SELENODONT ARTIODACTYLA (CAMELIDAE AND CERVIDAE) FROM THE LEISEY SHELL PITS, HILLSBOROUGH COUNTY, FLORIDA

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ABSTRACT

Two llama genera are represented in the Leisey Shell Pit by the largest samples of limb bones and dentitions known anywhere. *Palaeolama mirifica* has an especially distinctive dentition, with cervoid lower premolars, relatively low-crowned cheek teeth, thin cement, narrow but scallop-edged incisors, and shallow mandible. These features are contrasted with the more hypsodont, cement-bearing cheek teeth and thicker, wider incisors in *Hemiauchenia seymourensis*. The latter genus was a mixed feeder, whereas *Palaeolama* was probably a browser. Analysis of the Leisey 3A sample of *Hemiauchenia*, in which newborns, yearlings, and two-year-olds predominate, indicates that a catastrophic summer flood massively drowned a herd of these llamas. A small sample of *Odocoileus virginianus* constitutes the only evidence of ruminants at Leisey.

RESUMEN

En los depósitos de conchuelas de Leisey se encuentran representados dos géneros de llamas, siendo éstas las mayores muestras de huesos de extremidades y piezas dentarias encontradas en parte alguna. *Palaeolama mirifica* posee una dentición especialmente distintiva, con premolares inferiores con razgos cervoídeos, dientes post caninos con corona relativamente baja, cemento delgado, incisivos angostos y mandíbula poco profunda. Estas características contrastan con la dentición más hipsodonta de *Hemiauchenia seymourensis*. Este último género poseía una dieta mixta, mientras que *Palaeolama* era probablemente una especie ramoneadora. La muestra de *Hemiauchenia* proveniente de Leisey 3A está compuesta por neonatos, individuos de un año y predominantemente por individuos de dos años. El análisis de esta muestra indica que una inundación veraniega de características catastróficas causó la muerte por ahogo de estas llamas. Una pequeña muestra de *Odocoileus virginianus* constituye la única evidencia de rumiantes en Leisey.

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INTRODUCTION

Florida's Pleistocene fauna is remarkable for the frequent occurrence of two distinct genera of llama-like camelids and the absence of any larger non-lamine genera, such as *Camelops*, that characteristically appear in sites from western North America.   In Florida, the two llama-like genera, *Palaeolama* and *Hemiauchenia*, are frequently found together in apparent sympatry, as noted by Webb (1974); and this raises the question of how they maintained distinct ecological roles. The Leisey Shell Pit produces both of these lamine genera in extraordinary abundance. Indeed, at present each genus is more abundantly known at Leisey than anywhere else in the New World. *Palaeolama* is generally rare in North America, yet at Leisey it is the single most abundant vertebrate taxon, numbering over 120 individuals as a minimum estimate (see Pratt and Hulbert this volume). Although *Hemiauchenia* is only about half as abundant as *Palaeolama* at Leisey 1A, it nonetheless ranks among the ten most abundant mammalian taxa there.   At Leisey 3A, *Hemiauchenia*, mostly as young individuals, is almost exclusively sampled in an apparent catastrophic assemblage. It is quite remarkable that the world's richest assemblage of fossil llamas comes from an estuarine deposit in the southeastern United States, far from the center of diversity of living lamines in the Andes Mountains of South America.

Since their explosive appearance in the early Miocene, ruminants have played such a dominant role in most continental faunas that it is surprising to find a major Pleistocene lacuna in their North American history of dominance and diversity. The Leisey Shell Pit dramatically demonstrates the low ebb of ruminants during the Irvingtonian, despite their greater role both earlier and later in the faunal history of Florida. In this section we refer briefly to the one species of deer that occurs as a rare element at Leisey. A few concluding comments will place this ruminant in a phylogenetic and biogeographic perspective.

The first purpose of this chapter is to present the systematic identity of the one cervid and two camelid species from the Leisey Shell Pit, placing them in a broader taxonomic and geographic framework. The second purpose is to compare the principle adaptive features of the two llama taxa, including a brief population analysis of Leisey 3A *Hemiauchenia*, in order to elucidate their distinct ecological roles.

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen 1848
Suborder RUMINANTIA Scopoli 1777
Family CERVIDAE Gray 1821
Genus *Odocoileus* Rafinesque 1832
Odocoileus virginianus (Zimmerman 1780)

Description.-- The entire sample of ruminants from Leisey Shell Pit consists of about a dozen key elements, including antlers, maxillae, and mandibles, representing the genus *Odocoileus*. One virtually complete five-pointed left antler, UF 83250, clearly shows the anteriorly spiralling beam charcteristic of *O. virginianus*. All dentigerous elements have the morphology of *Odocoileus* teeth, and all Leisey material is of a comparable size; thus the entire sample is referable without serious doubt to this single species.

It is interesting to note in passing that of the three nearly complete mandibles, two (UF 84967 and 85327) represent two-year olds with slightly worn permanent premolars, and one (UF 81050) represents an individual at least four-years old with heavily worn cheek teeth. A palate (UF 81626) also pertains to a probable fourth-year adult. The adult male antler (noted above) must also belong to a buck at least four years old.

Discussion.-- *Odocoileus* appeared in North America in the early Blancan (as *O. brachydontus*). Essentially modern samples, referable to *O. virginianus*, are well documented from late Blancan to present (Kurtén and Anderson 1980). Some of the best early Irvingtonian evidence of that species comes from Inglis 1A. It is therefore not surprising to find such a modern species a little later at Leisey Shell Pit.

What is somewhat surprising is the paucity of *Odocoileus* at Leisey, and also the absence of any other ruminants, especially the pronghorn family Antilocapridae. In Florida during the late Blancan and earliest Irvingtonian, *Capromeryx*, a diminutive pronghorn, occurred quite abundantly in certain sites, notably Inglis 1A, but Inglis remains the youngest record of antilocaprids in Florida and eastern North America (Morgan and Hulbert this volume).

The low ebb in ruminant diversity occurred during the Irvingtonian, not only in Florida, but throughout most of North America, where most records of Bovidae and more diverse Cervidae are Rancholabrean. Following the late Miocene extinctions of archaic families, such as the Dromomerycidae and Moschidae, the only diverse and abundant family of North American ruminants during the Pliocene was the native Antilocapridae. Blancan ruminants include a few cervids
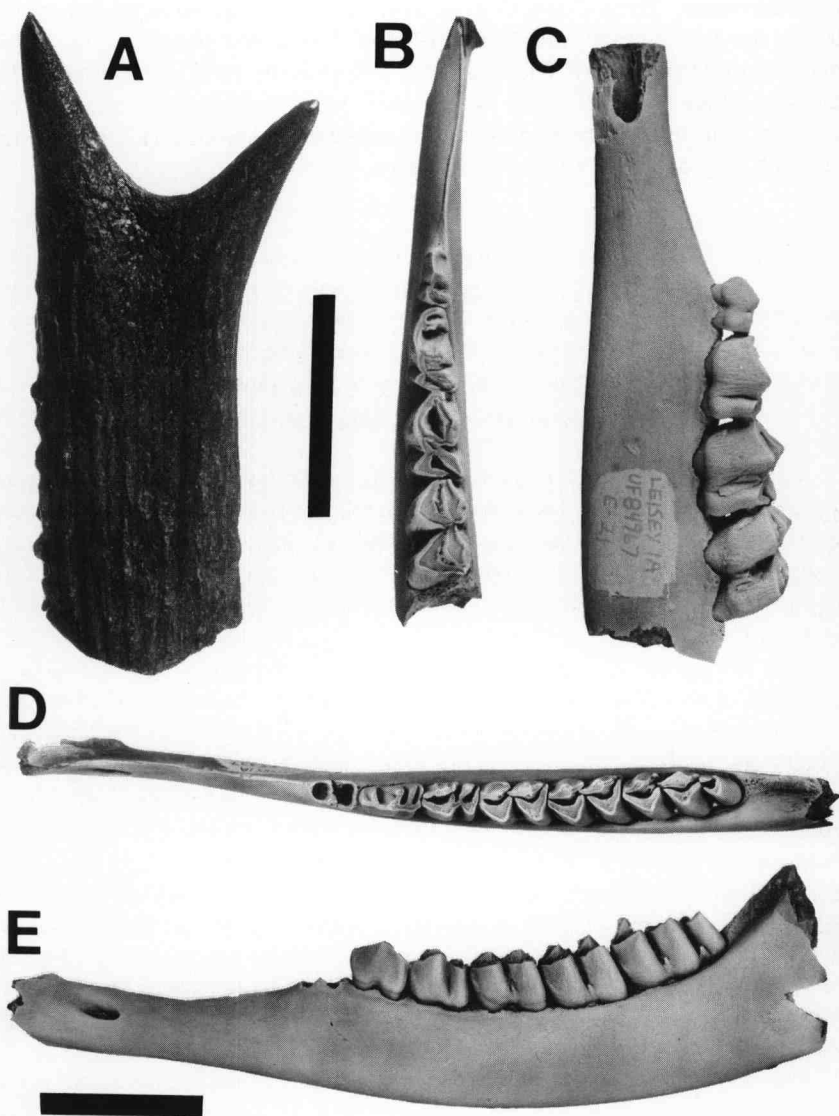
Figure 1. *Odocoileus virginianus* antler and mandibles from Leisey Shell Pit. (A) two-pointed antler, UF 81344. (B and C) lateral and occlusal views of left mandible bearing p2-m1, about two years old, UF 84967. (D and E) occlusal and lateral views of left mandible bearing p3-m3, about four years old, UF 81050. Scale bar = 30 mm.

such as *Bretzia* and an occasional ovibovine or bovine, but these are exceedingly rare occurrences. Even *Odocoileus* appears to have remained relatively rare until later in the Irvingtonian and Rancholabrean. Thus the ruminant-low in North America occurred during Blancan and Irvingtonian time. In eastern North America, where Antilocapridae were never very diverse, the ruminant-low is especially striking. Leisey represents an extreme case among rich late Cenozoic sites, with only one, rare species of ruminant.

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Suborder TYLOPODA Illiger 1811
Family CAMELIDAE Gray 1821
Subfamily CAMELINAE Gray 1821
Tribe LAMINI Webb 1965
Genus *Palaeolama* P. Gervais 1869
Palaeolama mirifica (Simpson 1929)

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Description.-- *Palaeolama* is the smaller of the two Florida Pleistocene lamine genera and has much shorter limbs than *Hemiauchenia*. It is especially well distinguished from *Hemiauchenia* and other known Camelidae by its complex p4 with multiple fossettids (Webb 1974). Numerous other distinctions, clearly brought out by the large samples from Leisey Shell Pit, are noted in the following description.

The deciduous premolars of *Palaeolama mirifica* are readily distinguished from those of *Hemiauchenia seymourensis* not only by their smaller size but also by several differences in character and proportion. Both genera retain a two-rooted second upper premolar in the milk series, a fact not known in earlier studies (e.g. Webb 1974). In *Palaeolama*, DP2 supports incomplete anterior and posterior lingual crests, much like the weaker variants in P3, described below. DP2 in *Hemiauchenia* is much narrower and lacks lingual crests. DP3 as in other camelids is submolariform. In *Palaeolama* the anterior moiety of DP3 is much smaller and transversely narrower than the posterior moiety. In *Hemiauchenia* the two parts of DP3 are more nearly equal, and thus more progressively molariform. DP4 is molariform in both lamine genera. In *Palaeolama* the two lingual roots of DP4 are closely appressed, and in some specimens proximally fused; whereas DP4 of *Hemiauchenia* has four widely separated roots.

The Leisey sample of lamine permanent upper premolars sheds new light on the limits of their variation. In *Palaeolama* P3 does not have a complete lingual crescent, but rather separate anterolingual and posterolingual crests, of which the anterior is usually the weaker. The P3 in Figure 2B shows a typical bipartite lingual cingulum. There is a slight trend for cingula to be stronger in later Pleistocene *Palaeolama* samples, but the distinction is nearly lost in the great variability of the Leisey sample. The lingual (third) root is moderately to strongly
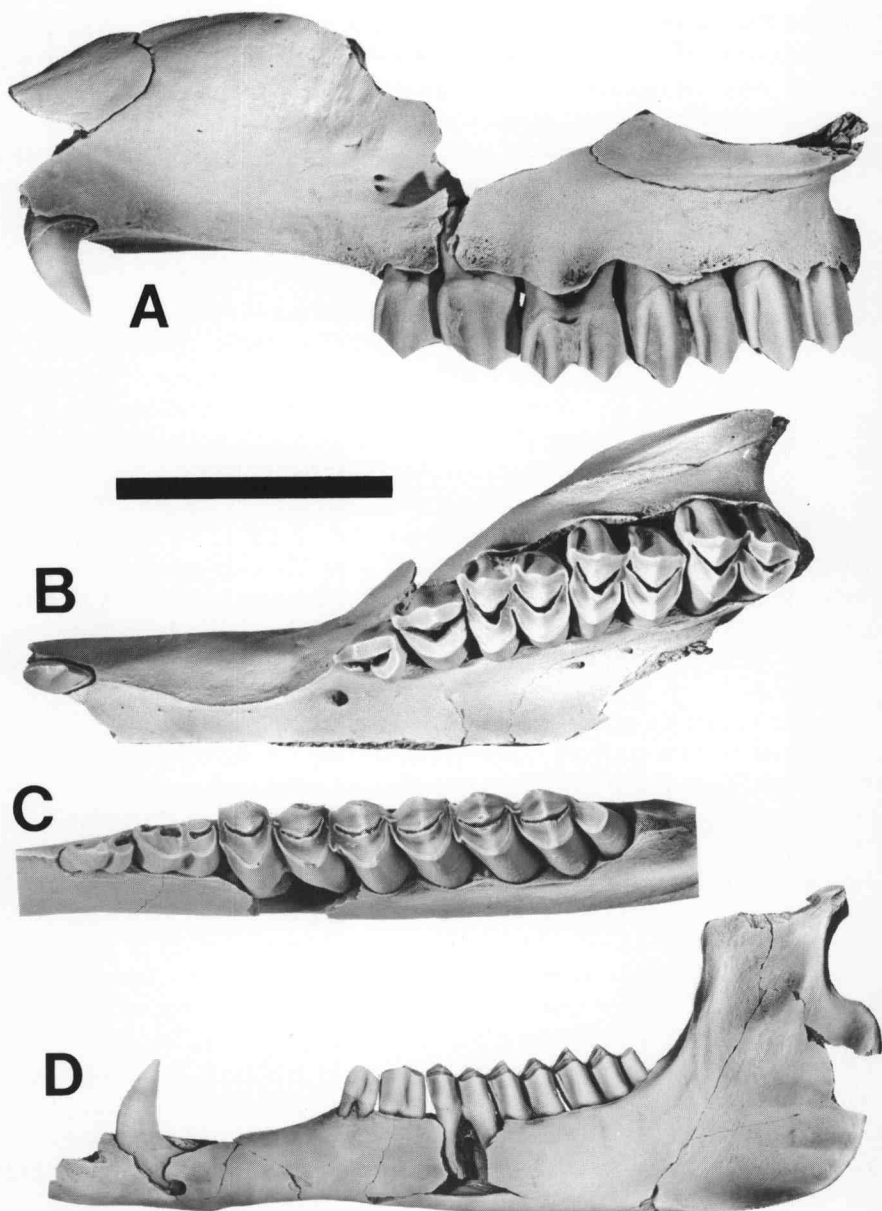
Figure 2. *Palaeolama mirifica* dentitions from Leisey Shell Pit. (A and B) lateral and occlusal views of left maxillary with C and P3-M3, UF 67077. (C and D) lateral and occlusal views of left mandible with c and p3-m3, UF 64233 (89548). Scale bars = 50 mm for A-C, 85 mm for D.

Table 1. Tooth measurements (in mm) of *Palaeolama mirifica* maxillaries from Leisey Shell Pit.

Specimen Number	P1-P3	P3-M3	M1-M3	LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2	LM3	WM3
UF 64268	-	-	-	-	-	17.96	-	16.72	20.12	-	-	-	-
UF 67080	-	-	-	12.40	8.21	14.56	14.32	-	-	-	-	-	-
UF 67078	-	-	-	-	-	-	-	15.19	18.50	19.64	-	-	-
UF 64279	-	81.65	54.35	11.45	-	12.78	13.82	14.36	18.11	17.24	20.00	16.80	18.83
UF 64276	-	54.26	78.40	10.31	9.78	12.05	14.88	16.65	16.85	17.80	20.41	17.52	19.12
UF 65304	-	-	-	-	-	-	-	-	-	17.40	20.76	18.88	21.61
UF 67079	-	-	-	-	-	-	-	11.02	19.46	20.57	22.96	-	-
UF 64728	-	-	-	12.15	8.12	17.80	13.63	15.04	17.21	-	-	-	-
UF 64277	-	82.01	55.70	11.32	7.02	14.12	14.45	17.06	19.07	16.95	19.52	19.08	19.33
UF 64283	-	-	58.55	-	-	14.40	15.17	15.90	18.80	18.82	22.06	20.00	20.35
UF 64287	-	-	-	-	-	-	-	-	-	19.20	21.25	19.95	21.30
UF 64280	-	-	-	-	-	-	-	-	-	16.65	21.75	20.75	20.13
UF 64282	-	82.21	57.05	-	-	13.52	13.87	15.20	17.52	17.75	20.55	19.10	20.52
UF 64286	-	-	-	12.00	8.15	12.86	13.68	16.60	18.52	-	-	-	-
UF 64285	-	-	-	10.57	9.76	11.80	13.77	-	-	-	-	-	-
UF 82839	-	85.47	60.90	10.14	9.50	13.00	14.76	16.00	19.23	19.05	22.20	22.01	21.80
UF 82621	-	86.95	60.15	12.35	9.71	14.40	15.36	16.88	19.77	20.00	20.88	19.81	19.72
UF 83263	-	-	57.20	-	-	13.50	14.42	15.90	20.01	17.85	22.78	19.50	20.67
UF 83265	-	-	-	12.18	8.50	-	-	-	-	-	-	-	-
UF 82131	-	-	-	-	-	-	-	-	-	19.34	21.05	22.44	20.85
UF 81945	-	-	63.75	-	-	-	-	11.70	20.29	19.32	20.16	23.17	21.62
UF 81943	-	-	62.19	-	-	-	-	12.24	17.30	20.12	20.95	20.70	19.97
UF 84150	-	77.97	55.90	9.93	-	11.40	14.67	15.95	19.46	18.57	23.15	18.28	21.52
UF 80097	-	80.35	56.10	11.70	9.40	12.78	14.34	15.00	18.94	17.90	19.91	18.82	20.50
UF 81456	-	85.32	58.00	12.16	9.95	12.78	14.76	14.80	19.40	18.60	22.16	21.30	20.97
UF 80119	-	88.85	61.51	12.05	10.61	14.65	15.91	16.35	19.30	19.67	22.22	22.63	21.72

Table 2. Tooth measurement (in mm) of *Paleolama mirifica* mandibles from Leisey Shell Pit.

Specimen Number	p1-p3	p3-m3	m1-m3	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3
UF 64233	52.51	92.62	68.11	10.70	5.95	14.49	7.83	17.84	13.89	20.43	15.09	27.55	15.06
UF 64237	-	-	65.72	-	-	-	-	15.00	14.25	17.26	14.35	25.81	14.57
UF 64236	-	89.71	65.04	-	-	-	-	17.22	13.46	16.85	14.70	25.91	14.87
UF 64235	-	-	64.75	-	-	-	-	17.34	12.50	18.40	14.74	27.04	14.27
UF 64234	-	-	68.89	-	-	15.04	-	15.93	-	20.71	15.26	29.30	15.22
UF 135671	-	-	69.32	-	-	-	-	16.25	14.69	19.35	15.52	29.15	15.01
UF 135673	-	94.53	67.74	9.24	5.58	14.81	9.52	16.26	13.33	19.82	14.68	28.22	15.21
UF 135672	66.34	91.08	65.41	-	-	12.97	8.68	16.88	13.52	19.76	14.12	27.31	14.78
UF 135674	-	96.34	68.67	-	-	12.39	8.52	16.22	13.16	19.34	14.22	27.37	15.31
UF 135675	-	94.49	66.86	-	-	13.83	9.00	15.95	14.51	19.26	15.72	28.75	15.81
UF 135676	-	102.64	75.30	13.59	10.25	14.76	11.92	19.86	20.52	23.25	22.14	22.02	22.15
UF 82800	-	92.64	70.27	7.46	4.47	12.93	8.53	16.72	13.35	19.92	15.21	30.94	16.03
UF 64234	59.30	98.95	72.97	10.41	5.70	14.48	7.14	17.33	14.07	17.61	13.93	29.38	15.00
UF 82450	-	94.05	67.42	-	-	13.28	9.13	16.19	13.50	18.91	14.86	26.90	15.13
UF 82126	-	102.82	74.44	9.40	5.43	14.22	8.48	17.73	13.44	21.15	14.27	29.56	14.62
UF 82620	-	104.40	75.36	13.38	9.55	14.45	15.24	20.24	19.76	22.60	20.43	29.92	20.31
UF 84363	-	97.80	69.83	10.18	5.70	13.45	8.32	18.16	14.12	20.00	14.31	28.45	15.30

developed.   Development of two lingual crests and a lingual root readily distinguishes P3s of *Palaeolama mirifica* from those of *Hemiauchenia seymourensis* in the Leisey samples.

Deciduous lower premolars of fossil llamas are also well represented for the first time in the Leisey sample. There is no evidence of dp2 in either genus. The first deciduous tooth in the mandibular series is dp3, a small triangular tooth, supported by two roots, and commonly bearing one posterior fossettid. It is smaller in *Palaeolama mirifica* than in *Hemiauchenia seymourensis*. In *Palaeolama* the last deciduous premolar, dp4, consists of three lobes, as in other camelids, with the anterior lobe considerably smaller and shallower than the succeeding ones. This tooth is supported by two widely separated roots and, variably, a small central root as well. By contrast the larger three-lobed dp4 of *Hemiauchenia* is fully three-rooted.

An important feature of the lower dentition, not previously documented in *Palaeolama mirifica*, is the absence of p1. UF 89548 is the most convincing voucher among several mature mandibles that clearly show the absence of this tooth. This is not a profoundly diagnostic feature, however, for, as discussed below, a similar tendency occurs in many populations of *Hemiauchenia*; and p1 is also normally absent in *Camelops* and modern llamas, this feature presumably having been achieved by parallel evolution.

The distinctive nature of the posterior lower premolars in *Palaeolama* has been fully described and illustrated by Webb (1974). In particular p4 has four lingual flexids or fossettids (which are enamel lakes formed from flexids in later wear) and these constitute the dental hallmark of *Palaeolama*. A similar diagnostic feature of p3 is the labial fold and three lingual flexids, which in particular wear stages may form a fossettid (very rarely two). In many respects lower premolars of *Palaeolama* more nearly resemble those of certain cervoid ruminants than those of other camelids (Fig. 2C).

The molar teeth of *Palaeolama* differ in character from those of *Hemiauchenia* in two major features. First they are less hypsodont. Clearly this feature must be applied cautiously, with ample attention to comparability of wear stages. Maximum crown height measured on the second lobe of m3 seldom exceeds 25 mm in *Palaeolama mirifica*, whereas in *Hemiauchenia seymourensis* that same dimension often exceeds 35 mm, for example in the unworn tooth of UF 65291 from Leisey 1A. Secondly, cementum development on the cheekteeth of *Palaeolama* is thin and largely confined to the gumline; whereas *Hemiauchenia* cheekteeth are heavily invested with cement over most of their external surfaces, much as in hypsodont horse teeth. At Leisey this gives the *Hemiauchenia* teeth a striking black demeanor. These two features are probably correlated as in many grazing mammals.

Several differences in the mandible also distinguish *Palaeolama mirifica* from *Hemiauchenia seymourensis*. The symphyseal region is shallower and more slender in *Palaeolama* than in *Hemiauchenia* (Fig. 2D). The maximum width of

that region, measured across the lower canines, ranges from 23 to 32 mm in the former and from 34 to 42 in *Hemiauchenia* The adaptive importance of this region is discussed further below. Based on Leisey samples, the overall length of the dentition is somewhat less in *Palaeolama mirifica* than in *Hemiauchenia seymourensis*: the mean length of p3-m3, taken from Tables 2 and 4, is 95.0 mm in *Palaeolama* (N=11), as compared to 104.6 mm in *Hemiauchenia* (N=17). Although these lengths vary widely with stage of wear, they nevertheless may be easily distinguished in normal mature stages. As might be expected of a less hypsodont animal, *Palaeolama* has an absolutely and relatively shallower mandible. The depth below the front of m3 in mature mandibles ranges from 37 to 45 mm, whereas in *Hemiauchenia* that depth ranges from 48 to 61 mm. The upper part of the masseteric fossa is deeply pocketed in *Palaeolama*, and shallow in *Hemiauchenia*; on the other hand, the posteroventral insertion area of the deep masseter is less fully expanded in *Palaeolama* than in *Hemiauchenia*. Finally, the angular "hook" is strongly inflected in *Palaeolama*, in contrast with the nearly straight alignment of that feature in *Hemiauchenia*.

It is beyond the scope of this paper to elaborate on the postcranial features of the Leisey llamas. A detailed analysis of both genera would make a valuable contribution. The relatively stocky features of *Palaeolama* described by Webb (1974) are clearly corroborated by the new collections from Leisey. Possibly these proportions form an adaptation for predator avoidance in scrubby or forested habitats as suggested by Graham (1992). It now seems doubtful that they evolved in the Andes as suggested by Webb (1974).

Discussion.-- The geographic distribution of *Palaeolama* in North America, thought by Webb (1974) to be restricted to Florida and the Texas Gulf Coast, extends as far north as Edisto Island, South Carolina (Roth and Laerm 1980), and southern Missouri (Graham 1992) and as far west as southern California (Conkling, pers. comm.). *Hemiauchenia* has a somewhat more northern range reaching as far north as Iowa and northwest to Idaho.

The precise relationship of *Palaeolama* to other lamines remains problematical. Clearly the rich sample of *P. mirifica* from Leisey Shell Pit provides an excellent basis for osteological comparisons; yet, as of this writing, no clearcut sister group, sharing any fundamental derived features of its dentition, has been recognized outside of the genus. Webb (1974, p. 210) stated that "... common ancestry of *Palaeolama* and the modern llamas is implied by shared morphological features, but it is not precisely documented. By the time the Tarija deposits had accumulated, the larger *Palaeolama* and the smaller *Lama* were already quite distinct. Nonetheless the two genera have some special features in common, including similar limb proportions and an Andean center of distribution." Harrison (1985) followed this proposal and placed *Palaeolama* as the sister group of living Laminae. This is hardly a convincing phylogenetic analysis. Until other shared features, besides limb proportions, and preferably cranial or

dental characters, are demonstrated in some other lamine genus, the relationships of *Palaeolama* and other llamas must be acknowledged as an unresolved polychotomy.

In the absence of a well defined sister group (not merely all other lamine genera), the geographic history of *Palaeolama* also remains problematical. Even if one were willing to follow the dubious practice of considering the place of its earliest stratigraphic appearance as most probably its place of origin, the continent of origin remains uncertain. In North America the early Irvingtonian occurrence at Leisey is the oldest record of *Palaeolama*. The nominal assignment of a much older llama to this genus, a proposed new species from the late Hemphillian Ocote local fauna near Guanajuato, Mexico by Dalquest and Mooser (1980), has been corrected by Montellano (1989) who assigned it to *Hemiauchenia* on the basis of more complete material. The oldest well-documented records of the genus in South America are those of the type species *P. weddelli* at Tarija, Bolivia, of Ensenadan (approximately middle Pleistocene; MacFadden et al. 1983) age. This species differs from the Leisey sample of *P. mirifica* mainly in its larger size. On this basis, one may suppose that the two samples are closely related, and therefore that they might indicate an early Pleistocene immigration from North America to South America, contrary to the suggestions of Webb (1974) amd Montellano (1989). On the other hand, Mones (1988) proposed a downward extension of the South American range of *Palaeolama* to Uquian (Plio-Pleistocene) based on associated faunal evidence (mainly the glyptodont, *Doedicurus*) in the upper San Jose Formation of Uruguay. Also, Marshall et al. (1984) cited an Uquian range for *Palaeolama* in Argentina, although the basis was not presented explicitly. Crucial resolution of this biogeographic problem will depend ultimately on resolution of the phylogenetic problem, that is on identifying the sister group of *Palaeolama*. We strongly deny the suggestion of Marshall et al. (1984:21) that *Hemiauchenia* (and other nominal South American taxa) "are most likely sub-genera of *Palaeolama*," for the many reasons described above. Presumably the critical evidence regarding the origins of *Palaeolama* resides in Pliocene sediments somewhere in low latitudes of the two American continents.

Genus *Hemiauchenia* H. Gervais and Ameghino 1880
Hemiauchenia seymourensis (Hibbard and Dalquest 1962)

Description.-- The rich samples of Leisey llamas shed new light on several features of this Plio-Pleistocene species, although in most respects they confirm the previous discussions of Webb (1974) and Breyer (1977).

Regarding deciduous premolars in *Hemiauchenia seymourensis*, several new observations can be made. First is the presence of DP2 as a narrow two-rooted tooth, lacking the lingual features observed in *Palaeolama*. As noted above, DP3 is more fully molariform, due to its larger size and more nearly equal anterior lobe,

than in *Palaeolama*. The DP4 is also relatively larger and has the two lingual roots more widely separated anteroposteriorly than in the corresponding tooth of *Palaeolama*. Among the lowers dp3 is two-rooted and much larger than in *Palaeolama*. The dp4 is also much larger than in that genus, and has the three lobes subequal, rather than reducing anteriorly. It is fair to state thus that *Hemiauchenia seymourensis* has a much more fully molariform deciduous dentition than *Palaeolama mirifica*.

Both upper P3 and lower p3 exhibit features worthy of further description. The lingual side of P3 in *Hemiauchenia* is remarkably narrow and incomplete in contrast with its tall, strong ectoloph. Typically there is a weak posterolingual cusp (seldom worthy of being called a crest) and no anterolingual feature at all (Fig. 3). In *Hemiauchenia* P3 is only two-rooted, lacking the third (lingual) root seen in the lingually more robust P3 of *Palaeolama*. These features were not noted in Breyer's (1977) excellent study, because he dealt only with the lower dentition.

The first lower premolar, p1, nearly always occurs as a distinct posterior caniniform above the posterior border of the symphysis, but its expression in the Leisey sample of *Hemiauchenia* is quite variable. UF 64216 exemplifies its tendency to be very slender and to be delayed in its eruption time until the molars are well worn.

Among the valuable statistics given by Breyer (1977:527) regarding the large late Blancan sample of *Hemiauchenia blancoensis* from the Broadwater local fauna in Nebraska, was the fact that p3 "... can be found in fewer than one in ten adults." Two of the eight mandibular dentitions in his figure one (1A and 1C) illustrate this tooth. It is therefore quite surprising to report that in the younger sample from Leisey, referred to *H. seymourensis*, a two-rooted p3 is present in virtually every specimen. This, along with slightly smaller size, helps distinguish the Irvingtonian species *H. seymourensis* from the Blancan species. It also suggests that the Florida sample was derived from a more primitive species of *Hemiauchenia* which had not nearly lost p3, although this could also represent a character reversal. Besides the ten specimens measured as parts of the relatively complete mandibles included in Table 4, there are many isolated lower third premolars; and, most importantly, there are two alveoli for p3 roots in every mandible that is appropriately preserved. The same regular occurrence of p3 extends even to the late Pleistocene samples of *Hemiauchenia macrocephala* in Florida as noted by Webb (1974). It appears that the third lower premolar was largely suppressed in Nebraska pre-Pleistocene samples of *Hemiauchenia*, whereas it continued to appear quite normally in Florida populations for some two million years longer. In the Leisey *H. seymourensis* this tooth is small, with closely appressed roots. Its relatively simple crown is about half as long as that of p4 (see Table 4) and consists of an apex anteriorly, and a greatly reduced posterolingual notch.

As noted above, the molars of *Hemiauchenia seymourensis* are considerably more hypsodont than those of *Palaeolama mirifica*. For example in UF 65291, the
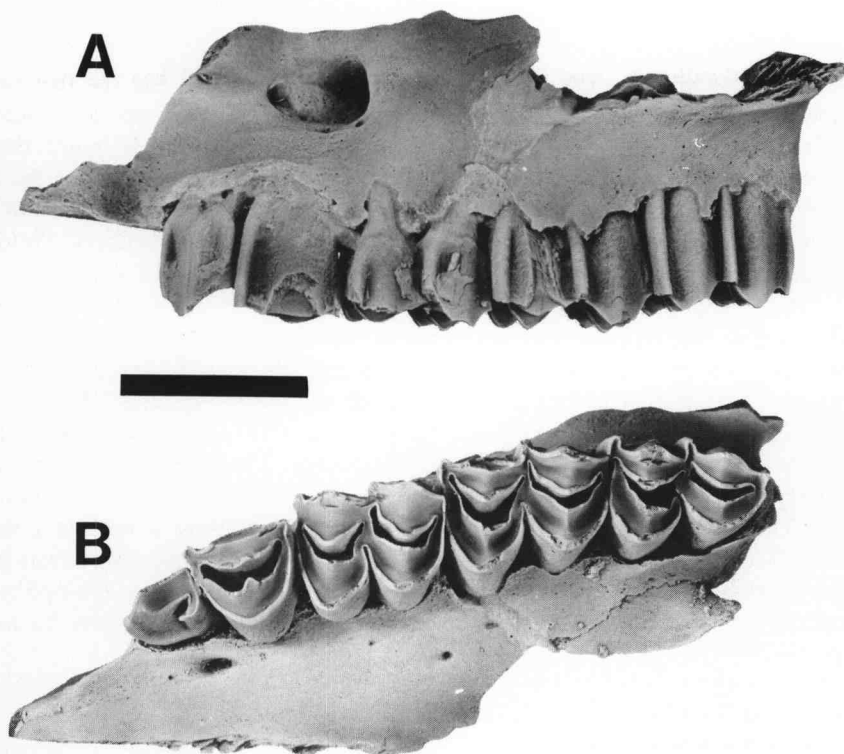
Figure 3. *Hemiauchenia seymourensis* left maxillary with P3-M3 from Leisey Shell Pit. (A and B) lateral and occlusal views, UF 81745. Scale bar = 30 mm.

second lobe of m3 has an unworn crown height of 35.5 mm. The cheek teeth also bear a heavy layer of cementum, giving most specimens in the Leisey sample a distinctively blackened and roughened surface. The llama buttresses at the anterior ends of the lower molars are well-developed and persistent, more so than in *Palaeolama*. These features are probably correlated with the greater hypsodonty of the cheek teeth in *Hemiauchenia*, as in many grazers. Other diganostic features of *Hemiauchenia* mandibles, such as their greater depth and broader symphysis, have been detailed above under *Palaeolama*. *Hemiauchenia* is also the larger of the two Florida Pleistocene lamine genera and has much longer limbs than *Palaeolama*. The striking differences in tibia and metatarsal proportions are illustrated in Figure 4.

Discussion.-- In North America *Hemiauchenia* is the more familiar genus with widespread occurrences in other parts of the continent, notably in California. There the Rancholabrean species, *H. macrocephala*, is well represented from the late Pleistocene sample at the McKittrick Tar Seep (Stock 1928). The geological

Table 3. Tooth measurements (in mm) of *Hemiauchenia seymourensis* maxillaries from Leisey Shell Pit.

Specimen Number	M1-M3	LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2	LM3	WM3
UF 64269	67.62	-	-	14.31	15.45	19.46	19.94	20.82	20.90	24.90	19.38
UF 82465	65.58	-	-	12.41	15.25	16.50	17.91	19.87	19.88	25.52	19.04
UF 64265	-	17.04	16.05	17.29	18.85	23.43	19.16	26.48	17.60	-	-
UF 64267	-	-	-	14.90	14.67	18.55	17.50	21.49	18.56	-	-
UF 64266	67.02	-	-	14.50	15.00	16.45	18.95	21.71	19.54	25.69	19.11

Table 4. Tooth measurements (in mm) of *Hemiauchenia seymourensis* mandibles from Leisey Shell Pit.

| Specimen Number	p1-p3	p3-m3	m1-m3	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3
UF 89548	65.02	94.05	68.15	-	-	13.93	8.20	16.95	13.57	19.12	15.51	27.55	15.26
UF 89548	66.26	93.16	67.55	-	-	13.90	7.83	16.57	13.40	18.87	15.06	27.96	15.44
UF 104500	45.01	115.27	83.51	9.64	6.04	17.86	9.91	20.65	13.95	25.37	13.92	34.05	12.93
UF 81407	-	92.03	62.15	10.22	5.56	14.93	8.71	17.14	14.18	18.78	14.50	27.80	15.08
UF 80053	48.04	114.35	77.96	8.71	5.28	16.00	8.19	20.16	13.88	20.97	15.32	32.87	14.98
UF 64232	59.96	98.39	70.64	10.05	-	14.86	8.76	17.14	13.12	19.15	14.54	28.44	13.86
UF 64231	-	-	-	-	-	-	-	-	-	18.57	14.40	-	14.25
UF 84225	-	98.23	70.15	-	-	14.36	7.42	18.05	13.47	20.55	14.36	28.50	14.52
UF 81745	-	102.01	72.42	12.94	7.72	15.00	15.12	21.48	19.95	24.79	19.72	27.15	17.54
UF 89542	47.93	101.38	72.53	-	-	-	-	17.38	13.82	21.01	14.12	31.10	14.57
UP 64215	50.83	107.07	78.40	-	-	15.96	8.85	18.35	14.38	22.41	15.37	33.16	15.33
UF 115504	48.26	114.25	83.68	11.36	6.21	19.05	9.61	21.95	13.37	27.20	14.37	34.14	14.14
UF 115504	50.47	115.46	86.69	10.09	6.07	19.15	9.82	21.68	13.94	26.06	14.74	35.30	13.57
UF 64216	39.74	-	-	-	-	16.60	8.03	19.61	13.62	24.82	14.24	-	-
UF 64218	-	103.64	74.26	-	-	16.31	8.97	18.00	14.62	20.45	15.44	32.93	14.50
UF 65291	-	115.22	84.63	11.23	4.57	16.96	7.21	21.45	13.3	27.24	13.86	31.66	
UF 81076	-	109.48	77.64	-	-	-	-	19.74	14.31	20.77	15.06	32.80	14.59
UF 81541	51.07	99.25	74.02	10.10	5.66	14.01	8.34	19.27	12.36	20.38	13.84	37.54	13.70
UF 65289	-	105.26	72.95	10.48	5.26	15.00	9.13	19.10	13.10	21.77	15.23	31.10	14.36
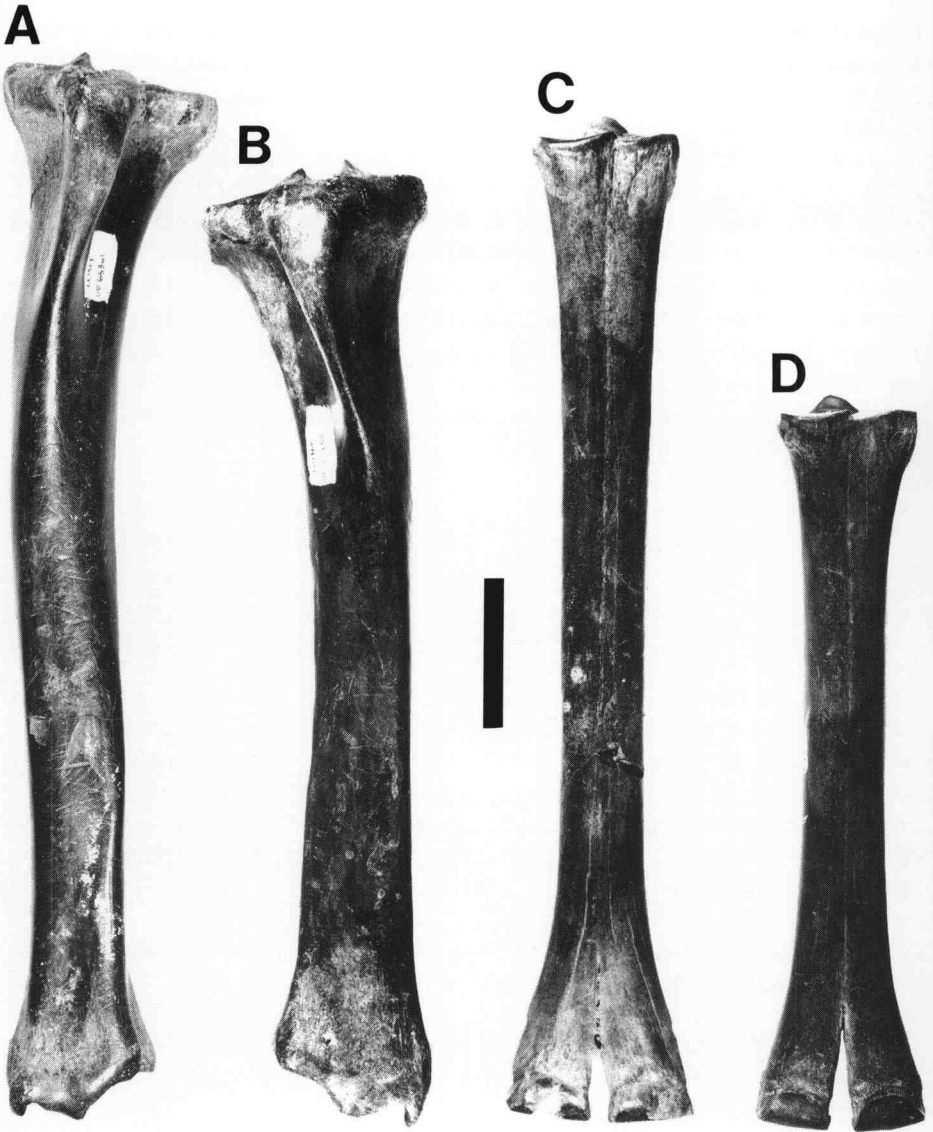
Figure 4. Camelid limbs, indicating different hind limb proportions of *Hemiauchenia* and *Palaeolama* from Leisey Shell Pit. (A) *Hemiauchenia*, UF 65361, and (B) *Palaeolama*, UF 65358, anterior views of tibiae. (C) *Hemiauchenia*, UF 66423, and (D) *Palaeolama*, UF 66401, anterior views of metatarsals. Scale bar = 55 mm for A-B, 50 mm for C-D.

range of *Hemiauchenia* extends back into the late Tertiary, through the Blancan at least into the Hemphillian. As outlined by Hibbard and Dalquest (1962), Webb (1974), and Breyer (1977), this evolutionary lineage progresses from *Hemiauchenia vera* through *H. blancoensis* and *H. seymourensis* to *H. macrocephala*. However, it cannot be a simple anagenetic sequence, as indicated by the retention of relatively large, two rooted p3 in Florida *H. seymourensis*, despite their near absence in earlier *H. blancoensis* from Nebraska. This genus ranged south into Mesoamerica (Dalquest and Mooser 1980; Montellano 1989), and spread by Uquian time into South America with the Great American Interchange (Webb 1974; Marshall et al. 1984). The fact that *Hemiauchenia* and *Palaeolama* were already distinct by early Irvingtonian in Florida suggests that they immigrated from North America to South America as separate taxa. On the other hand, as noted above, this question remains open until a sister group for *Palaeolama* has been clearly identified.

ADAPTATIONS AND ECOLOGICAL SEPARATION

The rich Leisey sample of two kinds of llamas forcefully raises the question of how such similar genera can occur together so abundantly in the same deposit. The answer dictated by ecological and evolutionary theory (sometimes known as Cabrera's Law) is that their niches must be divided effectively, so as to minimize competition for limiting resources. The special taphonomic conditions at Leisey 3A, which apparently accumulated a single population of *Hemiauchenia seymourensis* but no *Palaeolama*, strongly support the view that in life the two genera subtly separated the spheres of their activities. We will return to that separate glimpse of *Hemiauchenia* life history.

Osteological Evidence.-- First, however, another broader approach, depends upon interpreting from their osteology some of the major adaptive differences between *Palaeolama* and *Hemiauchenia*. Conclusions from such a morphological approach may be tested to a degree by comparison with data about their habitat preferences derived from independent evidence of their biogeographic distributions and taphonomic profiles.

In the Leisey Shell Pit *Hemiauchenia* exceeds *Palaeolama* by a bit more than 10 percent in length of cheek-tooth row (p3-m3) given above. Clearly there is ample room for a far more detailed quantitative analysis of interspecific and inatraspecific variation. In light of the diverse literature on niche separation within ecological guilds, this size difference falls below the ordinary expectation that dimensional differences among similar sympatric species should be doubled, emphasizing the expectation that there should be other adaptive bases for niche separation.

The most striking osteological differences between *Palaeolama mirifica* and *Hemiauchenia seymourensis* occur in the dentition. The crown heights of unworn molars in *Hemiauchenia* are half again as great as those in *Palaeolama.* In that case, because *Hemiauchenia* lower molars are proportionally narrower, their hypsodonty indices range from about 1.4 to 2.2, whereas the hypsodonty indices for lower molars of *Palaeolama* from Leisey range from about 0.7 to 0.9.

A related distinction concerns the development of cement on the cheek teeth in these lamines. *Hemiauchenia* consistently has a heavy coat of cementum enveloping its cheek teeth, whereas *Palaeolama* usually exhibits only thin patchy cement near the alveolar borders of its cheek teeth. This contrasting development of cementum in the two lamine taxa is not surprising, since generally in herbivorous mammals the presence of heavy cementum is correlated with increased hypsodonty, usually in grazers.

A third dental distinction is the well known feature of the lower premolars, in which these teeth are more "deer-like" in *Palaeolama* and more typically "camel-like" in *Hemiauchenia*. The important point to make here is that the functional significance of these premolar differences points in the same direction as the hypsodonty difference in the other cheek teeth, namely toward softer browsing adaptations in *Palaeolama*, and toward coarser grazing or mixed-feeding adaptations in *Hemiauchenia*.

A final very significant dental difference between these two lamine genera concerns the incisor arcade. Figures 5A and B illustrate the symphyseal region of *Palaeolama mirifica*, in which the symphysis is narrow and the incisors are imbricated and narrowly procumbent. By contrast the symphysis of *Hemiauchenia seymourensis* is much broader with more broadly splayed incisors. The incisors themselves further exemplify this distinction; for in *Hemiauchenia* each lower incisor is transversely wider and dorsoventrally thicker than its homologue in *Palaeolama* (Figs. 5C-F). Also in *Hemiauchenia* the roots maintain a large caliber, whereas the diameters of *Palaeolama* roots rapidly diminish posteriorly. Especially distinctive is the upper surface of the third lower incisor in *Palaeolama*; for it expands anteriorly, overlapping i2 and develops a scalloped (or delicately notched) wear surface. This lateral lobation is reminiscent of that in most giraffids (Hamilton 1978) (Figs. 5A, B). Graham (1992) notes unusually deep wear on these grooves and we confirm that in many specimens of *Palaeolama* from Leisey. Presumably these surfaces play an important role in grasping and stripping leaves and twigs in a browsing mode of feeding.

The adaptive significance of lower incisor and mandibular symphyseal morphology in ungulates has been emphasized by several recent investigators (Gordon and Illius 1988, Solounias et al. 1988; Janis and Ehrhardt 1988). The latter authors showed that among living camelids, all characterized as intermediate feeders, the widths of the lateral incisors had particularly great value as an indicator of dietary preferences, with greater width implying coarser fodder.
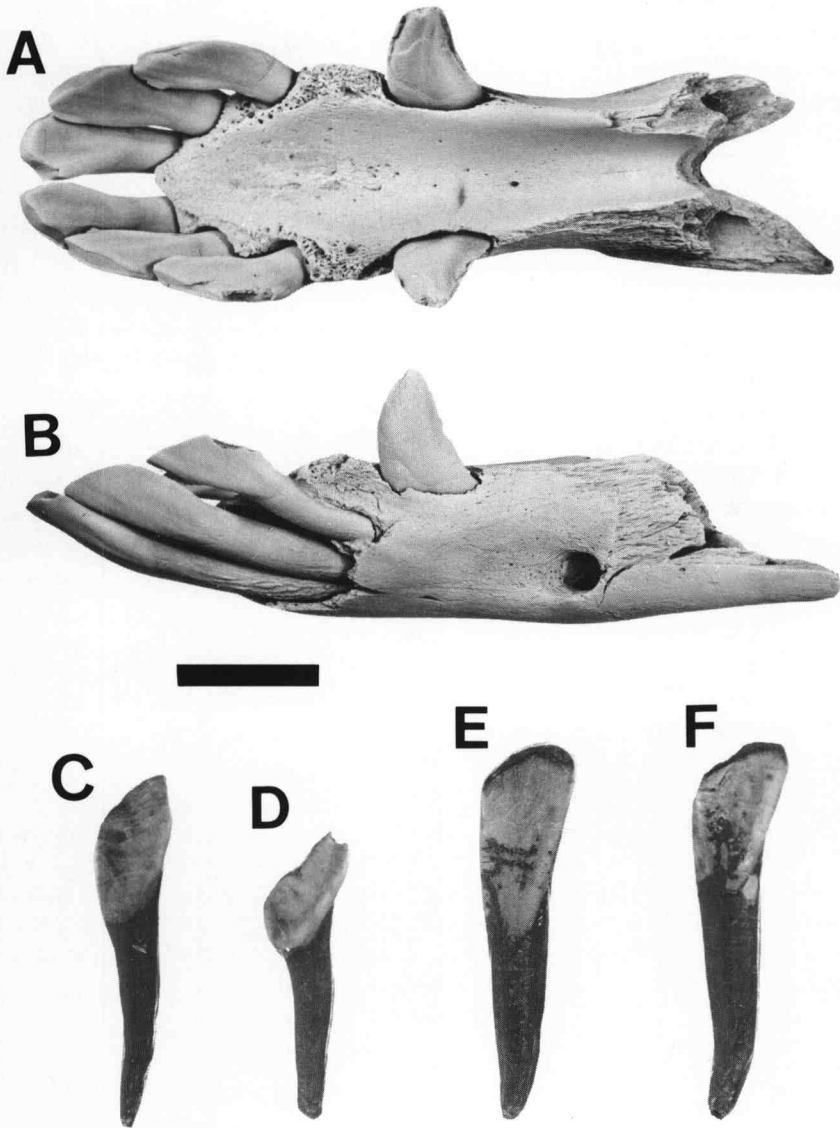
Figure 5. Mandibular symphysis and incisors of *Palaeolama mirifica* and *Hemiauchenia seymourensis* from Leisey Shell Pit. (A) occlusal and (B) lateral views of symphyseal region of *Palaeolama*, UF 81742. (C) left i2, UF 81743, and (D) left i3, UF 81744, dorsal views of *Palaeolama*. (E) left i2, UF 81746, and (F) left i3, UF 81747, dorsal views of *Hemiauchenia*. Scale bar = 20 mm.

The rich samples of postcranial material from Leisey warrant detailed analysis; such a study, however, is beyond the scope of this contribution. From the general phylogenetic context of advanced Camelidae, one can assert that the stocky proportions of *Palaeolama* are derived, and that the long limbs of *Hemiauchenia* generally resemble those of other Late Cenozoic camelids. The relatively short limbs of *Palaeolama* may represent an adaptation to rugged topography such as Andean slopes. This view appears reasonable when applied to the modern llamas of South America, although they are by no means confined to mountainous habitats; but it seems more tenuous in the context of the Gulf Coastal Plain in North America. More plausible perhaps is the suggestion of Graham (1992) that stout limbs were more adaptive to predator escape in scrubby and forested habitus.

Taken together these morphological distinctions between *Palaeolama* and *Hemiauchenia* strongly suggest that the former was primarily a browser, whereas the latter was a mixed feeder. Many features of the *Hemiauchenia* dentition, including its greater hypsodonty, thick cementum, and more powerful incisors, suggest a grazing dental mechanism, in contrast to a browsing mechanism for *Palaeolama*. While these analogies are useful in clarifying the general distinctions between these lamine genera, it must be remembered that in fact the environment around Leisey Shell Pit also supported several equid taxa, which surely separated themselves ecologically from *Hemiauchenia*. The morphological distinctions developed here support the probability that *Palaeolama* was more a browser and *Hemiauchenia* more a mixed feeder, thus providing the predicted basis for ecological separation in the same region.

Age Analysis of Leisey 3A Population.-- The following analysis is based on the nearly complete mandibles, with most cheek teeth in position, from the Leisey 3A sample of *Hemiauchenia seymourensis*. The stages of tooth eruption and wear were compared with the tables developed from known-age llamas and alpacas from Peru by Wheeler (1982). In two cases where a pair of mandibular rami appeared to represent a single individual, only one side was included in the final tally. Although no mandibles represent individuals less than a year old, there are several isolated deciduous teeth that indicate newborn llamas with ages that could range from birth to three months. Presumably the jaws of this age were too fragile to be preserved under depositional conditions that prevailed at Leisey 3A. Likewise at the mature end of the scale there is only one mandible representing an individual over two years of age (it happens to be about nine), although there are a number of well-worn teeth to indicate that mature and even gerontic individuals were present in the *Hemiauchenia* population at Leisey 3A. The tabulation, based on resonably complete mandibles and milk teeth, is presented as Figure 6. Similar results, with discrete age-classes and a predominance of yearlings and two-year olds, are indicated by the fusion-stages of *Hemiauchenia* metapodials at Leisey 3A.
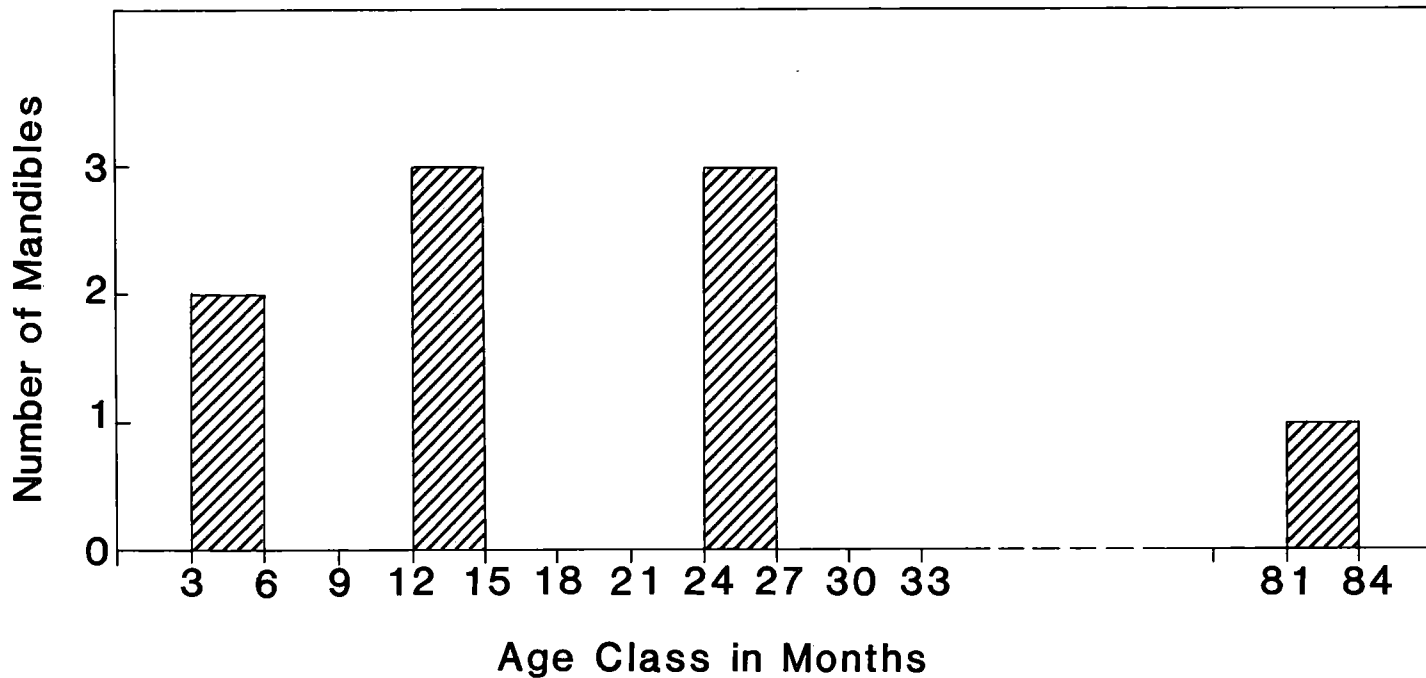
Figure 6. Age classes (in months) of *Hemiauchenia seymourensis* mandibles and milk teeth from Leisey 3 A. Note that the three predominant groups are newborns, yearlings, and two-year-olds, with full-year gaps between. These data indicate a catastrophic assemblage which caused the demise mainly of young animals.

This simple census provides a few conclusions about the nature of deposition at Leisey 3A and also about the population structure of the *Hemiauchenia seymourensis* that was abundantly preserved therein. The fact that this species alone accounted for the vast majority of large-bodied vertebrate fossils in the site indicates that a herd of this species experienced mass mortality in the focus of a catastrophic depositional event. The catastrophic nature of the llama sample is corroborated by the fact that each of the younger age classes met its demise at approximately the same month, regardless of whether they were newborns, yearlings, or two-year-olds (Fig. 6). The same evidence shows that the catastrophic episode occurred within the first three months after the birthing time of year; presumably this means summer, since most ungulates time completion of their gestation for the spring when nutrients are at their best. If the catastrophic event took place in the summer, that raises the possibility that the episode in this Florida coastal setting was a hurricane or at least a severe summer storm.

A similar mass mortality of partly articulated skeletons, representing a herd of extinct titanotheres, was described by Turnbull and Martill (1988). The numbers, age distribution, and dispersal of skeletons are broadly comparable. In each case one can eliminate a scenario of continuous deposition with repeated annual migrations as an explanation, because the sample is so strongly biased toward a single species.

The catastrophe that deposited the *Hemiauchenia* herd at Leisey 3A took place on the margin of an estuary. Possibly it was a summer hurricane. The relatively low numbers of fully mature individuals (over two years of age) trapped at Leisey 3A suggests that they may have been better able to swim to safety. The very young ages were the main victims.

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