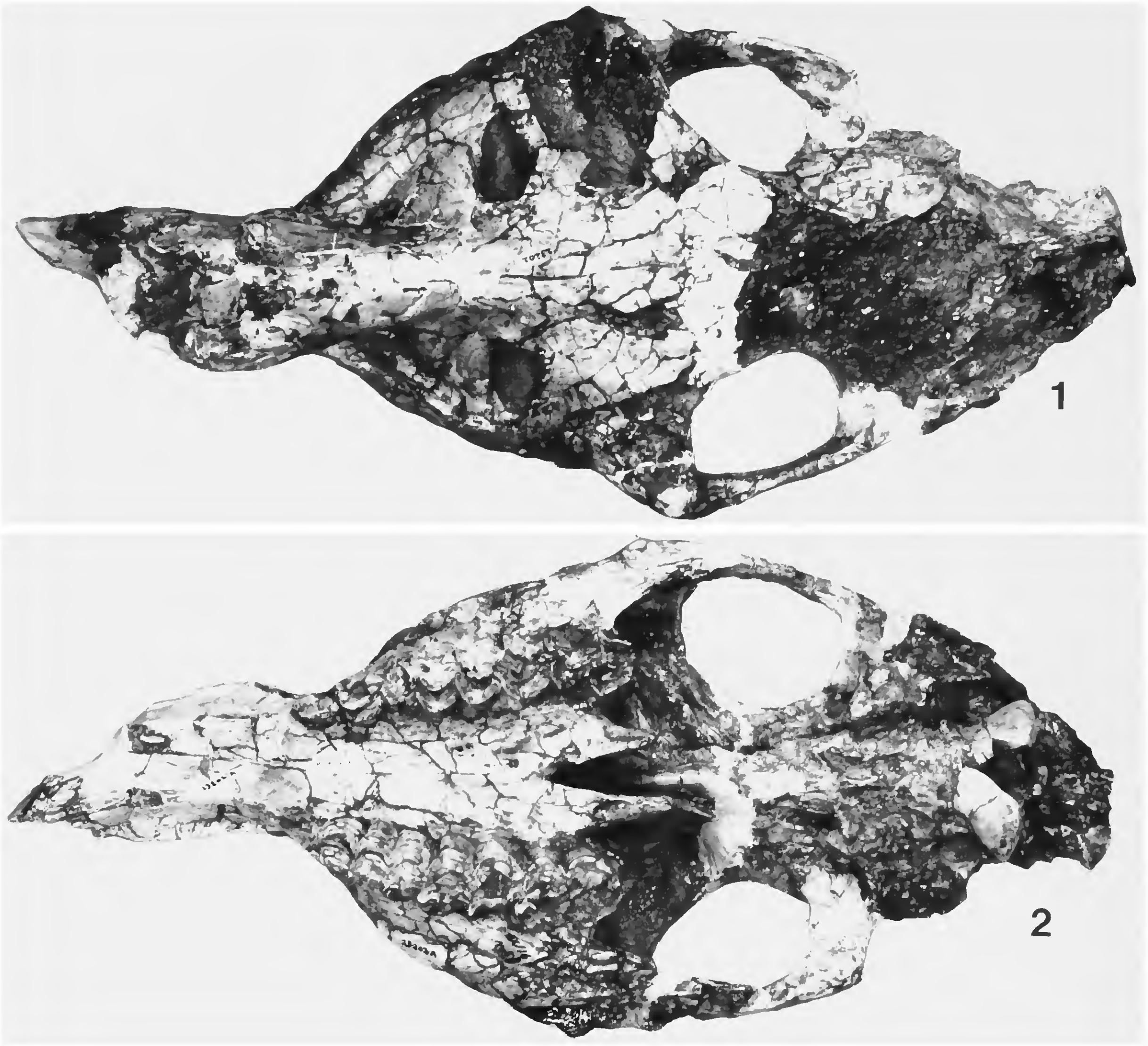


FIGURE 10.—*Megacamelus merriami*, new combination, from Keams Canyon, Arizona, F:AM 23202A, skull: *1*, dorsal view; *2*, occlusal view. (× ¼.) Note the large lacrimal vacuities.

camel were not enlarged, it was in comparison to the extreme development observed in *Gigantocamelus spatulus* and *Titanotylopus nebraskensis*. P^1 is caniniform and only slightly smaller than I^3. P^3 is large with an incomplete internal crescent. P^4 is not much longer than P^3 but much wider due to its complete internal crescent. Only the parastyle shows much development on P^4, but a strong parastyle and mesostyle are present on each molar. The teeth are higher crowned than those of *Megatylopus gigas* or *Titanotylopus nebraskensis*.

The mandible is long and massive but still smaller than that of *Gigantocamelus spatulus* or *Titanotylopus nebraskensis*. The mandibular proportions of *M. merriami* agree well with those of *G. spatulus;* however, *M. merriami* does not display the degree of variation in the symphyseal

TABLE 4.—Measurements (cm) of the postcrania of *Megacamelus merriami*, new combination, from Keams Canyon (O.R.= observed range, $\bar{X}$ = sample mean, s.d. = standard deviation).

Element	No.	O.R.	$\bar{X}$	s.d.
Atlas				
length of centrum	2	6.75–6.80	6.77	
posterior height	1	9.36		
Scapula				
maximum length	2	61.53–64.06	62.79	
maximum width	1	38.35		
glenoid fossa				
antero-posterior	3	9.37–10.56	9.87	
transverse	3	9.17–10.61	9.66	
Humerus				
length	1	53.27		
distal width across trochlea	5	10.60–11.70	11.14	
Radius-ulna				
maximum length	4	72.65–85.70	80.33	
articular length	4	66.03–75.50	71.22	
proximal width	6	10.19–11.52	10.87	0.43
distal width	5	10.40–12.62	11.39	
Metacarpus				
length	7	48.39–54.29	51.08	2.07
proximal width	8	8.11–11.64	9.12	1.10
distal width	7	11.38–12.30	11.88	0.33
Femur				
length	1	60.89		
proximal width	1	16.07		
distal width	2	13.98–15.34	14.66	
width of patellar surface	3	5.07–5.79	5.46	
Tibia				
length	1	67.00		
distal width	2	10.95–11.45	11.20	
Astragalus				
length (tibial to tarsal surface)				
medial	7	8.19–8.98	8.57	0.34
lateral	7	8.85–9.80	9.47	0.30
distal width	7	6.03–6.65	6.39	0.21
Calcaneum				
length	4	17.68–19.56	18.64	
maximum antero-posterior	4	7.21–8.30	7.90	
Metatarsus				
length	5	48.37–50.58	49.44	
proximal width	2	8.06–9.37	8.71	
distal width	4	10.01–10.75	10.35	
Proximal phalanx				
length	21	11.05–13.80	12.41	0.84
proximal width	21	4.55–5.73	5.08	0.35
distal width	22	3.82–5.14	4.42	0.41
Medial phalanx				
length	18	7.22–8.47	7.76	0.34
proximal width	18	3.74–4.99	4.19	0.27
distal width	17	3.26–4.21	3.79	0.25
Distal phalanx				
length	6	3.16–4.16	3.71	0.34
width of articular surface	6	2.45–2.80	2.60	0.13

region observed in *G. spatulus* by Meade (1945:532) or Hibbard and Riggs (1949:847). Meade, in the Mt. Blanco sample, and Hibbard and Riggs, in the Keefe Canyon sample, found jaws with widely splayed and canines and transversely arrayed incisors as well as jaws with more vertically oriented canines and more conventionally arrayed incisors. Hibbard and Riggs (1949), Webb (1965), and Breyer (1976) have attributed such variation to sexual dimorphism. In the Keams Canyon sample the incisors are procumbent and arrayed in a more shallow arc than in *Titanotylopus*. The canines are very large, but only slightly splayed. No specimen displays the degree of canine flare and incisor-row bluntness characteristic of *G. spatulus* (Cope, 1893, pl. 21; Barbour and Schultz, 1939, fig. 9; Meade, 1945, pl. 54; Hibbard and Riggs, 1949, fig. 8). A groove is present between the median incisors on the ventral symphyseal surface, as noted by Cope (1893:71) and Meade (1945:532).

The lower dentition consists of I_{1-3}, C_1, $P_{1,3,4}$, M_{1-3}. The incisors have spatulate crowns that with much wear assume a more rounded, peg-

FIGURE 11.—*Megacamelus merriami,* new combination, from Keams Canyon, Arizona: *1, 4,* F:AM 23216, mandible, occlusal and lateral views; *2, 3,* F:AM 23239A, partial ramus bearing deciduous P_{2-4} and M_1 emerging, occlusal and lateral views. (× ¼.)

like appearance. The canines bear the strong anterointernal and posterior enamel ridges typical of *G. spatulus.* P_1 is present in all specimens and usually well developed. An exception is F:AM 23218, one of the smallest individuals, in which P_1 is correspondingly small. The cheek tooth series is quite similar to that of *M. spatulus.* Meade (1945:533) reports an anteroexternal style or "llama buttress" on $M_{2,3}$ of one specimen and notes the presence of this feature in figures of *M. spatulus* from Lisco. No indication of a "llama buttress" is present in *M. merriami.*

The limbs and feet of *M. merriami,* especially the metapodials and phalanges, do not exhibit the shortening in relation to the basal length of the skull seen in *G. spatulus.* Hence, Barbour and

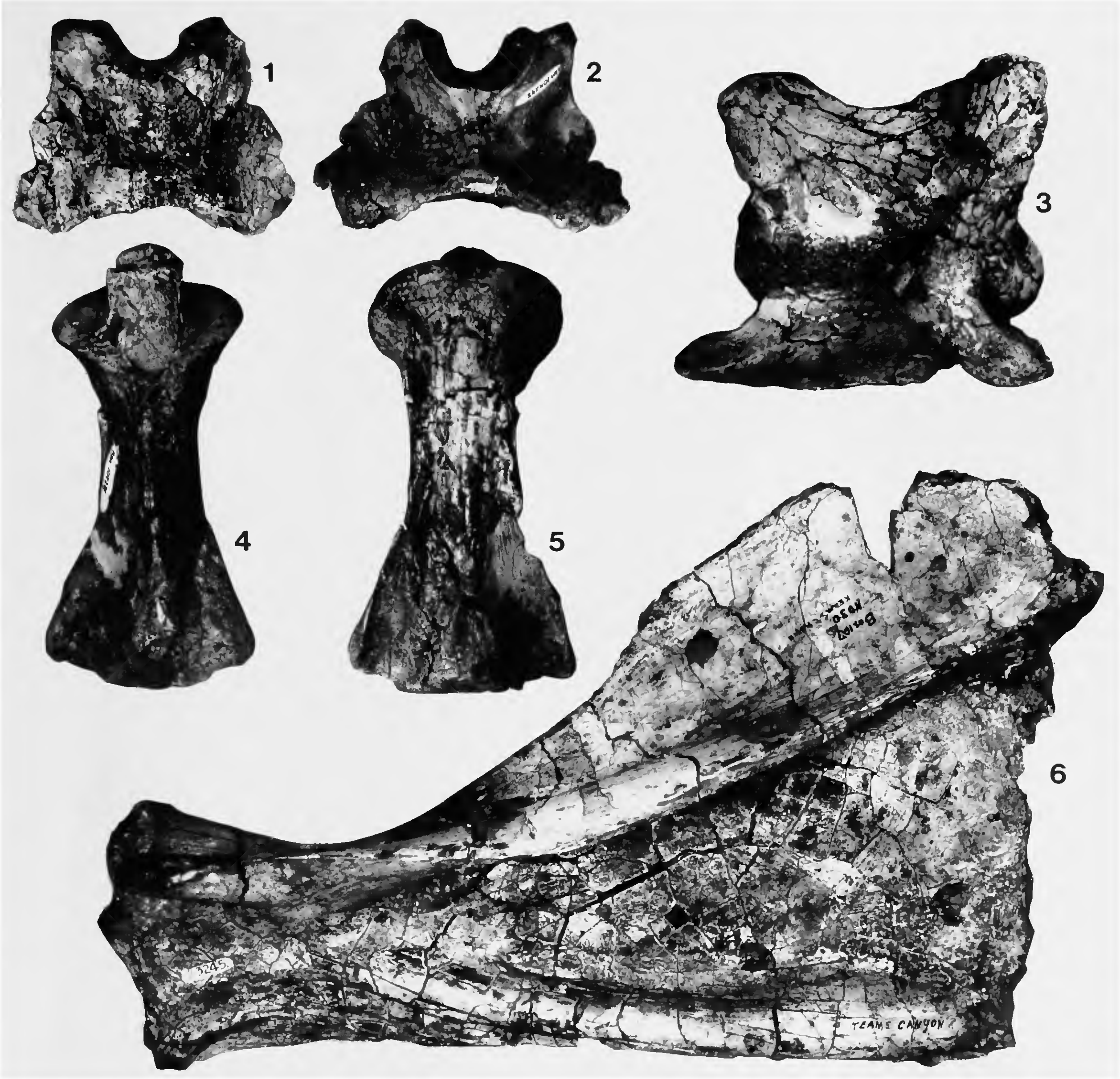


FIGURE 12.—*Megacamelus merriami,* new combination, from Keams Canyon, Arizona: *1, 2,* F:AM 104293, atlas, dorsal and ventral views; *3,* F:AM 104281, sixth cervical vertebra, lateral view; *4, 5,* F:AM 104284, axis, dorsal and ventral views; *6,* F:AM 23245, left scapula, lateral view. (× ¼.)

Schultz (1939:24) remarked that "the skeletal elements appear to be more massive in the Nebraska form" (= *G. spatulus*). The limbs of *M. merriami* are, however, shorter and stockier than those of *Megatylopus.*

DISCUSSION.—*Megacamelus merriami* is most closely related to *Gigantocamelus spatulus* but differs from it in the presence of the large, caniniform I^3, smaller size, less shortened limbs, and lower-crowned teeth. Breyer (1983:305) re-

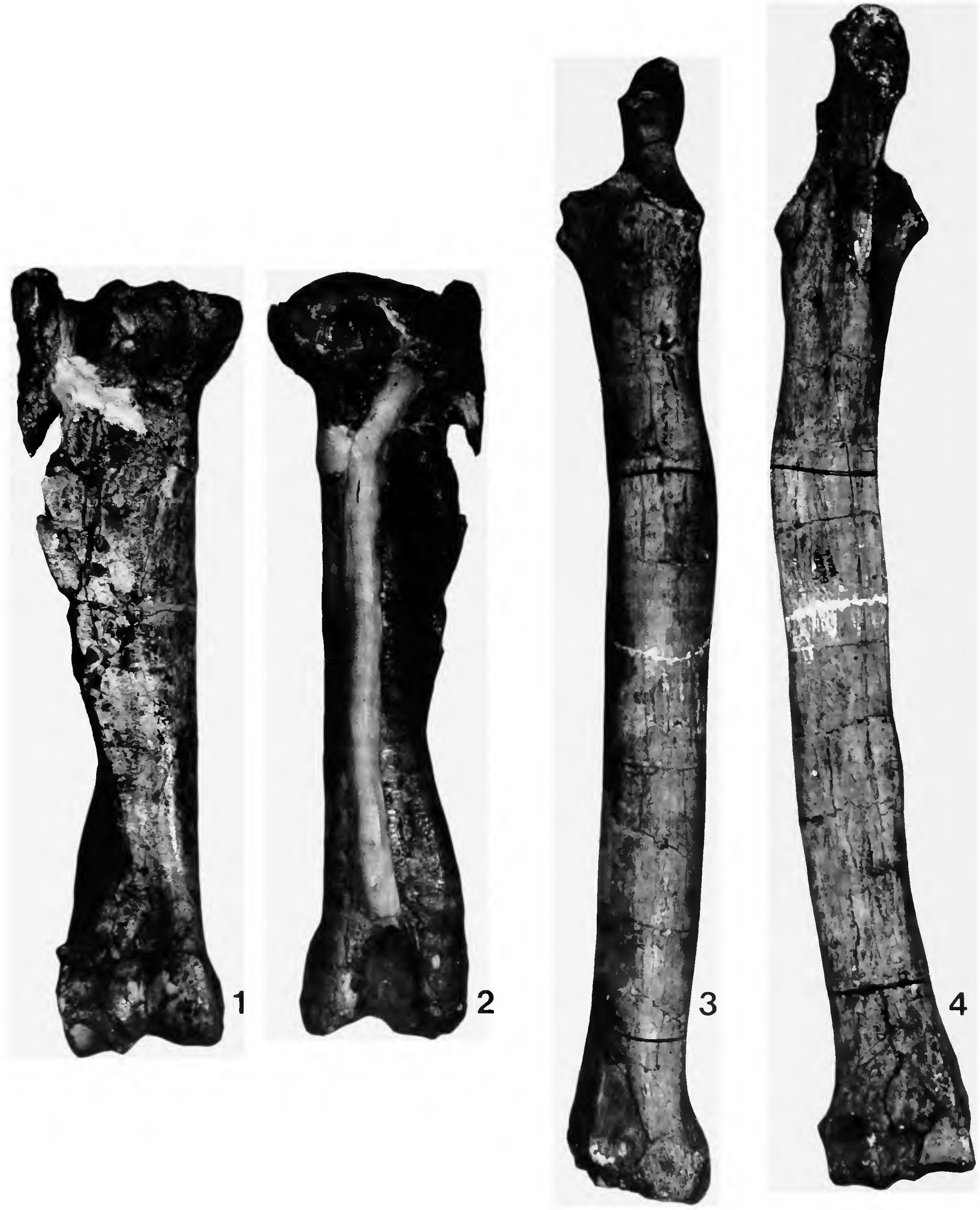


FIGURE 13.—*Megacamelus merriami*, new combination, from Keams Canyon, Arizona: *1, 2,* F:AM 23256, humerus, anterior and posterior views; *3, 4,* F:AM 23262, radius-ulna, anterior and posterior views. (× ¼.)

ferred the Keams Canyon material to *Titanotylopus nebraskensis* on the basis of the projection of the mandibular symphysis beyond the canines. This condition is primitive for camelines and hence not a valid criterion. Moreover, several characters such as the presence of P_1 in all specimens, greater degree of hypsodonty, and the greater distance between C_1 and P_3 preclude the referral of the Keams Canyon camel to *Titanotylopus*.

Camelus Linnaeus, 1758

TYPE-SPECIES.—*Camelus dromedarius* Linnaeus, 1758:65.

Camelus is the smallest of the giant camels. The two extant species, *G. dromedarius* (monogibbose) and *C. bactrianus* (digibbose), range throughout most of the arid and semi-arid regions of the Old World. *Camelus bactrianus* is native to Chinese Turkestan and Mongolia, where small wild populations still exist (Walker, 1964:1374). Both *C. bactrianus* and *C. dromedarius* have been domesticated for several thousand years, and the original native range of the latter species can no longer be determined.

Camelus has an extensive fossil record in the Pleistocene of the Old World and has been found in association with human artifacts and remains (Gauthier-Pilters and Dagg, 1981:5). Camels migrated from North America via Beringea near the end of the Tertiary, probably during the late Ruscinian. *Camelus* (*Paracamelus*) Schlosser (1903) occurs in several late Pliocene localities in the People's Republic of China. As yet no fossil material of *Camelus* or *Paracamelus* has been recovered from North America.

FIGURE 14.—*Megacamelus merriami*, new combination, from Keams Canyon, Arizona: *1, 2,* F:AM 104311, scaphoid, medial and lateral views; *3, 4,* F:AM 104323, lunar, medial and lateral views; *5, 6,* F:AM 104325, cuneiform, medial and lateral views; *7, 8,* F:AM 104312, pisiform, medial and lateral views; *9, 10,* F:AM 104359, trapezoid, posteromedial and anterolateral views; *11, 12,* F:AM 104360, magnum, proximal and distal views; *13, 14,* F:AM 104343, unciform, proximal and distal views; *15, 16,* F:AM 23279, metacarpus, anterior and posterior views. (× ¼.)

FIGURE 15.—*Megacamelus merriami,* new combination, from Keams Canyon, Arizona: *1, 2,* F:AM 23293, femur, anterior and posterior views; *3, 4,* F:AM 23296, tibia, anterior and posterior views. (× ¼.)

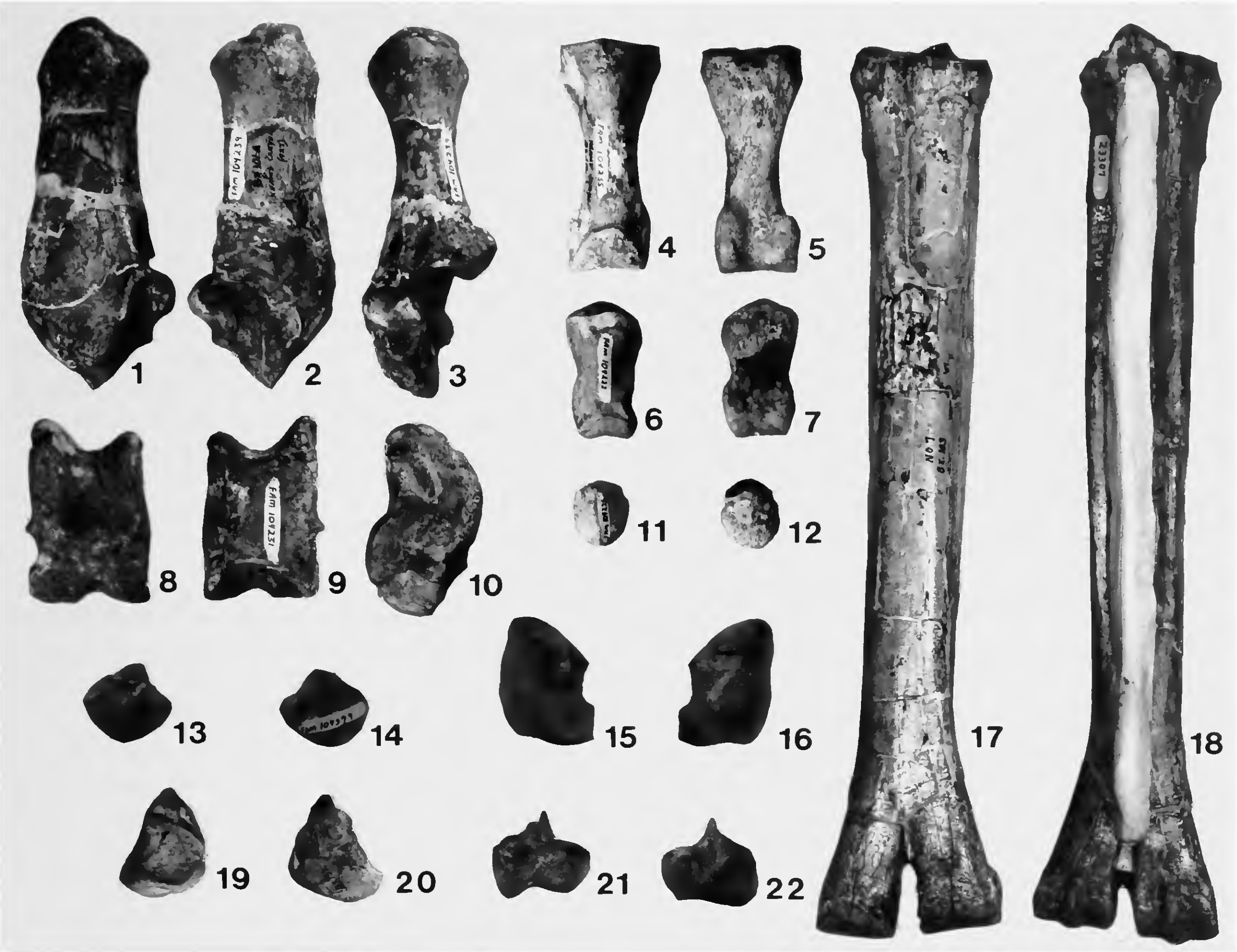


FIGURE 16.—*Megacamelus merriami*, new combination, from Keams Canyon, Arizona: *1–3*, F:AM 104239, calcaneum, lateral, medial, and anterior views; *4, 5*, F:AM 104255, proximal phalanx, anterior and posterior views; *6, 7*, F:AM 104222, medial phalanx, anterior and posterior views; *8–10*, F:AM 104231, astragalus, anterior, posterior and lateral views; *11, 12*, F:AM 104226, distal phalanx, anterior and posterior views; *13, 14*, F:AM 104379, ectocuneiform, proximal and distal views; *15, 16*, F:AM 104366, cuboid, proximal and distal views; *17, 18*, F:AM 23307, metatarsus, anterior and posterior views; *19, 20*, F:AM 104310, navicular, proximal and distal views; *21, 22*, F:AM 104375, distal fibula, medial and lateral views. (× ¼.)

Blancocamelus Dalquest, 1975

TYPE-SPECIES.—*Blancocamelus meadei* Dalquest, 1975:37.

This genus is represented solely by *B. meadei*, described by Dalquest (1975:37) from Mt. Blanco, Texas. Dalquest noted that although Meade (1945:538) was aware of the uniqueness of this camel, he mistakenly applied to it an unpublished name, *Leptotylopus percelsus*, from a 1924 manuscript of W.D. Matthew. As used by Meade, the name was a nomen nudum. The taxon to which Matthew had applied the name in manuscript was subsequently identified as *Tanupolama (= Hemiauchenia) blancoensis*. Thus, the genus was left without a valid name until Dalquest (1975) proposed *Blancocamelus meadei* for it.

Blancocamelus is known only from postcranial elements. Its limbs are exceedingly long, but quite slender, evoking mental images of a giant *Hemiauchenia*. Indeed, the posterior surface of the proximal phalanx presents an asymmetrical, W-shaped scar for the attachment of the suspensory ligament that is quite like that of *Hemiauchenia* (Breyer, 1976, fig. 2). Although Meade (1945) and Kurtén and Anderson (1980:302) have speculated upon the possible affinities of *Blancocamelus* and the aepycamelines, I prefer for the present to group it with the lamines. With the exception of a possible occurrence in the Blancan Red Light fauna of Texas (Akersten, 1972:29), *Blancocamelus* is restricted to the type-locality (Figure 4).

Camelops Leidy, 1854

TYPE-SPECIES.—*Camelops kansanus* Leidy, 1854:172.

Camelops is by far the best known of the lamines, giant or otherwise. It occurs from the late Blancan into the early Holocene in localities throughout the western United States (Kurtén and Anderson, 1980, fig. 15.4). Since its description by Leidy (1854:172), the genus *Camelops* has undergone a bewildering series of synonymies, referrals, and revisions. Much of this morass was clarified by Webb (1965), who followed Savage (1951) in recognizing five species: *C. kansanus* Leidy (1854:172), *C. hesternus* (Leidy, 1873:255), *C. huerfanensis* (Cragin, 1892: 258), *C. sulcatus* (Cope, 1893:84), and *C. minidokae* Hay (1927:93). These five species plus *C. traviswhitei* Mooser and Dalquest (1975:341) were recognized by Kurtén and Anderson (1980).

Camelops, especially the later species, is very hypsodont with large lacrimal vacuities and marked maxillary fossae. The skull is long and does not display the rostral shortening characteristic of other lamines such as *Hemiauchenia*, *Lama*, and *Vicugna*. The mandible is long with a sharp diastemal crest and uninflected angular processes. The dental formula is I^{1}_{3} C^{1}_{1} P^{2}_{1} M^{3}_{3}. In *Camelops* I^{3} and C^{1}_{1} are reduced, laterally compressed, and recurved rather than enlarged and rounded in cross section as in the giant camelines. $P^{1,2}_{1,2,3}$ are lost and P^{3}_{4} are reduced. The molars are relatively narrow with external styles less strongly developed than in the camelines.

The limbs of *Camelops* are sturdy and the metapodials less slender than those of the other lamines. The area of attachment for the suspensory ligament on the posterior surface of the proximal phalanx is distinctive (Breyer, 1974, fig. 2B). *Camelops hesternus*, *C. traviswhitei*, and *C. huerfanensis* are the only species considered within the scope of giant camels. More detailed descriptions of *Camelops* are given in Savage (1951) and Webb (1965).

Summary

The trend toward gigantism in camelids is first evident in *Aepycamelus* in the late Clarendonian and continued throughout the rest of the Cenozoic (Figure 17). Eight camelid genera are treated as giant camels in this paper.

Megacamelus merriami, new combination, is proposed for the large, late Hemphillian camel from Mt. Eden and Keams Canyon. The giant camels from Mt. Blanco, Lisco, and Keefe Canyon are referred to *Gigantocamelus spatulus*. *Titanotylopus* is applied only to *T. nebraskensis*. *Megatylopus major* is transferred to *Aepycamelus*.

The Camelini were all very large camels, but

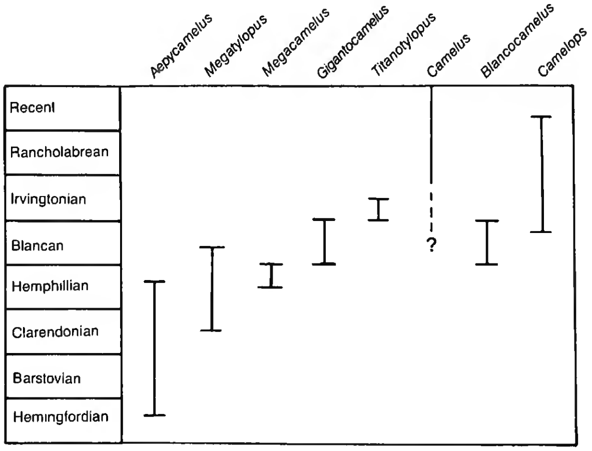


FIGURE 17.—Temporal distribution of the giant camels.

only two giants occur among the Lamini, *Camelops* (*C. hesternus*, *C. traviswhitei*, and *C. huerfanensis*) and *Blancocamelus* (if, indeed, this genus belongs in the Lamini and not the Aepycamelinae). Most camels were considerably smaller. It is intriguing that, in spite of over 40 million years of evolution in North America, and regardless of body size, camels became extinct in their place of origin following successful emigration to South America and Asia.

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