REVISION OF THE CAMELINAE (ARTIODACTYLA, TYLOPODA) AND DESCRIPTION OF THE NEW GENUS ALFORJAS[1]

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ABSTRACT

A cladistic analysis of the subfamily Camelinae indicates the presence of two major groups of camels in the Neogene. One group includes the extant lamines of South America and their fossil relatives. The other group includes *Camelus* and its sister group, the gigantic North American genera *Megatylopus* and *Titanotylopus*. *Alforjas taylori,* a new genus and species of lamine camel, is described from the Edson local fauna (Hemphillian) of western Kansas.

INTRODUCTION

The Camelinae constitute one of the most widely distributed and abundant elements in the Neogene faunas of North and South America. In North America the fossil record of the Camelinae may be traced from the relatively primitive middle Miocene protolabidine camels through the later Cenozoic to the extant genera currently restricted to Asia and South America.

Wortman (1898) produced one of the earliest revisions of the Camelinae, and subsequently several workers have revised all or part of the group. Matthew left an extensive unpublished manuscript on the Camelidae (Osborn Library, American Museum of Natural History) in addition to the phylogeny that he suggested in 1918. The most recent phylogeny of the Camelinae was proposed by Webb (1965) in his perceptive and detailed "Osteology of *Camelops*." The relationships suggested in this paper differ somewhat

from those of Webb, and are based upon a cladistic analysis of the group. Characters used in analysis are termed apomorphic (derived) or plesiomorphic (primitive), with an autapomorphic character unique to a particular taxon and a synapomorphic character shared by more than one taxon. For more detailed discussions of phylogenetic systematics, see Hennig (1966), Brundin (1968), and Wiley (1976); for deductive testing of hypotheses, see Popper (1968a, b). Museum acronyms appearing in this paper are: KUVP, University of Kansas Museum of Natural History, F:AM, Frick Collection, American Museum of Natural History, and AMNH, American Museum of Natural History.

Measurements.—All measurements are in centimeters unless otherwise indicated. The measurements of diastemata and incisors (I), canines (C), premolars (P), and molars (M) were taken on the teeth themselves unless otherwise noted. Upper molars were measured for length along the

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[1] Manuscript received March 9, 1979.

occlusal surface of the ectoloph. Width equals the maximum distance transverse to the long axis of the tooth. The mandibular symphysis was measured on the ventral surface from the posterior border of the first lower incisor to the posterior end of the symphysis. Width of the lower molars was measured transversely across the middle of the anterior portion of each tooth. Mean and standard deviation were calculated only for those elements with a sample size of four or more. For additional meristic data, see tables in Harrison (1979).

RELATIONSHIPS OF THE CAMELINAE

The cladogram in Figure 1 graphically shows inferred relationships of the Camelinae discussed in this paper. Characters appearing at nodes 1 through 23 on the cladogram are listed and then discussed in regard to their polarity and distribution among the Camelinae and outgroup taxa. Table 1 summarizes the distribution of several of the characters utilized in this study.
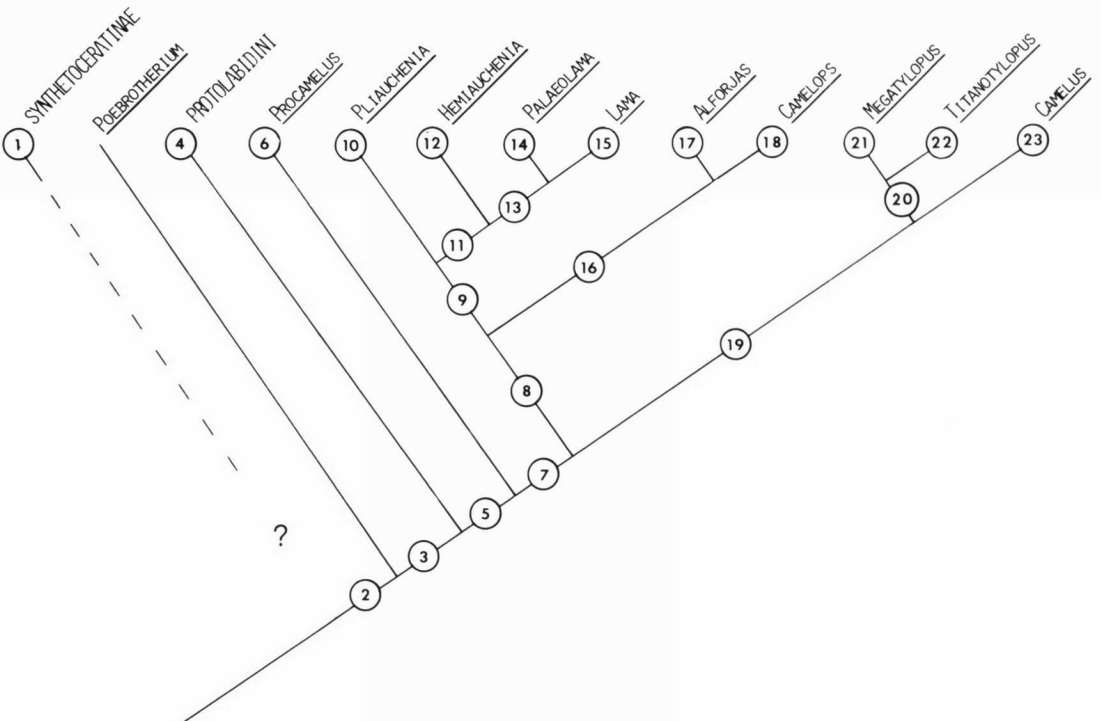

Fig. 1. Cladogram showing proposed relationships of the subfamily Camelinae.

Node 1. The Synthetoceratinae (Fig. 1) are distinguished by the following synapomorphies:

A. Single-shafted rostral horn formed of fused maxillary processes.

B. Paired supraorbital horns derived from the frontals.

Node 2. *Poebrotherium* and the Camelinae are united by:

A. Extreme reduction of metapodials II and V.

B. Divergent distal metapodials III and IV.

C. Anteriorly, the vertebrarterial canal passes through base of neural arch; posteriorly, vertebral artery is confluent with neural canal.

D. Tympanic bulla inflated and filled with spongy, cancellous bone.

Poebrotherium is not distinguished by an autapomorphy and is primitive relative to the Camelinae for all known characters.

Node 3. The Camelinae are a monophyletic group sharing:

A. Buccinator fossa weak.

B. Rostrum elongate.

Node 4. The Protolabidini have been characterized by Honey and Taylor (1978) as sharing:

A. Anterior nares laterally expanded.

B. Rostrum narrow.

Node 5. The Camelinae exclusive of the Protolabidini are united by:

A. Metacarpal length exceeds that of metatarsus.

B. Metapodials completely fused.

C. I^1 absent.

Node 6. *Procamelus* is the sister taxon to the remaining camelines. It retains several primitive characters, but has almost completed the loss of I^2.

Node 7. At Node 7 it becomes apparent that two main tribes (see following classification) comprise the bulk of the Camelinae. These two tribes are united by:

A. I^2 absent.

B. P^2 absent.

C. P_2 absent.

D. Raised posterolateral edges on the proximal end of the first phalanx.

E. Erythrocytes ovoid.

Node 8. The Lamini are united by:

A. Configuration of the anterior end of the nasals.

B. Lower molars with anteroexternal style (= llama buttress of Webb, 1965).

Node 9. *Pliauchenia, Hemiauchenia, Palaeolama,* and *Lama* share the following apomorphic characters:

A. Lacrimal vacuity reduced.

B. Rostrum shortened.

Node 10. *Pliauchenia* is primitive in all known characters relative to the remaining genera in the Lamini.

Node 11. *Hemiauchenia, Palaeolama,* and *Lama* are united by:

A. P^1 and P_1 small.

B. P^3 small.

Node 12. The autapomorphy distinguishing *Hemiauchenia* is extreme elongation of the limbs and cervical vertebrae.

Node 13. *Palaeolama* and *Lama* form a natural group in sharing:

A. P^1 absent.

B. P_1 absent.

C. Maxillary fossa reduced.

D. Lower molars with moderately strong anteroexternal style.

Node 15. *Lama* differs from *Palaeolama* in having:

A. P_3 absent.

B. Metacarpal length subequal to metatarsal length.

C. Lower molars with strong anteroexternal style.

D. Lacrimal vacuity greatly reduced.

E. Nasals extremely retracted.

F. P_4 greatly reduced.

Node 16. *Alforjas* is most closely related to *Camelops* in sharing a greatly increased degree of hypsodonty in comparison to the other Lamini. Width of the cheek teeth in *Alforjas* is reduced in relation to crown length and height, resulting in a very slim, hypsodont dentition.

Node 17. *Alforjas* is primitive in all known characters relative to *Camelops*.

Node 18. *Camelops* is derived relative to *Alforjas* in having:

A. Cheek teeth extremely hypsodont.

B. P^1 absent.

C. P_1 absent.

D. P_3 absent.

E. Dorsal surface of mandibular condyle transversely concave.

F. Suspensory ligament scar extends to center of shaft and has a raised center.

Node 19. The Camelini, consisting of *Camelus* and the giant North American forms, is

TABLE 1.—*Summary of Character Distribution in the Camelinae and Outgroup Taxa.*

Character	Camelinae		
	Procamelus	*Alforjas*	*Camelops*
1. I^1	lost	lost	lost
2. I^2	very reduced	lost	lost
3. I^3	present	present	present
4. C^1	laterally compressed	reduced; laterally compressed	very reduced; laterally compressed
5. C_1	laterally compressed	reduced; laterally compressed	very reduced; laterally compressed
6. P^1	present	present	lost
7. P_1	present	present	lost
8. P^2	present	lost	lost
9. P_2	present	lost	lost
10. P^3	present	internal crescent incomplete	internal crescent incomplete
11. P_3	present	present	lost
12. P_4	present	present	reduced
13. Anteroexternal style on lower molars	absent	weak	moderate
14. Crown height	moderately high	moderately high	extremely high
15. Premaxilla	light to moderate	light	light
16. Lacrimal vacuity	....	large	very large
17. Maxillary fossa	....	moderately large	large
18. Nasals	flattened	arched	very arched
19. Rostrum	long	long	long
20. Zygomatic arch	curved	curved	curved
21. Postglenoid foramen	moderately large	small	small
22. Postglenoid process	small	small	moderately small
23. Postglenoid facet on mandibular condyle	centrally positioned; transversely elongated	centrally positioned; transversely elongated	centrally positioned; transversely elongated
24. Diastemal crest on mandible	sharp	sharp	very sharp
25. Angular process on mandible	moderate; inflected	small; inflected	moderate; inflected
26. Dorsal surface of mandibular condyle	concave-convex	concave-convex	concave
27. Metacarpal length vs. metatarsal length	metc.>mett.	metc.>mett.	metc.>mett.
28. Metapodial elements III and IV	fused	fused	fused
29. Suspensory ligament scar on first phalanx	close to proximal end; no raised areas	posterolateral edges raised	extends to center of shaft, posterolateral edges and center raised

TABLE 1.—(Continued from preceding page)

	Camelinae			
	Hemiauchenia	*Palaeolama*	*Lama*	*Megatylopus*
1.	lost	lost	lost	lost
2.	lost	lost	lost	lost
3.	present	present	present	large; caniniform
4.	reduced; laterally compressed	recurved; laterally compressed	strongly recurved; laterally compressed	very large; rounded
5.	reduced; laterally compressed	recurved; laterally compressed	strongly recurved; laterally compressed	large; rounded
6.	present	lost	lost	present
7.	present	lost	lost	present
8.	lost	lost	lost	lost
9.	lost	lost	lost	lost
10.	low internal crescent weak to absent	internal crescent variable	very reduced; internal crescent incomplete	internal crescent incomplete
11.	present	present	lost	present
12.	present	present	very reduced	present
13.	moderately strong	strong	very strong	absent
14.	moderately low	moderately high	moderately high	moderately low
15.	light	light	light	thick; robust; heavy
16.	reduced	reduced	very reduced	large
17.	moderately large	reduced	reduced	reduced
18.	very arched	very arched	very arched	moderately flattened
19.	short	short	very short	long
20.	curved	curved	curved	curved
21.	very large	small	very small	large
22.	small	small	small	large
23.	medially positioned; round	medially positioned; round	medially positioned; round	medially positioned; vertically elongated
24.	sharp	sharp	sharp	reduced; rounded
25.	small; inflected	small; inflected	small; inflected	large; strongly inflected
26.	slightly concave-convex	convex	convex	convex
27.	metc.$>$mett.	metc.$>$mett.	metc.$\approx$mett.	metc.$>$mett.
28.	fused	fused	fused	fused
29.	posterolateral edges raised	posterolateral edges raised	posterolateral edges raised	posterolateral edges raised

TABLE 1.—(Continued from preceding page)

Character	Camelinae		Outgroup Taxa
	Titanotylopus	*Camelus*	*Syndyoceras*
1. I^1	lost	lost	lost
2. I^2	lost	lost	lost
3. I^3	large; caniniform	present	lost
4. C^1	very large; rounded	large; rounded	large
5. C_1	large; rounded	large; oval to rounded	incisiform
6. P^1	present	reduced	lost
7. P_1	present	reduced	present
8. P^2	lost	lost	present
9. P_2	lost	lost	present
10. P^3	internal crescent incomplete	internal crescent incomplete	present
11. P_3	present	lost	present
12. P_4	present	reduced	present
13. Anteroexternal style on lower molars	absent	absent	absent
14. Crown height	high	high	brachyodont
15. Premaxilla	thick; robust; heavy	moderate to heavy	moderate to light
16. Lacrimal vacuity	reduced or occasionally absent	very reduced	absent
17. Maxillary fossa	reduced	reduced or absent	absent
18. Nasals	flattened	flattened	....
19. Rostrum	long	short	long
20. Zygomatic arch	curved	straight	curved
21. Postglenoid foramen	large	large	....
22. Postglenoid process	large	large	....
23. Postglenoid facet on mandibular condyle	medially positioned; vertically elongated	medially positioned; vertically elongated	....
24. Diastemal crest on mandible	reduced; rounded	reduced; rounded	....
25. Angular process on mandible	large; strongly inflected	large; strongly inflected	absent
26. Dorsal surface of mandibular condyle	convex	convex	....
27. Metacarpal length vs. metatarsal length	metc.>mett.	metc.≈mett.	....
28. Metapodial elements III and IV	fused	fused	unfused
29. Suspensory ligament scar on first phalanx	posterolateral edges extremely rugose	extends to center of shaft; posterolateral edges and center raised	....

TABLE 1.—(Continued from preceding page)

	Outgroup Taxa		
	Synthetoceras	*Oxydactylus*	*Poebrotherium*
1.	lost	present	present
2.	lost	present	present
3.	lost	$\approx C^1$ in size; caniniform	moderately large; caniniform
4.	moderately large alveolus	moderately large; laterally compressed	small
5.	small; incisiform	moderately large; laterally compressed	moderately large
6.	lost	present; 2 roots	present; 2 roots
7.	lost	present; 2 roots	present; 1 root
8.	lost	present; 2 roots	present; 2 roots
9.	lost	present; 2 roots	present; 2 roots
10.	present	present	present
11.	present	present	present
12.	present	present	present
13.	absent	absent	absent
14.	moderately high	brachyodont	brachyodont
15.	moderate to heavy	moderate	light
16.	absent	present	present
17.	absent	moderately large	....
18.	....	flattened	flattened
19.	long	long	moderately long
20.	curved	curved	curved
21.	absent	large	small
22.	absent	very small	very small
23.	absent	small; medially positioned	very small; medially positioned
24.	long; sharp; curved	moderately sharp	sharp
25.	absent	small; little or no inflection	very small; very slightly inflected
26.	flat	flat	flat to convex
27.	metc.<mett.	metc.≤mett.	metc.<mett.
28.	unfused	unfused	unfused
29.	posterolateral edges slightly raised	very close to proximal end; no raised areas	very close to proximal end; no raised areas

united by:

A. Angular process on mandible enlarged and strongly inflected.
B. Postglenoid foramen large.
C. Postglenoid process on skull long with correspondingly large facet on mandibular condyle.
D. C^1 and C_1 enlarged and rounded in cross section, especially in males.
E. Auditory bulla ventrally flattened.
F. Diastemal crest on mandible low and rounded.
G. Maxillary fossa reduced.

Node 20. In addition to their large size, *Megatylopus* and *Titanotylopus* share:

A. Caniniform I^3 medium to large in size.
B. Premaxilla thickened and heavy.

Node 21. *Megatylopus* is distinguished by reduced P_3 and P_4.

Node 22. *Titanotylopus* is distinguished by:

A. Increased hypsodonty.
B. Metapodials shortened in relation to basal length of skull.

Node 23. The apomorphic features characterizing *Camelus* are:

A. Paroccipital process reduced.
B. Metacarpal length subequal to metatarsal length.
C. Maxillary fossa reduced or absent.
D. Zygomatic arch straight.
E. Nasals retracted.
F. Center of suspensory ligament scar raised (Fig. 2C).

The following classification, exclusive of outgroups, is derived from the cladogram (Fig. 1).

Subfamily	CAMELINAE
Plesion	PROTOLABIDINI
Plesion	*Procamelus*
Tribe	LAMINI
Subtribe	LAMINA
	Pliauchenia
	Hemiauchenia
	Palaeolama
	Lama
Plesion	CAMELOPINA
	Alforjas
	Camelops
Tribe	CAMELINI
Plesion	MEGATYLOPINA
	Megatylopus
	Titanotylopus
Subtribe	CAMELINA
	Camelus

The term plesion refers to "fossil groups or species, sequenced in a classification according to the convention that each such group is the plesiomorph sister-group of all those, living and fossil, that succeed it" (Patterson & Rosen, 1977). The term is particularly useful because the group so designated may carry any conventional rank. Thus, the Protolabidini, a group composed exclusively of extinct taxa, is designated a plesion, but may retain the hierarchical rank of tribe. The designation of *Procamelus* as a plesion renders unnecessary the creation of a rank to contain this taxon alone. The subtribes Lamina and Camelina and the plesions Camelopina and Megatylopina, bearing subtribal rank, are suggested herein, but due to their low rank will probably meet with little use by future workers. This classification retains three of Webb's four tribes at their original hierarchical level, and thus causes minimal disruption of familiar nomenclature.

The Protoceratidae, of which the Synthetoceratinae are a subfamily, have undergone a remarkable number of systematic fluctuations since their original description by Marsh (1891). This group has been variously aligned with the Pecora, the Tragulina, the Hypertragulidae, and the Leptomerycidae. Although Scott (1899) initially placed *Protoceras* in the Leptomerycidae, he (1940) was one of the first to suggest tylopod affinities for the group. Stirton (1967), in discussing *Lambdoceras*, also referred the Protoceratidae to the Tylopoda. Patton and Taylor (1971, 1973), in the most exhaustive examination of the Protoceratidae to date, followed Scott and Stirton in referring this group to the Tylopoda. Unfortunately, the supporting characters, primarily pertaining to the distal limbs and feet, are primitive. They do, however, offer many valid reasons for excluding the Protoceratidae from the Pecora and the Tragulina. I have as yet been unable to discover a derived character linking the Protoceratidae and the Camelidae, but I agree with Patton and Taylor that they are a probable sister-group to the Camelidae and thus belong in the Tylopoda. At the risk of being criticized for employing such an archaic line of evidence, I note, as have many previous workers, the almost identical geographic distribution of the protoceratids and the camels.

As difficult as are the external relationships

of the Protoceratidae, internally they comprise two cohesive subfamilies, which are distinguished largely by the form of the cranial armament. The Protoceratinae exhibit either paired parietal horns or an occipital horn, whereas the Synthetoceratinae bear a maxillary horn and paired frontal horns.

Poebrotherium was selected as an outgroup taxon because of its basal relationship to the camelid line. The characters at Node 2 (Fig. 1) apply not only to *Poebrotherium* and the Camelinae, but to the remainder of the Camelidae as well. Very early in camelid history, metapodials III and IV became the major weight-bearing digits with concomitant reduction to small vestiges of metapodials II and V. Fusion of metapodials III and IV into a canon bone commenced quite early also and developed independently in several subfamilies. Perhaps the most unusual derived character shared by the Camelidae is the disposition of the vertebrarterial canal. Only in camels is the vertebral artery confluent with the neural canal in the posterior half of cervical vertebrae two through six. In the anterior half of each vertebra, it passes through a canal contained within the base of the neural arch. In other artiodactyls the vertebrarterial canal is contained within the transverse processes of the cervical vertebrae, and at no point is the artery confluent with the neural canal.

The Camelinae are united by two characters, a weakly developed buccinator fossa and an elongate rostrum. The buccinator fossa became progressively deeper in the Protolabidini, but is reduced or absent in most of the remaining Camelinae. In both the Lamini and the Camelini, the elongate rostrum has been considerably shortened.

The Protolabidini have recently been revised by Honey and Taylor (1978). I agree with their findings, and in order to avoid duplication, I do not discuss the Protolabidini at the generic level, but instead treat them as a single unit in the cladogram. The narrow rostrum and laterally expanded anterior nares typical of the advanced protolabidine *Michenia* are characters that may also be observed in a less specialized state in the lamine *Hemiauchenia*. Honey and Taylor (1978, p. 422) maintained that although some similarities exist between the two groups, "a relationship between the Lamini and derived species of *Michenia* is unlikely. . . ."

The remaining Camelinae have lost the upper first incisor, which is present in *Poebrotherium* and *Oxydactylus*. The metacarpals were primitively shorter than the metatarsals; however, they became progressively longer in both the more specialized protolabidines and in the rest of the Camelinae until they exceeded the metatarsals in length. Only in the most derived of the Lamini (*Lama*) and the Camelini (*Camelus*) is this trend reversed and the metapodials are subequal in length, although early indications of this reversal may be discerned in *Palaeolama* and *Titanotylopus*.

Procamelus, described by Leidy (1858), has long functioned as a catchall genus for medium- to large-sized camelids of late Miocene and early Pliocene age. I have designated it as the sister taxon to the Lamini and Camelini because of its generally primitive appearance. *Procamelus* did not develop any of the derived features of the Lamini or the Camelini; however, future much-needed revision of the genus will probably indicate that it is more closely related to the latter tribe. I am inclined to agree with Webb (1965, p. 37), who suggested that "some large, Late Clarendonian species of *Procamelus,* like *P. grandis* or *P. occidentalis,* is the nearest North American ancestor to the extant Asian camels."

The Lamini and Camelini have lost I^2, P^2, and P_2. Reduction and loss in the incisor and premolar series is a trend seen in every camelid lineage. The most extreme reduction occurs in the two extant genera, *Camelus* (retains small $P^1{}_1,{}^3{}_3,{}^4{}_4$) and *Lama* (retains only small $P^3{}_3,{}^4{}_4$). Character D at Node 7 (Fig. 1) refers to the configuration of the insertion surface of the major suspensory ligaments. Figure 2 illustrates this feature in *Hemiauchenia, Titanotylopus,* and *Camelus.* Primitively, the insertion scar is very close to the proximal end of the first phalanx and rather flat, as in *Poebrotherium* and *Protolabis.* In a more specialized state, the scar is larger and extends further down the phalangeal shaft. The posterolateral corners are raised and form what Breyer (1974) termed a "W-shaped scar" (e.g., Fig. 2A, *Hemiauchenia*). Independently, in both *Camelus* and *Camelops,* the center of the scar has become raised as well as the posterolateral edges, thus straightening the W-shaped border in *Camelus* and rounding it in *Camelops.* The scar extends further down the shaft in *Camelops.*
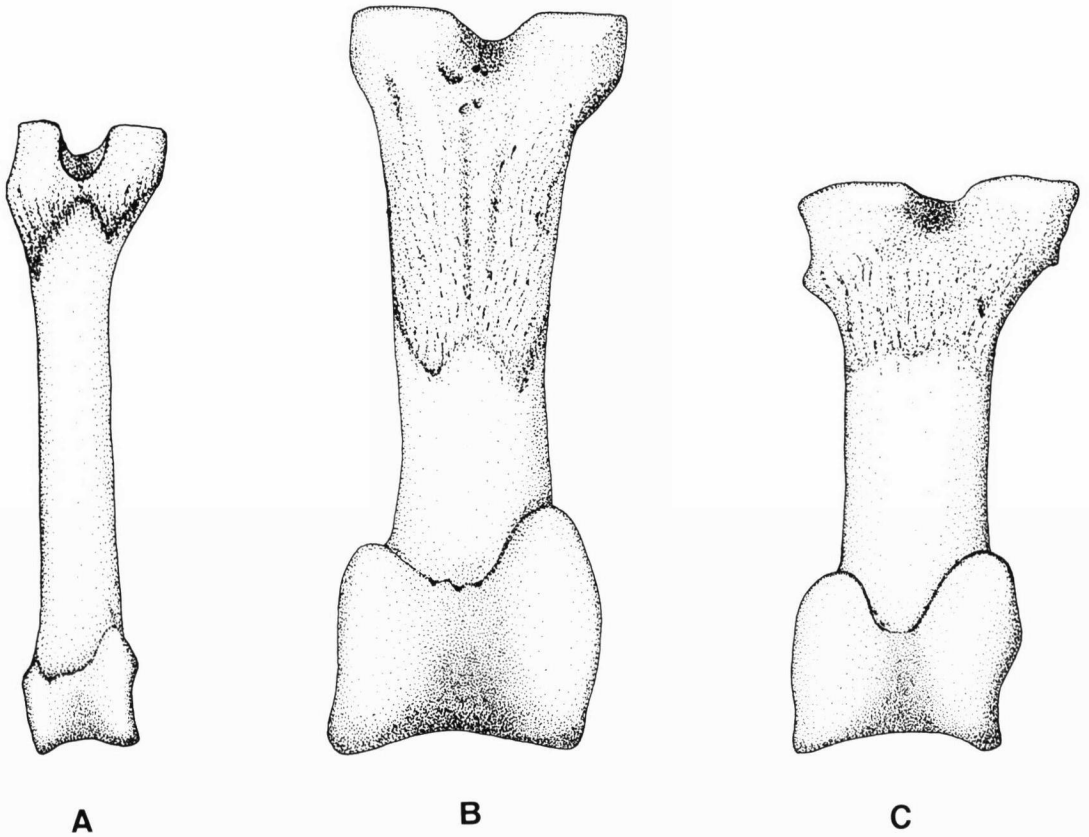
Fig. 2. Posterior surface of the proximal phalanx of three camels, illustrating the configuration of the rugose attachment site of the major suspensory ligaments; all × 1. A, *Hemiauchenia;* B, *Titanotylopus;* C, *Camelus.*

Among the Mammalia, the presence of ovoid or elliptical erythrocytes is a feature unique to extant camels (Grassé, 1955; Koopman, 1967). For this reason, I choose to place this character at Node 7 on the cladogram (Fig. 1) instead of deriving it independently for both *Lama* and *Camelus.* The inference that the fossil lamines and camelines also had ovoid erythrocytes is an admittedly untestable hypothesis; however, I find it preferable to the idea of multiple development of such an unusual character.

One of the characters uniting the Lamini is the configuration of the anterior end of the nasals. Primitively, the nasals were slightly arched, and a transverse section taken through the anterior end of the nasals reveals a low, flat curve (Fig. 3A). The derived condition is a high arch, which is bilobate in *Lama* (Fig. 3B). Secondly, the lower molars of all lamines exhibit a style on

the anteroexternal corner (=llama buttress of Webb, 1965). This style is strongly developed in *Lama* and *Camelops,* but is quite weak in *Alforjas.* Although Webb stated that this character occasionally occurs in *Megatylopus,* I have not encountered it in the specimens that I studied.

The lacrimal vacuity is primitively large in *Poebrotherium,* but became reduced in size in the Lamini and the Camelini. The reduced size of the lacrimal vacuity may be functionally related to the shortening of the rostrum that commonly accompanies it.

The extremely long limbs and cervical vertebrae characteristic of *Hemiauchenia* are also found in the Aepycamelinae, a problematical group whose relationship to the Camelinae is presently undetermined. Moreover, such typically lamine characters as strongly arched nasals and lower molars with an anteroexternal style occa-

sionally appear in later species of *Aepycamelus*. An examination of the aepycamelines and the possibly related oxydactylines is beyond the scope of this paper; however, future investigation may reveal synapomorphies indicative of a close relationship between the Laminae and the Aepycamelinae.

The maxillary fossa is well developed in such genera as *Poebrotherium* and *Oxydactylus*, but is reduced or absent in the more advanced Lamini and Camelini. Primitively, the angular process on the mandible is small as in the Protoceratidae, *Poebrotherium*, and the Lamini, and becomes enlarged and strongly inflected in the Camelini. In *Camelops* the angular process is moderately well developed, but is not inflected. Primitively, the diastemal crest on the mandible is quite sharp as in the Synthetoceratinae, *Poebrotherium*, and *Oxydactylus*. In the Camelini this crest is low and rounded. The upper third incisor is commonly reduced in most of the Camelinae; however, in two genera, *Megatylopus* and *Titanotylopus*, this tooth is large and caniniform.

In 1965, Webb proposed a division of the Camelinae into four tribes: the Protolabidini, "a horizontal ancestral group"; the Lamini, consisting of *Pliauchenia*, *Tanupolama*, *Palaeolama*, and

Lama; the Camelopini, consisting of *Megatylopus* and *Camelops;* and the Camelini, consisting of *Procamelus*, *Titanotylopus*, *Paracamelus*, and *Camelus*. Honey and Taylor (1978) have effectively demonstrated that the Protolabidini are too derived to have given rise to the modern camelids. The discrepancies between Webb's phylogeny and that presented in this paper center around the tribe Camelopini. Webb has demonstrated repeatedly that *Camelops* is more closely related to *Lama* than to *Camelus*, and I concur (Fig. 1). I do not, however, agree that the genus *Megatylopus* is ancestral to *Camelops*. On the contrary, I believe that it is more closely allied to *Titanotylopus* and *Camelus*.

One of the major criteria employed by Webb in the delineation of his tribes and, in particular, in support of a *Megatylopus-Camelops* lineage is the degree of basicranial-basifacial flexion. Osborn (1912) applied the term cytocephaly to this parameter and offered preliminary data on its distribution in certain ungulates, particularly the Equidae. The degree of flexion is obtained by measuring the angle between the plane of the basicranium and that of the palate. This character may be of some value in distinguishing taxa exhibiting radically different degrees of flexion;
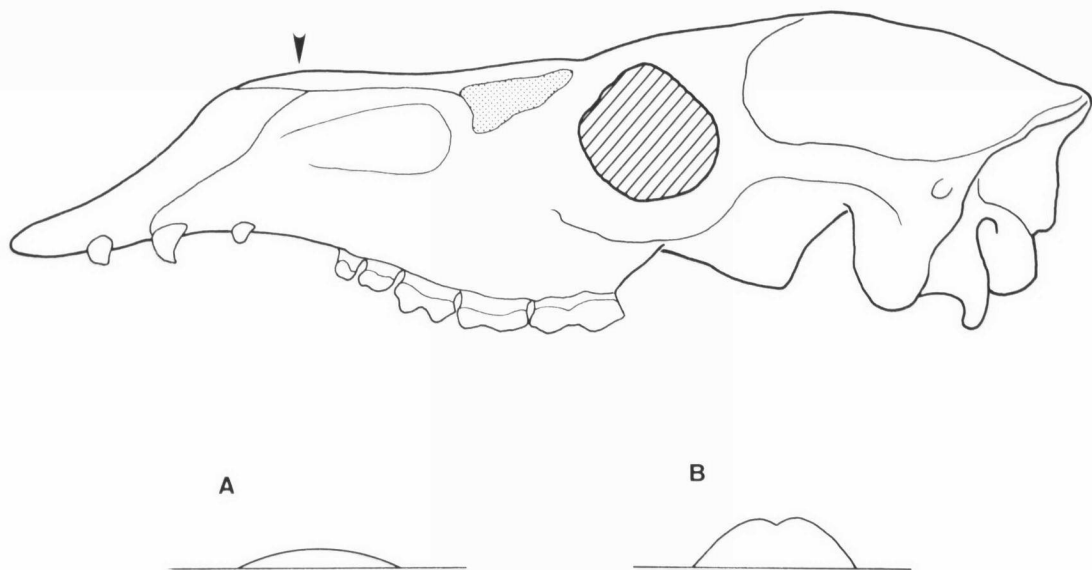

Fig. 3. Diagram comparing the degree of arching in a cross section through the nasals at a point indicated by the arrow. A, Camelini type; B, Lamini type.

however, within the Camelinae, there is a considerable amount of overlap in the degree of flexion exhibited by the component genera, even between the taxa representing the extremes of variation, *Camelus* and *Lama*. Webb (1965, p. 4) presented data on the degree of flexion in several cameline genera. Flexion ranges from 0° to 5° in *Camelus* ($n=5$) compared with 8° to 15° in *Lama* ($n=6$); the ranges are separated by a hiatus of 3°. Based on a larger sample from collections of the Mammalogy Department of the American Museum of Natural History, I recorded the following ranges: *Camelus* ($n=9$), –4° to 8° and *Lama* ($n=9$), 5° to 15°. The larger sample reveals a greater degree of individual variation as well as an overlap of 3° between *Camelus* and *Lama*.

Data on basicranial-basifacial flexion is especially difficult to obtain from fossil material. Fossil skulls, a rare commodity to begin with, are commonly too deformed to permit of an accurate assessment of flexion. The fragile, cancellous basicranial and basifacial regions of the skull are by their very nature most affected by crushing, warping, and other taphonomic deformation. The type skull of *Megatylopus gigas* (AMNH 14071), described by Matthew and Cook (1909), has been extensively restored with plaster in the basicranial area, thus compromising any measurement of flexion. Neither the type of *M. gigas* nor a referred skull from the Edson local fauna offer conclusive support for a high degree of flexion.

Additional characters cited in support of a *Megatylopus-Camelops* lineage are a large lacrimal vacuity and an elongate rostrum. Both of these characters are primitive for the Camelinae.

Moreover, the presence in *Megatylopus* of such derived characters as the enlarged and rounded canines, reduced maxillary fossa, reduced and rounded mandibular diastemal crest, thickened, heavy premaxilla, and large postglenoid foramen indicates a close alignment with *Titanotylopus* and *Camelus,* and precludes an ancestral relationship to *Camelops.*

Conclusions.—The Camelinae are divided into three tribes, Protolabidini, Lamini, and Camelini, with the latter two tribes composing the bulk of the subfamily. *Procamelus* is proposed as the primitive sister taxon to the Lamini and Camelini; however, additional study of this genus may result in its referral to the Camelini. The Lamini consists of *Pliauchenia, Hemiauchenia, Palaeolama, Lama, Alforjas,* and *Camelops.* *Alforjas* is a new lamine genus most closely related to *Camelops.* The Camelini consists of *Megatylopus, Titanotylopus,* and *Camelus.* The tribe Camelopini (Webb, 1965), which consisted of *Megatylopus* and *Camelops,* is discarded.

The family Camelidae is a fascinating and yet challenging subject for research. It is fascinating because camels represent a diverse and highly successful radiation that has only with the end of the Pleistocene been restricted to the two extant genera, *Lama* and *Camelus.* It is challenging because of the parallelism which is so typical of the group. Almost every major character complex, be it reduction of incisors and premolars, facial shortening, fusion of the metapodials, increased hypsodonty, or shortening or lengthening of limbs, is found in more than one camel lineage. It is this duplication that renders camelid systematics so difficult and so complex.

SYSTEMATICS

Family CAMELIDAE Gray, 1821
Subfamily CAMELINAE Zittel, 1893
Tribe LAMINI Webb, 1965
Genus ALFORJAS Harrison, new genus

Type species.—*Alforjas taylori* Harrison, new species.

Diagnosis.—A medium-sized lamine camel with transversely arched anterior nasals, a weak to absent anteroexternal style on the lower molars, a long rostrum, and moderately hypsodont teeth. *Alforjas* differs from *Pliauchenia, Hemiau-*

chenia, Palaeolama, and *Lama* in its greater height of crown, larger size, and longer rostrum. *Alforjas* is most closely related to *Camelops,* but differs in the loss of P_1^1 and P_3, configuration of the suspensory ligament scar on the first phalanx, greater hypsodonty, and larger size.

Etymology.—*Alforjas* (pronounced al-fór-has), is the Spanish name for the panniers or saddle bags used on the domestic lama; it also carries a regional, colloquial meaning of lumps or humps.

TABLE 2.—Alforjas taylori: *Measurement of Skull and Upper Dentition.*

		Hypodigm		
Measurement	Holotype	Number	Observed range	Sample mean (SD)
Length, premaxilla to occipital crest	42.54	0	....	....
Length, premaxilla to occipital condyles	40.00	0	....	....
Length, premaxilla to posterior nares	24.54	0	....	....
Width across C¹	4.15	0	....	....
Minimum width at postorbital constriction ..	....	1	6.50	....
Width across I³	3.69	0	....	....
Width across M³	8.53	1	9.59	....
Width across occipital condyles	6.58	0	....	....
Length, occipital crest behind condyles	3.20	0	....	....
Length, I³-M³	21.05	0	....	....
Length, P³-M³	12.15	4	12.33-14.08	13.30(0.81)
Diastema I³-C¹	1.47	0	....	....
Diastema C¹-P¹	1.58	0	....	....
Diastema P¹-P³	2.71	2	2.67-2.69	....
I³, Length	1.17	0	....	....
Width	0.80	0	....	....
C¹, Length	1.42	0	....	....
Width	0.99	0	....	....
P¹, Length	0.92	1	0.76	....
Width	0.57	1	0.50	....
P³, Length	1.87	4	1.85-1.91	1.89(0.03)
Width	1.21	3	1.17-1.32	....
P⁴, Length	....	6	2.18-2.37	2.27(0.07)
Width	2.17	5	1.83-2.01	1.94(0.06)
M¹, Length	....	8	2.29-3.78	3.00(0.43)
Width	....	7	2.32-3.08	2.64(0.26)
M², Length	2.84	9	3.12-4.03	3.63(0.27)
Width	2.76	7	2.28-2.86	2.51(0.19)
M³, Length	3.56	8	3.49-4.14	3.78(0.22)
Width	2.60	5	2.00-2.51	2.20(0.19)

Description and discussion.—The holotype of *Alforjas taylori* (F:AM 40821) is the skull of a fairly old individual, possibly a female (Pl. 1). The left side of the skull is damaged from the lacrimal vacuity back to and including the parietal. The rostrum is essentially intact and has suffered little deformation. Neither zygomatic arch is complete. The anterior basicranial region, consisting of the presphenoid, vomer, posterior palatine, and parts of the alisphenoid and orbitosphenoid, is missing. The muzzle is moderately long and slender as in *Camelops* and little facial shortening has occurred.

The premaxilla is broader anteroposteriorly in *Alforjas* than in *Lama* or *Hemiauchenia* and resembles that of *Camelops*, although the anterior tips are not so large. The medial premaxillary processes join loosely and extend posteriorly in a sharply pointed wedge, the tip of which reaches beyond the posterior alveolar border of C¹.

The maxilla is constricted between C¹ and P³ as in all of the lamines. The diastemal crest between P¹ and P³ is heavier and more curved than in *Lama* or *Hemiauchenia* and in this resembles *Camelops*. The two halves of the maxilla join medially to form a low ridge that bisects the palate from C¹ to P³. The palatine notch does not extend as far anteriorly in *Alforjas* as it does in other lamines, reaching only to the back of M³, as opposed to the middle or back of M². The most anterior part of the palatine-maxillary suture lies at the level of the middle of M².

Although in the type skull the depth of the maxillary fossa is somewhat exaggerated due to the rupture of the fragile inner wall, it is deeper than in *Lama* or *Hemiauchenia*. The fossa extends medially and posteriorly to undercut a portion of the maxilla so that the posterior and

dorsal borders form an overhanging shelf. Among lamines, this fossa is larger only in *Camelops*. The fossa, which begins as a shallow depression above the P^1-P^3 diastema, reaches its maximum depth at about the level of the posterior half of M^1.

The anterior opening of the infraorbital canal is somewhat crushed and obscured in the type skull; however, the hypodigm contains three additional partial skulls (F:AM 40822, 104409, and 104410) in which the anterior infraorbital foramen opens in the maxilla dorsal to the posterior part of P^4 or the anterior part of M^1. The opening is more rounded, as in *Camelops,* rather than dorsoventrally oval as in *Lama* and *Hemiauchenia*. The posterior opening of the canal is obscured in all of the specimens.

The nasals, like the rest of the rostrum, have undergone little shortening; they remain long and slender as in *Camelops*. They are strongly arched transversely (Fig. 3) as in the other lamine camels, and lack the swelling dorsal to the maxillary fossa seen in *Lama* and *Hemiauchenia*.

The frontals are very slightly depressed between the orbits. The most anterior point of the nasofrontal suture lies dorsal to the anterior edge of M^2, which is considerably further back than in *Lama* or *Hemiauchenia*. The posteromedial trending slash in the dorsal border of the orbit is particularly pronounced in the type skull. The temporal crests are heavier than in *Lama*.

The lacrimal is broken or distorted in each of the Edson Quarry specimens, and consequently, its position in relation to the posterior border of the lacrimal vacuity cannot be determined. In the type it appears to be excluded by united extensions of the frontal and maxilla. The lacrimal vacuity is large, although its original dimensions are exaggerated by breakage. The vacuity is larger than in *Hemiauchenia* or *Lama,* and resembles that of *Camelops*.

The parietals are smoothly rounded. The sagittal crest is broken in all specimens. It merges posteriorly with the lambdoidal crest that runs along the edge of the broad supraoccipital. The supraoccipital overhangs the condyles to a greater extent than in *Lama*. The paroccipital process of the exoccipital is hooked anteriorly at the tip and is longer than in *Lama*. The basioccipital extends forward between the inflated auditory bullae to

meet the basisphenoid posterior to the anterior edges of the bullae as in *Camelops*. This suture occurs anterior to the bullae in *Hemiauchenia* and *Lama*. The postglenoid process is small as is the postglenoid foramen. The external auditory meatus is tubular and opens just posterior to the postglenoid foramen.

The upper dentition consists of I^3, C^1, $P^{1,3,4}$, $M^{1,2,3}$. I^3 is almost as long anteroposteriorly as C^1 and is separated from it by a diastema approximately equal to that between C^1 and P^1. Both I^3 and C^1 are recurved, but not to the extent seen in *Lama* and *Hemiauchenia*. P^1 is reduced to a small, single-rooted nubbin, smaller than in *Hemiauchenia*. The cheek teeth are higher crowned than in any of the lamines with the exception of *Camelops*. P^3 is triple rooted, although the two posterior roots exhibit a tendency to become united. The internal crescent is incomplete. P^4 is large and not much reduced. The anterior and median molar styles resemble those in *Hemiauchenia,* but the external ribs are less well developed. In the type skull the dentition is very worn; the right P^4 and M^1 are missing, as is the anterior half of the left M^1.

TABLE 3.—Alforjas taylori: *Measurements of Mandible and Lower Dentition.*

Measurement	Number	Observed range	Sample mean (SD)
Length of symphysis	3	6.28-7.06	....
Length, C_1-M_3	3	19.25-19.99	....
Length, P_3-M_3	6	12.46-13.29	12.89(0.35)
Diastema I_3-C_1	3	0.41-0.89[a]	....
Diastema C_1-P_1	4	1.19[a]-2.05	1.66(0.36)
Diastema P_1-P_3	6	2.86-4.24[a]	3.41(0.47)
C_1, Length	3	0.97-1.42	....
Width	3	0.46-0.85	....
P_1, Length	3	0.69-0.88	....
Width	3	0.39-0.42	....
P_3, Length	6	1.21-1.44	1.29(0.08)
Width	6	0.62-0.75	0.70(0.05)
P_4, Length	9	1.91-2.12	2.03(0.07)
Width	10	1.04-1.24	1.15(0.08)
M_1, Length	13	2.24-3.31	2.69(0.30)
Width	11	1.39-1.71	1.57(0.09)
M_2, Length	14	2.81-3.92	3.34(0.32)
Width	13	1.41-1.96	1.72(0.14)
M_3, Length	9	3.85-4.65	4.15(0.26)
Width	11	1.31-1.89	1.62(0.17)
Width of condyle	6	2.76-3.32	3.07(0.20)
Width across C_1	3	3.57-4.76[b]	....

[a] Alveolar measurement.
[b] Deformation may have caused slight inaccuracy in measurement.

The deciduous upper dentition is represented in the Edson Quarry sample by $dP^{2,3,4}$ (Pl. 4, figs. 1, 2). The difference in degree of hypsodonty between *Hemiauchenia* and *Alforjas* is particularly apparent in the unworn deciduous dentition. DP^2 has a low, incomplete internal crescent. DP^3 is an elongate triangle with the anterior crest not so strongly developed as in *Hemiauchenia*. DP^4 is molariform.

The mandible of *Alforjas* (Pls. 2, 3) is deeper than that of *Hemiauchenia* or *Lama* in the region of the cheek teeth to accommodate the more hypsodont crowns. The symphysis is proportionately shorter in *Alforjas* than in *Hemiauchenia* or *Lama*, with the anterior border broadened as in *Camelops*. The coronoid process is long and hooked posteriorly, although not so long as in *Lama*. The angular process is larger and more strongly inflected, and the mandibular condyle bears a larger postglenoid facet than in *Lama*. The dorsal surface of the condyle is transversely concave medially and transversely convex laterally, as opposed to continuously convex in *Lama*.

The lower dentition consists of $I_{1,2,3}$, C_1, $P_{1,3,4}$, and $M_{1,2,3}$. The incisors are more broadly spatulate in *Alforjas* than in *Lama* or *Hemiauchenia*, and they tend to wear in an even, transverse line as in *Camelops*. C_1 is a thin, posteriorly recurved blade that is separated from I_3 by a short diastema. C_1 is proportionately larger in *Alforjas* than in *Camelops*. P_1 is a small, single-rooted, caniniform tooth. It is located above and occasionally slightly posterior to the mental foramen. P_3 is double rooted and bears a less reduced anterior crest than in *Hemiauchenia*. P_4 is not as laterally compressed as that of *Hemiauchenia*. On the molars the internal styles

are reduced, and the anteroexternal style (= llama buttress of Webb, 1965) is present although weak.

All of the lower deciduous premolars are represented in the Edson Quarry sample (Pl. 2, fig. 1; Pl. 3, fig. 1). DP_2 is single rooted but larger in relation to $dP_{3,4}$ than in *Hemiauchenia*. DP_3 is not so narrow as in *Lama*. DP_4 is larger than in *Hemiauchenia*, but the configuration is very similar except for the greater height of crown.

In the Edson Quarry sample of *Alforjas*, the only atlas (F:AM 101586) is missing the lateral wings (Pl. 4, fig. 3). The notch between the cotyloid process and the condylar articular surface dorsal to it is moderately deep as in *Hemiauchenia* and, to a lesser extent, *Lama*. This notch is very shallow in *Camelops*. The posterior end of the median hypapophysis bears a much larger knob than in *Hemiauchenia* or *Lama*. The hypapophysis itself is heavier as in *Camelops*. In *Camelops* the posterior median portion of the centrum is very thick and heavy as if it had overgrown and engulfed the hypapophysis and its terminal knob. The thickness of the centrum and the knob approach this condition in *Alforjas*. The ventral median condyloid surfaces extend further onto the ventral surface of the centrum in *Alforjas* and *Camelops*.

Although the axis is close in length to that of *Hemiauchenia*, it is proportionately much heavier (Pl. 4, fig. 4). The dorsal spine is higher and more curved in *Alforjas* and *Camelops* and terminates in a more anterior position than in *Lama* or *Hemiauchenia*. Furthermore, the postzygopophysis is more deeply divided in *Alforjas* and *Camelops* than in *Lama* or *Hemiauchenia*.

The humerus is not so long and slender as in *Hemiauchenia* (Pl. 4, figs. 5,6). The tubercle

TABLE 4.—Alforjas taylori: *Measurements of Deciduous Upper and Lower Dentition.*

Tooth		Length			Width	
	Number	Observed range	Sample mean (SD)	Number	Observed range	Sample mean (SD)
dP^2	7	0.72-1.09	0.92(0.14)	7	0.26-0.52	0.41(0.11)
dP^3	13	2.32-3.01	2.72(0.21)	13	1.21-2.02	1.67(0.21)
dP^4	10	2.43-3.40	3.08(0.32)	10	1.58-2.25	1.86(0.24)
$dP^3\text{-}M^2$	1	11.64	....	....	....	....
dP_2	19	0.48-0.77	0.61(0.08)	18	0.16-0.36	0.30(0.06)
dP_3	30	1.09-1.84	1.53(0.16)	28	0.54-0.94	0.77(0.07)
dP_4	28	3.29-4.26	3.88(0.23)	27	0.99-1.55	1.22(0.15)
$dP_3\text{-}M_2$	2	11.51-11.72	....	....	....	....

on the lateral epicondyle is as heavy as in *Camelops*. Total curvature of the shaft is less in *Alforjas* and *Camelops* than it is in *Lama*. Only one humerus in the Edson Quarry sample retains the proximal end, although the tuberosities have been broken off, leaving only the head.

The radius-ulna is always shorter and stockier than that of *Hemiauchenia* (Pl. 5, figs. 7, 8). The lateral tuberosity on the proximal end of the radius is larger and more protuberant in *Camelops* and *Alforjas* than in *Hemiauchenia* and *Lama*.

The scaphoid is larger than in *Lama* or *Hemiauchenia* and the lateral edge of the posterior proximal surface slopes less steeply (Pl. 5, fig. 1). On the distal surface of the lunar, the facets for the magnum and the unciform appear to be separated by a groove rather than a ridge as in the rest of the lamine camels (Pl. 5, fig. 2), but this may be due to breakage. Except by its larger size, the cuneiform is difficult to distinguish from that of *Hemiauchenia* and *Lama*, although the facet for the pisiform extends further onto the posteromedial surface in *Alforjas* and *Camelops* (Pl. 5, fig. 3). The magnum is more L-shaped than in *Lama*. The posterior process is larger and is separated from the posterior unciform facet by a groove that is not present in *Lama or Hemiauchenia* (Pl. 5, fig. 4). The posterior knob of the unciform is blunt and heavy in *Alforjas* as in *Camelops* but not in *Hemiauchenia* or *Lama* (Pl. 5, fig. 5). A small concavity on the posteromedial corner of the distal side is present in *Lama* and *Camelops*, but is absent in *Alforjas* and in *Hemiauchenia*.

The metacarpus is always longer than the metatarsus. It is proportionately heavier than in *Lama* and much heavier than in *Hemiauchenia;* it is not, however, so stocky as in *Camelops* (Pl. 5, figs. 6, 9, 10). The trapezoid facet on the proximal surface of the third metacarpus is relatively larger in *Alforjas* and *Camelops* than in *Lama* and *Hemiauchenia*, and the crest that separates it from the magnum facet is more strongly developed. Moreover, the distal condyles are more massive and divergent in *Alforjas* and *Camelops* and exhibit more flare on the posterolateral edges.

The first phalanx is not so slender as in *Lama* or *Hemiauchenia*. The shaft is heavier and the proximal articular surface is proportionately wider in relation to the shaft (Pl. 7, figs. 7, 8). The attachment scar for the suspensory ligaments is of an uneven W-shape as in *Hemiauchenia* and *Lama*, but it extends further down the shaft. As in many camelids, the distal condyles are asymmetrical.

A distal third of a tibia (F:AM 104511) has been tentatively referred to *Alforjas* on the basis of its larger size and heavier shaft (Pl. 6, figs. 6, 7, 8). Moreover, the distal fibula is also larger than that of *Hemiauchenia* or *Lama* (Pl. 6, fig. 3). The posterior border of the calcaneal facet curves back onto the posterior surface for a short distance in *Camelops* and *Alforjas*, but not in *Lama* or *Hemiauchenia*.

The posterior edge of the calcaneum is more heavily ridged and more rugose in *Alforjas* (Pl. 6, figs. 4, 5) than in *Hemiauchenia* or *Lama*. In *Camelops* and *Lama* a small facet occurs on the posteromedial corner of the distal end between the cuboid and the astragalar facets. This area is occupied by a shallow trough in *Hemiauchenia* and *Alforjas*. The trough on the posterior side of the tuber calcis is wider and shallower in *Alforjas* and *Camelops* than it is in *Lama* or *Hemiauchenia*. The shaft of the calcaneum tends to be heavier as in *Camelops;* the anterior edge, especially, is more rounded than in *Lama* or *Hemiauchenia*.

In the astragalus of *Alforjas*, the groove that divides the parasustentacular facet is more distally placed than in *Hemiauchenia* or *Lama*, but not so much as in *Camelops* (Pl. 6, figs. 1, 2). The sustentacular facet continues smoothly into the trochlear valley in *Alforjas*, *Camelops*, and *Lama*, and is without the 'step' that is present in *Hemiauchenia*.

The styloid process of the cuboid is not so sharply pointed as in *Lama;* it is heavier than in *Camelops*, although not as high (Pl. 7, figs. 5, 6). The navicular facet on the medial side of the styloid process is much larger in *Alforjas* and *Camelops* than in *Lama*. In *Lama* this facet is separated from the posteromedial navicular facet by a wide, shallow groove. In *Alforjas*, this groove is narrow and deeper. In *Camelops* this groove is usually absent, and the two facets fuse into one.

The transverse width of the navicular is greater in *Camelops* and *Alforjas* than in *Lama* and *Hemiauchenia*, thus giving the element a

more circular proximal outline (Pl. 7, figs. 1, 2). The two posteromedial cuboid facets are separated by a groove as in *Lama* and *Camelops*, not joined as in *Hemiauchenia*. The facet for the

TABLE 5.—Alforjas taylori: *Measurements of Axial Skeleton, Forelimb, and Hindlimb.*

Element	Measurement	Number	Observed range	Sample mean (SD)
		AXIAL SKELETON		
Atlas	Length of centrum	1	2.98	....
	Posterior height	1	5.67	....
Axis	Length of centrum	2	17.41-18.02	....
	Anterior width	3	6.22-6.57	....
	Width across transverse processes	2	6.76-7.29	....
		FORELIMB		
Humerus	Maximum length	0	....	....
	Proximal width across tuberosities	0	....	....
	Distal width across trochlea	16	5.70-7.27	6.30(0.47)
Radius-ulna	Maximum length	0	....	....
	Articular length	5	38.70-43.64	41.04(1.81)
	Proximal width	8	5.77-6.51	6.02(0.23)
	Distal width	6	6.10-7.13	6.65(0.34)
Scaphoid	Height	2	2.44-2.72	....
	Anteroposterior	2	3.85-4.36	....
Lunar	Height	1	3.03	....
	Anteroposterior	1	3.32	....
Cuneiform	Height	1	3.06	....
	Anteroposterior	1	4.02	....
Magnum	Height	3	1.83-1.90	....
	Anteroposterior	3	3.12-3.43	....
Unciform	Height	2	1.85-1.87	....
	Anteroposterior	2	4.09-4.35	....
Metacarpus	Length	10	27.96-33.55	31.34(1.78)
	Proximal width	21	4.77-6.42	5.33(0.36)
	Distal width	9	6.28-7.45	6.91(0.41)
		HINDLIMB		
Tibia	Length	0	....	....
	Proximal width	0	....	....
	Distal width	1	7.48	....
Distal fibula	Height	2	3.23-3.43	....
	Anteroposterior	2	3.75-3.89	....
Astragalus	Height (tibial to tarsal surface)			
	Medial	3	6.02-6.32	....
	Lateral	4	6.38-6.93	6.71(0.24)
	Distal transverse	4	4.23-4.60	4.45(0.16)
Calcaneum	Height	9	12.00-13.71	12.84(0.70)
	Anteroposterior	11	5.21-6.17	5.57(0.33)
Navicular	Height	2	2.67-3.01	....
	Anteroposterior	2	4.42-4.48	....
Ectocuneiform	Height	1	1.44	....
	Anteroposterior	1	2.62	....
Cuboid	Height at styloid process	3	3.36-4.08	....
	Anteroposterior	3	5.13-5.45	....
Metatarsus	Length	12	26.07-32.79	29.75(2.22)
	Proximal width	15	4.33-5.45	4.79(0.36)
	Distal width	12	5.65-6.92	6.39(0.37)
First phalanx	Length	2	8.82-8.83	....
	Proximal width	2	2.68-3.04	....

articulation with the styloid process of the cuboid is large as in *Camelops.*

The groove that separates the medial process of the ectocuneiform from the cuboid facet is shallow to absent in *Alforjas* and *Camelops* as opposed to more pronounced in *Hemiauchenia* and *Lama* (Pl. 7, fig. 3). The metatarsus is shorter than the metacarpus. It is proportionately much more robust and stocky than in *Hemiauchenia* or *Lama.* (Pl. 7, figs. 4, 9, 10).

Conclusions.—*Alforjas* is a medium-sized camel with a skull and dentition larger than in any of the Lamini except *Camelops.* The limb elements have undergone some shortening in relation to the basal length of the skull, but not nearly to the extent observed in *Palaeolama* or *Lama.* Crown height in *Alforjas* is exceeded within the Lamini only in *Camelops.* The F:AM material from Edson Quarry, including the type specimen, was originally referred to "*Submegatylopus,*" a nomen nudum used in an unpublished manuscript of Childs Frick. The name is indicative of the superficial resemblance that *Alforjas* bears to *Megatylopus,* as well as the difference in size.

Three genera of camels occur in many of the middle to late Hemphillian faunas of North America. These genera are usually *Hemiauchenia, Megatylopus,* and *Alforjas.* Undescribed material in the F:AM collections from Coffee Ranch, Hemphill County, Texas, and from the Mormon Mesa area, Clark County, Nevada, is very similar to the Edson Quarry material and may be referred to *A. taylori.* Additional material from the Wray area, Yuma County, Colorado, and the Guymon area, Texas County, Oklahoma, is probably referable to the genus *Alforjas.*

ALFORJAS TAYLORI Harrison, new species

Holotype.—F:AM 40821, skull.

Type locality.—Edson Quarry, SW¼ sec. 25, T. 10 S., R. 38 W., Sherman County, Kansas.

Type horizon.—Ogallala Formation of late Hemphillian age.

Diagnosis.—Same as for genus.

Etymology.—The species is named for Beryl E. Taylor in recognition of his extensive and valued work with the Tylopoda.

Referred material.—From F:AM: 104409-104411, partial skull; 24676, 24676A, 24677, 40820, 40846, 104412-104421, maxillae; 40809, 40812, 40815, 40819, 40820, 40824, 40827, 104422-104427, 104430-104441, 104443-104446, 104449, lower jaws; 101586, atlas; 101585, 104537, axes; 104478-104493, humeri; 104494-104510, radii-ulnae; 101584, 104517, scaphoids; 101583, lunar; 101582, cuneiform; 101581, 104521, 104522, magna; 101580, 104514, unciforms; 40811, 40832, 40838, 40841, 40842, 104450-104459, 104466, 104475-104477, metacarpi; 104511, partial tibia; 104523-104529, 104531, 104532, calcanea; 104515, 104516, astragali; 104533, distal fibula; 101579, cuboid; 101578, navicular; 40810, 101590, 104460-104464, 104468-104474, metatarsi; 101589, first phalanx; 104518, second phalanx; 101587, metatarsus with associated tarsal elements and phalanges.

From KUVP: 527, 528, 3215, 3229, 3458, maxillae; 3214, 3216, 3217, 3219, 3221, 3224, 3226, 3257, 3264, 3512, 3590, 3725-3729, 3734, lower jaws; 3285, axis; 3528, 3531, 5617, humeri; 3527, 3593, 3824, radii-ulnae; 3236, 3517, 3522, 3785, 3824, metacarpi; 3538, 3824, calcanea; 3542, astragalus; 3533, metatarsus; 3523, metatarsus with associated cuboid; 3225, 3234, 3244, 3596, first phalanges.

Description and discussion.—*Alforjas taylori* is now the only described species of *Alforjas* and was named to validate the genus. Although one might speculate about which characters distinguish genus and which the species, I prefer to wait until the study of more material allows a better basis for speculation. Thus, the description and discussion of the genus also applies at the specific level.

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EXPLANATION OF PLATES

Alforjas taylori Harrison, new genus, new species

PLATE 1

FIGURE

1-3. Holotype, skull; F:AM 40821, dorsal, lateral, and palatal views, scale = 5.0 cm.

PLATE 2

FIGURE

1-3. Growth stages in mandibles; scale = 5.0 cm.—— *1*, Juvenile with complete deciduous dentition and M_1 germ; KUVP 3216, lateral view.——*2*, Young adult with dP_4 in place and M_2 erupting; KUVP 3214, lateral view.——*3*, Mature adult with M_3 in place; KUVP 3725, lateral view.

PLATE 3

FIGURE

1-3. Growth stages in mandibles; occlusal views of specimens in Plate 2, figures 1, 2, and 3 respectively. See Plate 2 legend for specimen numbers and scale.

PLATE 4

FIGURE

1,2. Deciduous upper dentition; KUVP 528, occlusal and medial views, ×0.5.

3. Atlas; F:AM 101586, dorsal view, ×0.5.

4. Axis; KUVP 3285, dorsal view, ×0.5.

5,6. Humerus; F:AM 104478, anterior and posterior views, scale = 5.0 cm.

PLATE 5

FIGURE

1. Scaphoid; F:AM 101584, medial view, ×0.5.

2. Lunar; F:AM 101583, lateral view, ×0.5.

3. Cuneiform; F:AM 101582, posterior view, ×0.5.

4. Magnum; F:AM 101581, proximal view, ×0.5.

5. Unciform; F:AM 101580, proximal view, ×0.5.

6. Metacarpus; F:AM 40842, proximal view, scale = 3.25 cm.

7,8. Radius-ulna; F:AM 104497, posterior and anterior views, scale = 5.0 cm.

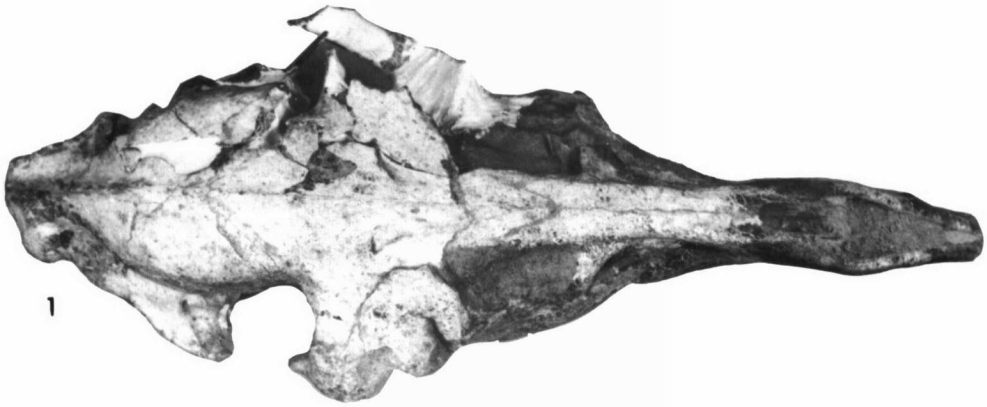*9,10.* Metacarpus; F:AM 40842, anterior and posterior views, scale = 5.0 cm.

PLATE 6

FIGURE

1,2. Astragalus; F:AM 101587, posterolateral and anteromedial views, ×0.5.

3. Distal fibula; F:AM 101587, medial view, ×0.5.

4,5. Calcaneum; F:AM 101587, anterior and medial views, ×0.5.

6,7. Partial tibia; F:AM 104511, anterior and posterior views, scale = 5.0 cm.

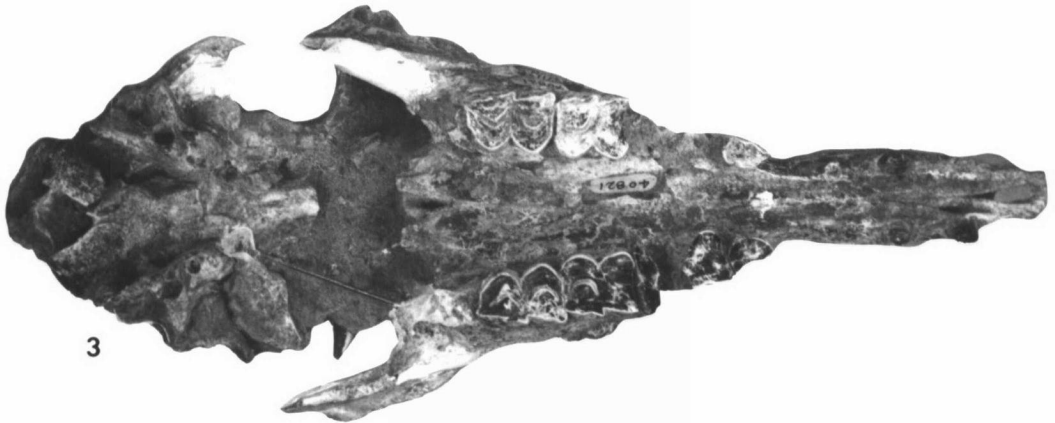*8.* Partial tibia; F:AM 104511, distal view, scale = 3.0 cm.

PLATE 7

FIGURE

1,2. Navicular; F:AM 101587, proximal and distal views, ×0.5.

3. Ectocuneiform; F:AM 101587, proximal view, ×0.5.

4. Metatarsus; F:AM 101590, proximal view, scale = 3.25 cm.

5,6. Cuboid; F:AM 101579, distal and proximal views, ×0.5.

7,8. First phalanx; F:AM 101589, anterior and posterior views, scale = 3.0 cm.

9,10. Metatarsus; F:AM 101590, anterior and posterior views, scale = 5.0 cm.