A NEW SPECIES OF *Hemiauchenia* (CAMELIDAE;LAMINI) FROM THE PLIO-PLEISTOCENE OF FLORIDA

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2003

I dedicate my thesis to my step-mother, Laura Oleshko Meachen, who passed away on October 12, 2002. She never got to see the finished product, but I am sure she would have been very proud of me. Laura, wherever you are, this is for you.

ACKNOWLEDGMENTS

First and foremost, I would like to thank my major advisor, Dr. S. David Webb. Although a valuable professional mentor, he was also like a caring member of the family. All the good advice he gave me, and all the interesting conversations I had with him I will never forget. I am sincerely glad that I had the pleasure of working with him before he retired this year. I will miss him dearly. I would also like to acknowledge the other members on my committee, Dr. Bruce MacFadden, who has also helped me in many ways and Dr. Richard Kiltie as well.

There are many graduate students with whom I have had the pleasure of working over the years. I would like to thank Diana Hallman for being like a big sister in many respects and also being my collaborator on projects and a good friend. I would like to thank Matt Mihlbachler, Brian Beatty and Andy Hemmings for all their advice and help.

I extend my thanks to the staff of the vertebrate paleontology collection at the FLMNH, Russ McCarty, who has been a great friend and mentor, Dr. Richard Hulbert, Art Poyer and especially Dr. Pennilyn Higgins for all the advice, proofreading and just being a darn good buddy.

My master's thesis was greatly improved by the FLMNH Lucy Dickinson fellowship in vertebrate paleontology.

Last, but certainly not least, I would like to thank all my friends and family. Without their help and support I would never be where I am today!

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Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

A NEW SPECIES OF *Hemiauchenia* (CAMELIDAE;LAMINI) FROM THE PLIO-PLEISTOCENE OF FLORIDA

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August 2003

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Major Department: Zoology

In 1974 paleontologists from the Florida Museum of Natural History (FLMNH) discovered a gracile llama that was originally thought to be *Hemiauchenia macrocephala*. It was discovered at the Inglis 1A fossil site in Citrus County, Florida. Upon further inspection and comparison of this material with known *H. macrocephala* material, Florida museum paleontologists decided that this was not *H. macrocephala*, but a new species altogether. More of this new lamine was also found at the De Soto Shell Pit fossil locality in De Soto County, Florida. Both fossils sites are latest Blancan, earliest Irvingtonian in age.

For the description of this new species, I conducted a thorough morphological analysis of the crania and postcrania, which I then compared to the morphology of *Hemiauchenia macrocephala, Palaeolama mirifica, "Hemiauchenia" minima*, *Hemiauchenia edensis* and extant lamines, *Lama* and *Vicugna*. The holotype for this new species was a right mandibular fragment including p4, m1, m2 and m3 from De Soto

Shell Pit in De Soto County, Florida (UF 210707). This specimen is housed in the FLMNH vertebrate paleontology collection.

This new lamine shares many homologous character states with *Hemiauchenia macrocephala* and *Hemiauchenia edensis*. However, the new lamine has postcrania that are always more slender than those of *H. macrocephala* and usually larger than *H. edensis*. It also has some unique dental features, such as the lack of a p3. This new species is placed in the genus *Hemiauchenia* based on several morphological characters: The length and gracility of the postcranial skeleton, the shape and form of the teeth and the striking resemblance that this new species shares with *H. macrocephala* and *H. edensis*.

From dental characters, post-cranial analysis and stable carbon isotope analysis it seems that this new species ate mainly browse with occasional grass mixed in, and preferred to dwell in savanna type environments. It was probably an agile cursor, using that ability as its main mode of predator evasion. It coexisted with *Hemiauchenia macrocephala* and other artiodactyls, but not with fellow lamine *Palaeolama mirifica*. This new species may have had an affiliation with the origin of the true (extant) llamas that crossed the Isthmus of Panama in the early Pleistocene, as did *Palaeolama*.

CHAPTER 1
INTRODUCTION

Family Camelidae

The family Camelidae includes the living camels, llamas, vicuñas, guanacos and alpacas. They originated in North America in the middle Eocene (approximately 54 MA) and remained endemic to North America until the late Miocene, when they dispersed to Asia and Africa and gave rise to the modern camels (Moya-Sola and Agusti 1989; Pickford et al. 1993; Pickford et al. 1995). In the early Pleistocene, they dispersed to South America to give rise to the modern lamines (Webb 1974). Camelids became extinct in North America in the late Pleistocene, along with most of the other endemic megafauna (Honey et al. 1998).

There were four major episodes of camelid diversification in North America. The first episode took place in the late Eocene through the middle Oligocene and consisted of the camelids *Poebrotherium* and *Paratylopus*. The second radiation took place from the late Oligocene through the early Miocene with the radiation of the stenomylines (*Blickomylus, Rakomylus*). These species became extinct in the middle Miocene. The third radiation of camelids took place in the same time span as the second radiation, and consisted of “higher camelids” or those that possessed metastylids on the lower molars. This radiation more than doubled the number of camelid genera. The fourth radiation of camelids occurred in the early to middle Miocene and produced the Camelinae (Lamini and Camelini) including all extinct and modern American lamines (Honey et al. 1998).

The first lamine fossils, represented by the genus *Alforjas* or *Pleiolama* (Webb and Meachen in press) originated in the Great Plains of North America approximately 11 million years ago. *Pleiolama* is thought to have given rise to the genus *Hemiauchenia* approximately ten million years ago. *Hemiauchenia* is thought to have engendered the extinct genus *Palaeolama*, and also the modern South American lamines. This transition is estimated to have taken place two million years ago (Wheeler 1995) (See Figure 1 for current lamine phylogeny).

The genus *Hemiauchenia* (syn. *Tanupolama*) was named by H. Gervais and Ameghino in 1880. This genus is in the Class Mammalia (Linnaeus 1758), Order Artiodactyla (Owen 1848), Suborder Tylopoda (Illiger 1811), Family Camelidae (Gray 1821), Subfamily Camelinae (Gray 1821) and Tribe Lamini (Webb 1965).

Cranial characteristics of this genus include a dental formula of I1/3, C1/1, P3/2-3, M3/3, a markedly low hypsodonty index (tooth crown height/tooth width or length), with only the genus *Palaeolama* having a lower hypsodonty index, laterally compressed and recurved canines, a sharp diastemal crest on the mandible, a swollen, narrow rostrum, and arched and retracted nasals, but not as far as in the genus *Lama*. The palatine notch is sharply V-shaped extending to the M2. Postcranial characters include, very long, slender limbs and cervical vertebrae (Harrison 1979), fused metapodials that are longer than the basal length of the skull, and a proximal phalanx with a W-shaped suspensory ligament scar (Honey et al. 1998). Most *Hemiauchenia* species were comparatively small camelids, barely larger than the domestic llama (Dalquest 1992), but some became larger than the modern camels.

The four species currently attributed to this genus are: *Hemiauchenia vera* (Matthew) from Florida, Texas, the Texas/Oklahoma panhandle, Kansas, Nebraska, Arizona, New Mexico, California, and Central Mexico; *Hemiauchenia blancoensis* (Meade) from Florida, Texas, the Texas/Oklahoma panhandle, Kansas, Nebraska, Arizona, New Mexico, Colorado, and Washington state; *Hemiauchenia macrocephala* (Cope) is known from Florida, Texas, California, and South America; and "*Hemiauchenia" minima* from Florida (Honey et al. 1998). Webb, MacFadden and Baskin (1981), however, suggested that a new genus name might be more appropriate for *"Hemiauchenia" minima.*

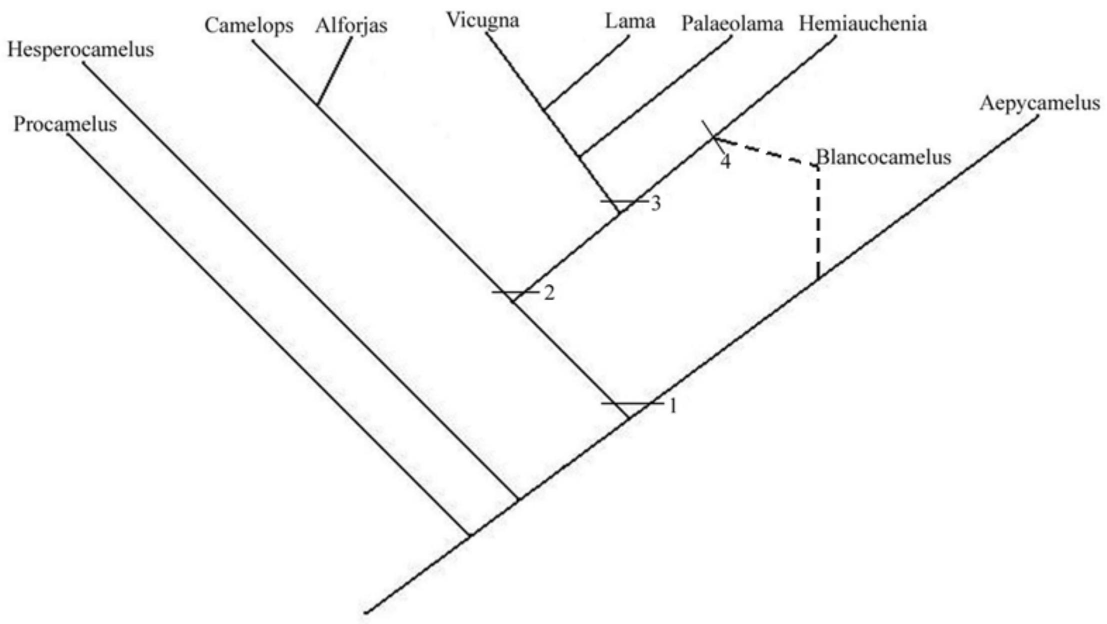


Figure 1: A modern phylogeny of the Camelinae, adapted from Honey et al. 1998. Numbered slash marks indicate synapomorphies of the clade above.

1.) LAMINI: arched nasals.
2.) I1-2 lost; P2/p2 lost; anteroexternal style present on lower molars.
3.) Small P1/p1; p3 small or absent; reduced lacrimal vacuity; shortened rostrum.
4.) HEMIAUCHENIA: extremely elongate metapodials, neck.

Hemiauchenia vera can be distinguished from other members of the *Hemiauchenia* genus by relatively brachydont (low-crowned) teeth, a large caniniform upper P1, and the retention of the lower p3. This species was found in the Hemphillian North American Land Mammal Age (Dalquest 1992). *Hemiauchenia blancoensis* is characterized by a shorter mandibular diastema than in *H. macrocephala*, but longer than *H. vera*; Caniniform upper P1, absent upper P2, upper P3 present or absent, and lower crowned molars than *H. macrocephala* (Breyer 1977). *Hemiauchenia blancoensis* is known from the late Blancan (2.5 to 2.0 MA)(Morgan and Hulbert 1995). *Hemiauchenia macrocephala* is the *Hemiauchenia* species that has been found at the widest range of fossil sites in Florida, and throughout North America. It occurs at localities that range in age from the late Blancan through the late Rancholabrean, 2.5 MA to 10 KA; (Morgan and Hulbert 1995; Webb and Stehli 1995).

H. macrocephala is characterized by long, robust limbs, large skeletal size, presence of a deciduous upper P2, a fully molariform deciduous upper P3, hypsodont (high-crowned) molars (hypsodonty index of 1.4 to 2.2), a thick layer of cementum on the teeth and a broad mandibular symphysis with incisors oriented in a vertical fashion, reminiscent of the lower incisors of a horse (Hallman and Meachen in review). It overlaps in time span and locality ranges in Florida with both *H. blancoensis*, in the late Blancan and a new species of lamine in the late Blancan to early Irvingtonian (Morgan and Hulbert 1995; Webb and Stehli 1995).

A New Species

In 1974 S. David Webb and other paleontologists from the Florida Museum of Natural History (FLMNH), then the Florida State Museum, discovered a gracile llama that was originally thought to be *Hemiauchenia macrocephala*. It was discovered at the Inglis 1A fossil site in Citrus County, Florida (Webb 1974). Upon further inspection and comparison of this material with known *H. macrocephala* material stored in the UF vertebrate paleontology collection, Florida museum paleontologists decided that this was not *H. macrocephala*, but a new species altogether. In the 1980s and 1990s, volunteers Steve and Suzan Hutchens and Reed and Barbara Toomey discovered more of this new llama material from the De Soto Shell Pit fossil locality in De Soto County, Florida, which they donated to the FLMNH vertebrate paleontology collection (Ruez 2001). The similarity of the fossils from these two sites as well as the same approximate age of the fossil localities, indicate the existence of a new llama species in the Plio-Pleistocene of Florida.

CHAPTER 2
MATERIALS AND METHODS

For the description of this new species, I conducted a thorough morphological analysis of the crania and postcrania, which I then compared to the morphology of *Hemiauchenia macrocephala, Palaeolama mirifica, "Hemiauchenia" minima*, and extant lamines, *Lama* and *Vicugna*. I also compared it to a lesser-known lamine species, *Hemiauchenia edensis* (Webb et al. in press). These comparisons formed the basis for two different series of interpretations, one systematic and the other ecological. The first purpose was to determine how this sample differed from other lamine samples and how its characteristics placed it in a phylogeny with other lamine clades. The second purpose of this comparison was to better understand the relationship between form and function in this and other lamines. The Anatomy of the Dromedary (Smuts and Bezuidenhout 1987) provided an authoritative basis for many of the descriptive features used in the comparisons. All structures in this new lamine were recognized as homologous structures in the dromedary camel. A Guide to the Measurement of Animal Bones from Archaeological Sites (Von den Dreisch 1976) was used to guide the postcranial measurements taken for this study.

This study did not concentrate only on the cranial material of this new species because of the small amount of cranial and dental material recovered from the two fossil localities in which this species is found. A large quantity of postcranial material was also incorporated to describe this new animal (Table 1).

All fossil specimens in this study are currently housed in the Florida Museum of Natural History Vertebrate Paleontology collection unless otherwise specified. All extant specimens are housed in the Florida Museum of Natural History Environmental Archaeology collections. The Florida Museum of Natural History specimens are designated with the prefix UF.

Cranial, dental, tarsal, carpal, and phalanx measurements were taken with digital calipers to the nearest 0.1 mm, as were the measurements of the widths and ends of the long bones. All other measurements were taken with manual sliding calipers to the nearest millimeter. The abbreviation "*M.*" denotes *Musculus*, for a particular muscle, followed by the rest of the anatomical Latin name, for example: *M. anconeus*. Lower-case letters indicate lower teeth and upper-case letters indicate upper teeth. To supplement the Florida fossil material used in this study, material from the American Museum of Natural History's Frick collection (abbreviated F:AM) was also utilized.

Table 1: Specimens of the new species of *Hemiauchenia* by locality.

Skeletal Element	Inglis 1A (Citrus County)	De Soto Shell Pit (De Soto County)
Cranial and Dental Material	UF 45493 maxillary fragment with M1 and M2	UF 210707 mandibular fragment with p4-m3, right. UF 210714 maxillary fragment with P4 and M1, right. UF 210715 mandibular fragment with m3, left. UF 210716 maxillary fragment with DP3 and DP4, left. UF 210717 lower m3, right.

Humeri	UF 176915 distal end of humerus.	UF 210702 distal end of humerus, right.
Radio-ulnae	UF 8917 complete radio-ulna.	UF 179636 distal end of radio-ulna. UF 210701 reconstructed radio-ulna, both ends intact, but no visible contact, left.
Femora	UF 176925 partial distal femur. UF 45275 and 45276 proximal femora including majority of shaft, but no distal ends.	
Astragali	UF 210722 (Inglis 1F) complete astragalus, right. UF 10281 complete astragalus.	UF 210706 complete astragalus, left.
Calcanea		UF 210709, left and 210710, right.
Metapodials	UF 176935 complete metatarsal. UF 18230 unfused metacarpal. UF 18236 distal end of metapodial.	UF 210720 proximal end of metacarpal, right. UF 210711 proximal end of metacarpal, left. UF 210726 proximal metacarpal fragment, right.
Phalanges	UF 179639, 18237, and 179638 three proximal phalanges. UF 97203 (Inglis 1B?) proximal phalanx. UF 177024 distal phalanx.	UF 210704, 210708, 210712, and 210703 four complete proximal phalanges. UF 210705 medial phalanx.

I performed stable carbon isotope analysis on the tooth enamel of this new species to better estimate feeding strategy. I then incorporated previous studies of artiodactyl postcrania to assess habitat usage.

For stable carbon isotope analysis, I used the following procedure. Tooth enamel from the P_4 or M_2 was sampled for carbon isotopic composition following Feranec and MacFadden (2000). The teeth were prepared by cleaning the enamel. This entailed removal of the outermost layer of enamel and any other material that adhered to the enamel surface. An enamel layer was then removed with a carbide dental drill bit in a Foredom Drill at low RPM to minimize vibration. Isotope samples were removed under a binocular stereomicroscope by manually passing the drill bit along the length of the buccal crown until approximately 10 mg of powdered enamel was obtained.

To each tooth enamel sample, 1 ml of 30% H_2O_2 was added to remove organic compounds. The samples were sealed and agitated until the enamel dissolved. The samples were left in the H_2O_2 solution overnight. Samples were then centrifuged at 10,000 RPM for five minutes. Following centrifugation, the solvent was discarded and the samples rinsed with deionized water. The rinse entailed addition of 1 ml of deionized water, agitation, centrifugation for five minutes at 10,000 RPM, and finally removal of the solvent. The samples were rinsed three times. After the final rinse, 1 ml of 0.1 N acetic acid was added to each sample to remove carbonates. Samples were left overnight. After treatment with acetic acid, the samples were centrifuged and the acetic acid discarded. The samples were given three deionized water rinses and a final rinse with ethanol. Vials were left open overnight in order for the samples to dry.

For isotope analysis samples were shipped to the University of Michigan and analyzed in the mass spectrometer lab at Ann Arbor. The following procedure was followed: 20 μg of sample was placed within a capped vial with a septum. Samples were placed in an autosampler that analyzes carbon isotope composition with the addition of phosphoric acid. Isotope concentrations were measured on a Finnigan mass spectrometer with measurements listed in δ-notation relative to a standard (VPDB). A correction of –0.10 ‰ was applied to the carbon results based on carbon isotope values of an internal UF standard (MEme, an *Elephas* molar) relative to VPDB (Hallman and Meachen in review).

CHAPTER 3
SYSTEMATIC SPECIES DESCRIPTION

Age and Occurrence

The two sites in which this new species occurs are Inglis 1A and the DeSoto Shell Pits, both on the west coast of south-central Florida (Figure 2). The Inglis 1A site is a sinkhole deposit with excellent fossilization. The site is approximately five meters below present sea level, but lacks any marine fossils, therefore it would seem that this deposition occurred at a time of low sea level (Morgan and Hulbert 1995). Larger animals may have fallen or climbed into the sinkhole and starved to death. The faunal assemblage indicates a more arid and open habitat than is present today in Citrus County. Large grazers dominated the savanna habitat of Inglis 1A. This fauna includes both the new Florida llama species and *Hemiauchenia macrocephala*. The nearby Inglis 1C site had a wetter, forested habitat with large numbers of browsers including the lamine species, *Hemiauchenia macrocephala* and *Palaeolama mirifica* with no evidence of the new llama species (Emslie 1998; Ruez 2001).

Inglis 1A was an important site because of its unique biochronologic and geographic position. The time that the site was deposited coincides with the acme of the Great American faunal interchange as well as a surge in native faunal diversity, and it lies along the broad subtropical Gulf Coastal Corridor. As a result, this site contains many fossils that give us clues into the Plio-Pleistocene faunal history of Florida as well as the faunal exchange with South America (Ruez 2001; Webb 1976). The presence of Blancan fauna and the absence of *Mammuthus* at Inglis 1A place it in the latest Blancan mammal age with a date of approximately 2.0-1.6 MA (Bell et al. in press; Morgan and Hulbert 1995).

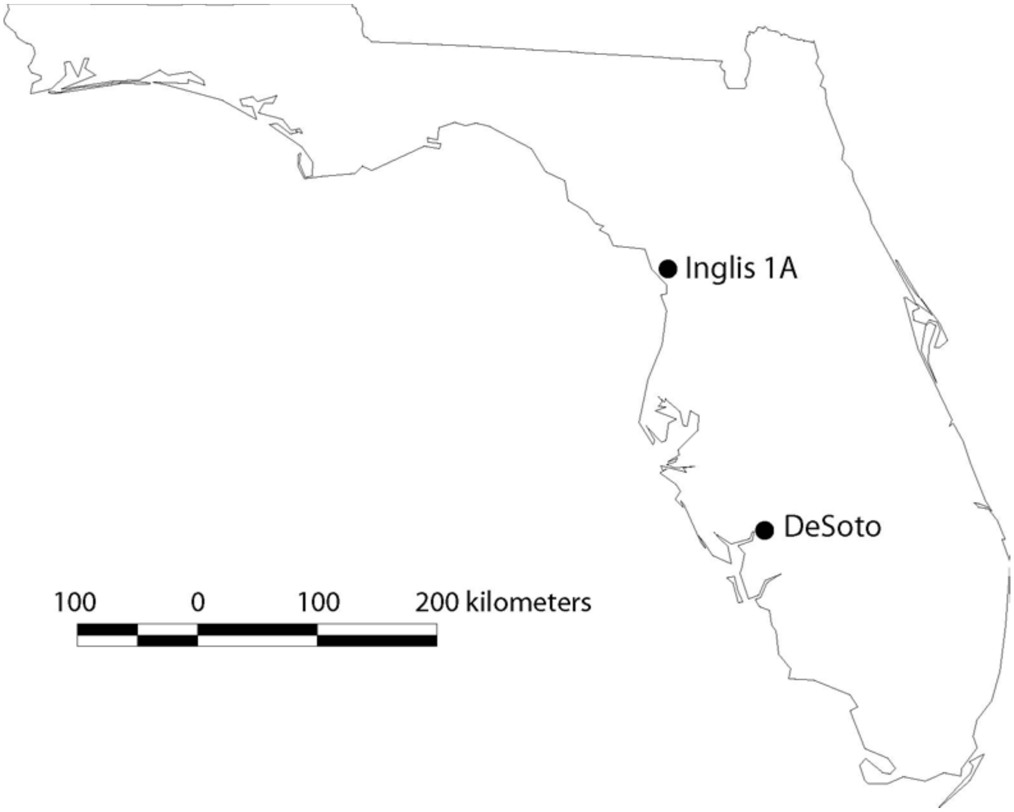


Figure 2: Map of Florida fossil sites where the new lamine species has been found.

The DeSoto local fauna is the designation for the vertebrate fauna from the organic layers in the Caloosahatchee Formation, which is exposed in three commercial shell mines in DeSoto County, Florida (Morgan and Hulbert 1995). The DeSoto site shares the late Blancan and early Irvingtonian type of fauna that Inglis 1A has and also lacks *Mammuthus*. However, at Inglis 1A the deposition occurred below present-day sea level, possibly during a glacial event, whereas DeSoto was deposited five to ten meters above present sea level in an interglacial period. Corals that were collected from the Caloosahatchee Formation gave Helium/Uranium dates of approximately 1.89 to 1.73 MA (Bender 1973; Morgan and Hulbert 1995).

Comparisons from the American Museum of Natural History

One important question is whether the new species from Florida is also represented in other undescribed samples of Plio-Pleistocene lamines. Only one specimen was found in the Frick American Museum collection that could possibly belong to the new species, an uncataloged astragalus from the Collins, Texas area, Blancan in age. Approximately the same size as the new species, it was 39.1 mm long and 24.7 mm wide.

Recently a single proximal phalanx was found at the 111 Ranch locality in Arizona that appears to be the new species. This fossil locality is Blancan in age at approximately 2 MA.

Several mandibles and astragali from the Panaca fossil site in Nevada showed similarity in the teeth, mandibles and metapodials. These specimens were slightly smaller than the new species, and they also differed by being Hemphillian in age.

There were several of these Hemphillian specimens from different locations along the southern/southwestern U.S. border in the Frick collection that were slightly smaller in size than the new species. Still other specimens of similar character are also found in Florida at the Bone Valley fossil site. They are all Hemphillian in age (approx. 5-7 MA) and seem to represent a small lamine originally named *Procamelus edensis* (Frick 1921) from the Mt. Eden fauna of southern California. Frick describes it as having lost the lower p2 and having a reduced lower p3. He describes the tooth crowns as fairly short and broad, and mentions the presence of the "camelid buttresses" (Frick 1921), a diagnostic dental character of lamines. According to Webb et al. (in press) this lamine is referable to *Hemiauchenia*, and not to *Procamelus*. They describe the lower molars as "…transversely compressed with angular lingual crescents, strong 'llama buttresses' and substantial midlingual stylids." They also mention that the enamel is mildly crenulated and lacks cementum (Webb et al. in press). This species from the Panaca site is also mentioned in more detail in Macdonald and Pelletier (1965).

Systematic Paleontology

Class Mammalia, Linnaeus 1758
Order Artiodactyla, Owen 1848
Suborder Tylopoda, Illiger 1811
Family Camelidae, Gray 1821
Subfamily Camelinae, Gray 1821
Tribe Lamini, Webb 1965
Genus *Hemiauchenia*, H. Gervais and Ameghino 1880

Holotype: UF 210707, Right mandibular fragment including p4, m1, m2 and m3 from De Soto Shell Pit in De Soto County, Florida.

Referred material: See Table 1 for a complete listing of all dental and postcranial specimens.

Diagnosis: This new lamine shares many homologous character states with *Hemiauchenia macrocephala* and a lesser-known species *Hemiauchenia edensis*.

However, the new lamine has postcrania that are always more slender than those of *H. macrocephala*. In some cases the postcrania are more elongate, in some cases, shorter. The postcrania of the new species are always longer and usually more robust than that of *H. edensis*. It also has some unique dental features, such as the lack of a p3. This new species is placed in the genus *Hemiauchenia* based on several morphological characters: The length and gracility of the postcranial skeleton, the shape and form of the teeth and the striking resemblance that this new species shares with *H. macrocephala* and *H. edensis*. Evidence for this generic assignment will be given in the description below. Only one speculative character of this new species is troubling with regard to the genus assignment, the possible lack of a p1. According to Honey et al. (1998), a character of the genus *Hemiauchenia* is that it possesses a p1. Since the evidence for the loss of this character in the new species is speculative at best, it will not be given much weight in this analysis. Also, it is possible, if this new species does truly lack a p1, that it still was most closely related to a *Hemiauchenia* species and should be assigned to that genus, despite the currently accepted genus description.

Dentition: (Table 2). No incisors, canines, first or second premolars have yet been found for the new species. The holotype for the new species is an incomplete right mandible with p4-m3 (Figure 3). The length of the diastema in the holotype is 39.2 mm. This specimen lacks a p3, and has no remnant of one. The lack or reduction of a p3 is a diagnostic feature of the genera *Lama* and *Vicugna* and a variable feature for the genera *Hemiauchenia* and *Palaeolama* (Honey et al. 1998). This feature is interesting because the lack of a p3 is a late Blancan character. The *Hemiauchenia* and *Palaeolama* individuals from the Irvingtonian seem to posses the p3 more often than not.

Table 2: Measurements of the new species' dentition in mm.

Catalog number	Tooth orientation	Length (anterior-posterior)	Width (lingually-labially)	Crown height
UF 210714	P4	13.8	10.9	14.5
UF 45493	M1	17.8	12.7	7.1
UF 210716	M1	21.8	14.3	11.4
UF 210714	DP3	21.5	16.2	11.0
UF 210716	DP4	22.6	15.4	12.8
UF 45493	M2	22.2	15.7	19.5
UF 210707	m1	13.9	9.9	Too worn
UF 210707	m2	19.9	12.1	8.4
UF 210707	m3	29.4	11.7	10.9
UF 210715	m3	26.5	11.8	8.9
UF 210717	m3	28.2	11.1	27.2

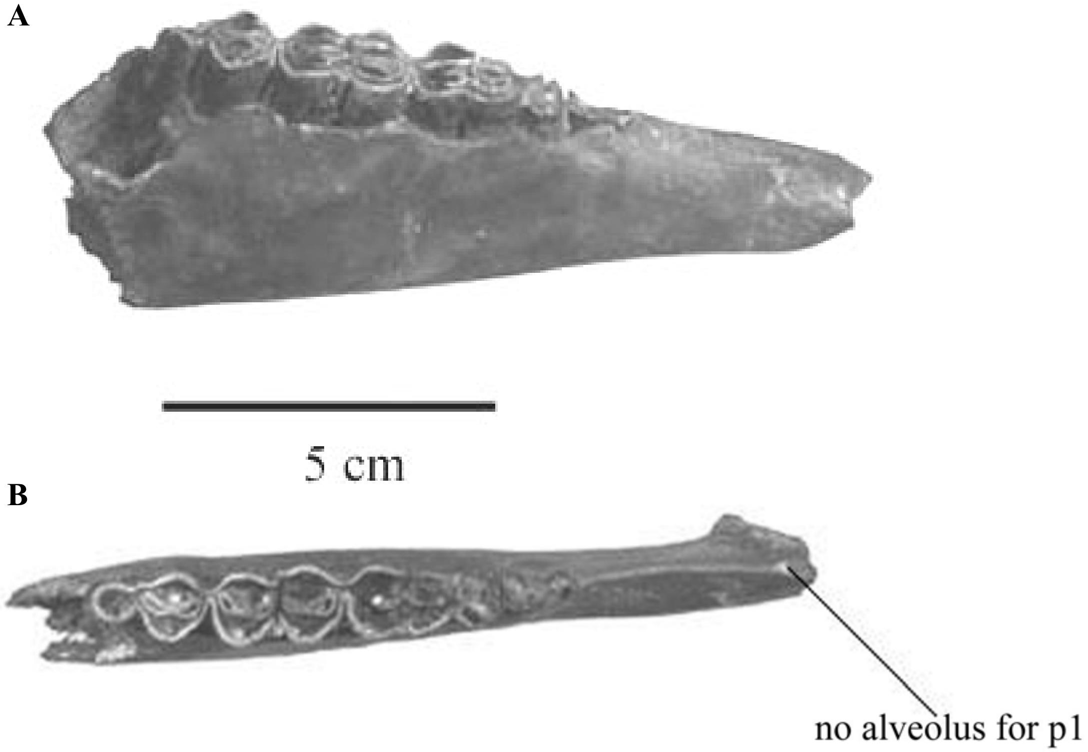


Figure 3: New *Hemiauchenia* species holotype, right mandible with p4-m3, UF 210707 from DeSoto Shell Pits, A. labial view, B. occlusal view.

Breyer's (1977) study on the interspecific jaw variation in *Hemiauchenia blancoensis* from the late Blancan Broadwater fossil locality in Morrill County, Nebraska, found that fewer than one in ten adults had a lower p3, or evidence of one. Juveniles possessed the Dp3 in most cases and after it was shed, the alveolus closed up leaving no trace that a Dp3 was ever present.

Webb and Stehli found, in their 1995 study on *Hemiauchenia macrocephala* and *Palaeolama mirifica,* from the Irvingtonian aged Leisey Shell Pits in Hillsborough County, Florida, that over half of the adult individuals possessed p3s. The Leisey Shell Pit fauna is slightly younger than the Broadwater fauna, Inglis 1A fauna or DeSoto Shell Pit fauna (Webb and Stehli 1995). The age of the Leisey fauna is early Irvingtonian, approximately 1.4-1.7 MA, from paleomagnetic dating of shells located within the vertebrate fossil layer (MacFadden 1995). Therefore, it seems likely that the new species possessed a deciduous p3, but when it was shed the alveolus closed, leaving no trace it was ever present, much like the Blancan species *Hemiauchenia blancoensis*. This presumption can be tested when juvenile mandibles of this new species are recovered. This new species is distinguishable from *H. edensis* in this regard, because *H. edensis* seems to always possess a small p3 with two nearly fused roots (Webb at al. in press).

Although it is difficult to discern with certainty, it appears that the new species also lacked a p1. On the holotype, the mandible is broken in half at the point where the two halves of the mandibular symphysis meet. Therefore, it can be determined whether this animal had an alveolus for the p1 where the two bones of the symphysis met. The new species evidently lacks this alveolus, arguing for an absent p1. Absence of the p1 is a character of the genera *Palaeolama*, *Lama* and *Vicugna.* In all previous studies

Hemiauchenia has been thought to possess the p1 (Honey et al. 1998). In this respect the new species differs from all other known *Hemiauchenia* species. However, larger samples may show that this feature of the type specimen is variable. At most it is a minor loss and it should not hold much weight in the decision about where in the lamine phylogeny to place this animal.

The mandible of this new species is deeper and more robust than the mandible of *H. edensis*. *H. edensis* has a very shallow mandible with an average width at the posterior end of the m3 of approximately 34 mm. This measurement is compared with 43 mm in the new species. The dental arcade is also comparably shorter in *H. edensis*, with an average length of approximately 72 mm, including the p3, compared to 75 mm in the new species without a p3.

The deciduous teeth, DP3 and DP4 are very molariform (Figure 4), and upon first examination, were thought to be M1 and M2. The DP3 presents the trilobate quality of artiodactyl deciduous premolars, but not very strongly. It almost appears to be a deformation of an M1. The DP4 is bilobate (molariform) and resembles an M2. However, these teeth do show the diagnostic root splay of deciduous premolars.

The P4 has a distinctly rounded and laterally flattened shape with an open "U-shaped" hollow crescent (Figure 5). In my observations, this "U-shaped" crescent is diagnostic of the genus *Hemiauchenia*. The genus *Palaeolama* has sharply pointed lophs with "V-shaped" crescents. The P4 appears to have little wear, and is in excellent condition. The P4 in *H. edensis* is considerably smaller with a maximum length of 11.6 mm and a maximum width of 9.3 mm. The P4 of the new species retains a rounded appearance from labial to lingual sides, whereas the P4 of *H. edensis* tapers toward the lingual side, forming a V-shaped premolar.

The molars of the new species are less robust in appearance than the molars of either *H. macrocephala* or *Palaeolama*. The enamel of the new species is thin, but the molars are coated in a complete layer of cementum in all specimens, much like the molars of *H. macrocephala*. By contrast, *Palaeolama* and *H. edensis* only have a thin patchy coating of cementum. The teeth of the new species show little crenulation. This small degree of crenulation is also indicative of *Hemiauchenia macrocephala*. The teeth of *Palaeolama* show comparatively more crenulation than is present in *Hemiauchenia*. Crenulation of the teeth is generally a browsing adaptation (Webb and Stehli 1995).

In the new species the M1 is shorter and smaller than that in *H. macrocephala*, as is the m3 (Figure 6). However, it maintains the same shape. Again the “U” shape of the hollow crescents is conserved. The shape of the tooth crown, although less hypsodont, also maintains the same pattern. The ribs of the molars (or the parastyle, mesostyle, and metastyle) are close in height to the cusps of the crescents as in *H. macrocephala.* I will discuss the functional significance of this concept in the next section. In *Palaeolama*, by contrast, the ribs appear to be considerably shorter than the cusps. In the new species, the anterior and posterior labial crescents are raised, but not sharply so, and the anterior and posterior lingual crescents are close in height to the former two structures. This contrasts strikingly with the condition in *Palaeolama* in which the anterior and posterior labial crescents are sharply pointed and form high peaks on the upper molars and there is a considerable size discrepancy in the heights of the lingual and labial crescents.

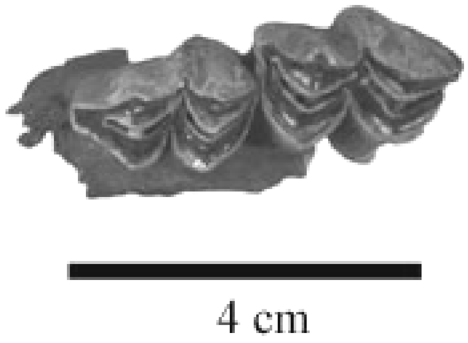


Figure 4: Maxillary fragment of new species with deciduous P3 and P4, UF 210716, occlusal view.

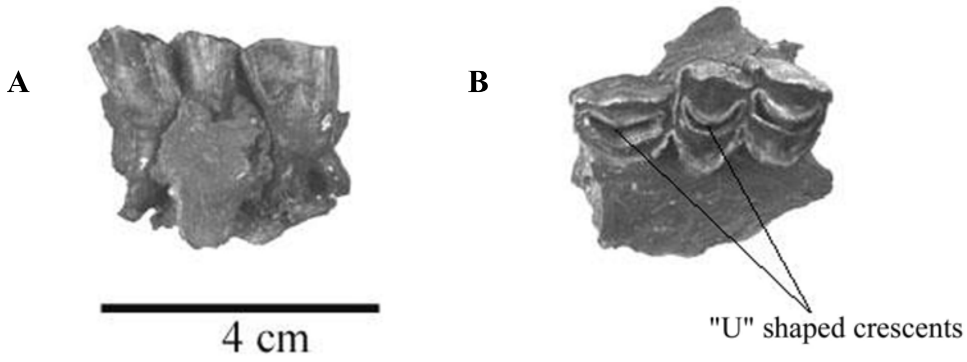
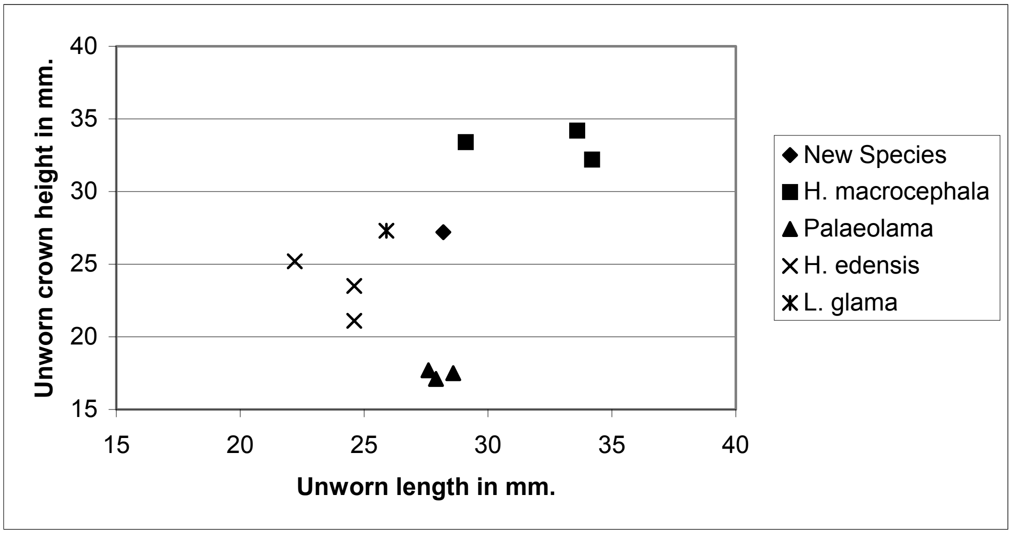


Figure 5: Maxillary fragment of the new species with P4 and M1, UF 210714, A. labial view, B. occlusal view.

The M2 of the new species has a very similar appearance to the M1, except that it is slightly larger and more robust.

The lower dentition of the new species is much more transversely compressed than that of either *H. macrocephala* or *Palaeolama*, but less so than that of *H. edensis*. On the lower m3 (Figures 7 and 8), the anterior enamel folds on the molars, referred to as “llama buttresses” are very prominent in the new species, which helps it sustain a great deal of interdental wear in an anterio-posterior direction. In *H. edensis* the m3 is not only smaller, but the "llama buttresses" are also less robust and have a posteriorly curved orientation, as opposed to the vertically oriented buttresses of the new species (Figure 9). The crown height in the unworn m3 suggests that the new species may have incorporated some grass into its diet, but not as much as *H. macrocephala* (Figure 10). The posterolophid on the m3 is rather robust in this species, and has a completely longitudinal orientation when compared with other lamine teeth, which have a more transversely curved orientation.



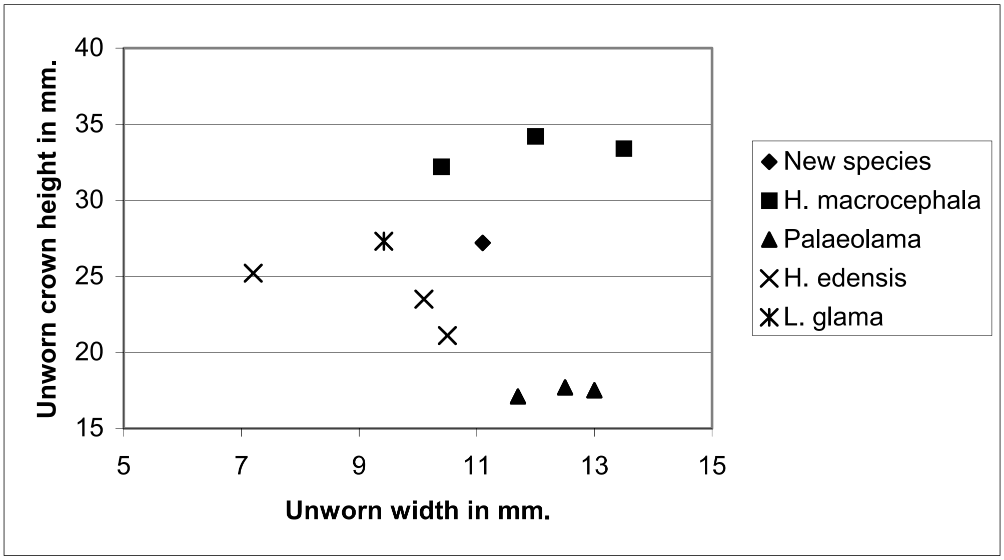


Figure 6: Lower m3 measurements for five lamine species in mm, plotting unworn crown heights against unworn anterio-posterior lengths and unworn widths lingually-labially.

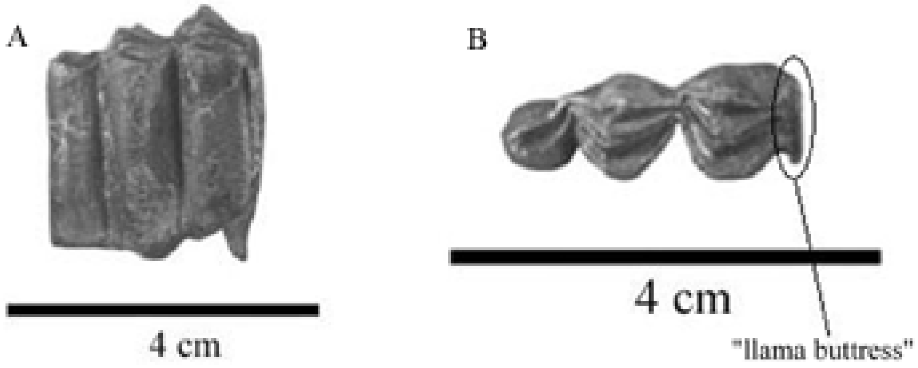


Figure 7: Lower right m3 of new species, UF 210717, A. labial view, B. occlusal view

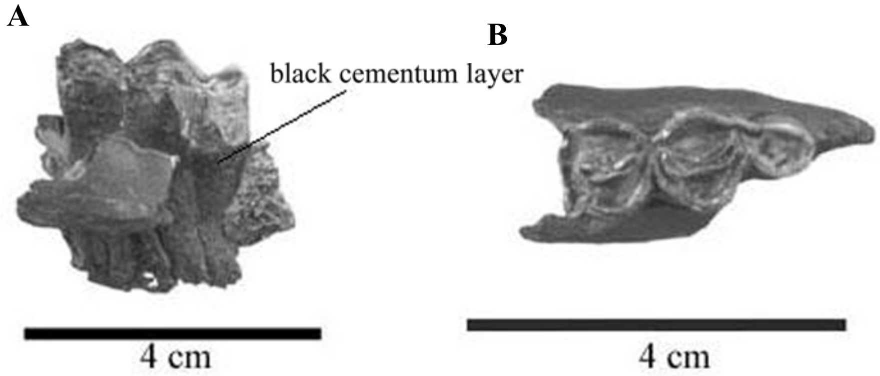


Figure 8: Lower left m3 with mandibular fragment of new species, UF 210715, A. labial view, B. occlusal view

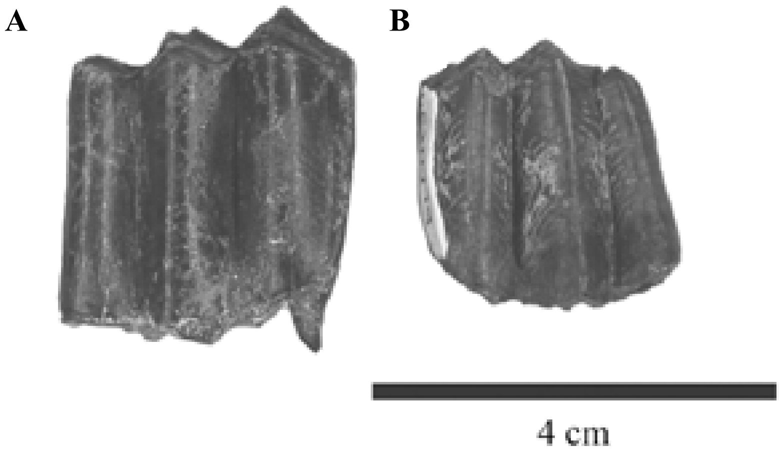


Figure 9: Lower m3s of A. new *Hemiauchenia* species (right) and B. *Hemiauchenia edensis* (left) for comparison.

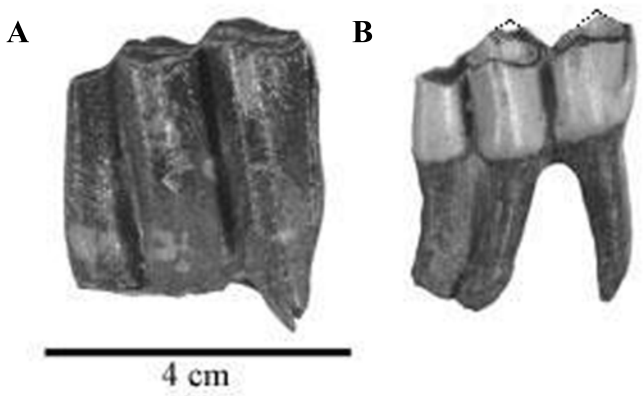


Figure 10: A. *Hemiauchenia macrocephala* and B. *Palaeolama mirifica* m3s for comparison, labial view. Note the cementum layer and crown height on the *H. macrocephala* tooth, and the cusp reliefs (mesostyle to cusp) and cusp tip shape on both, *Palaeolama* cusps are slightly broken, dotted lines indicated original relief.

Postcranial: There was a great deal of material found representing the postcranial skeleton of the new species. The long, slender nature of the limb bones is the most striking feature of this new species.

Only two distal ends of the humerus were recovered for the new species (Table 3 and Figures 11 and 12). The size of the humerus differentiates it from both *H. macrocephala* and *Palaeolama* (Figure 13). These distal humeri were approximately one-half the depth and two-thirds the width of the latter two species.

Table 3: Measurements of the new species' humeri in mm.

Catalog number	Breadth of distal end (BD)
UF 176915	36.8
UF 210702	40.9

The dimensions of the humeri of the new species were almost identical to those of extant lamines and *H. edensis*. The humeri of the new species were slightly more robust then either of the other species, especially in the olecranon fossa, the fossa radialis, and the thickness of the humeral shaft. There also appears to be more surface area for the attachment of the *M. flexor carpi ulnaris, M. flexor digitorum profundus, M. extensor digitorum lateralis,* and *M. extensor digitorum communis*. With regards to *H. edensis*, the epicondylus lateralis and the epicondylus medialis were both more flattened and robust in the new species. The humeri of the new species were much less robust than those of either *H. macrocephala* or *Palaeolama*.

The radio-ulna is the most complete postcranial element for the new species, and also seems to be the most diagnostic postcranial element for this species (Table 4 and Figures 14 and 15).

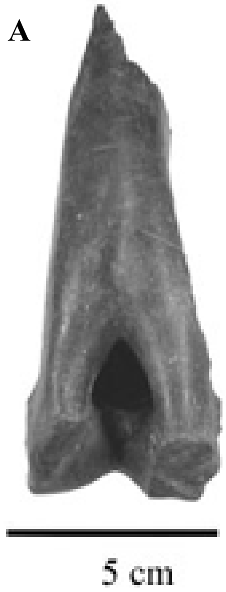


Figure 11: Distal humeri from new *Hemiauchenia* species, A. UF 210702, B. UF 176915, posterior view

Figure 12: Distal humeri of the new species, A. UF 210702, B. UF 176915, anterior view.

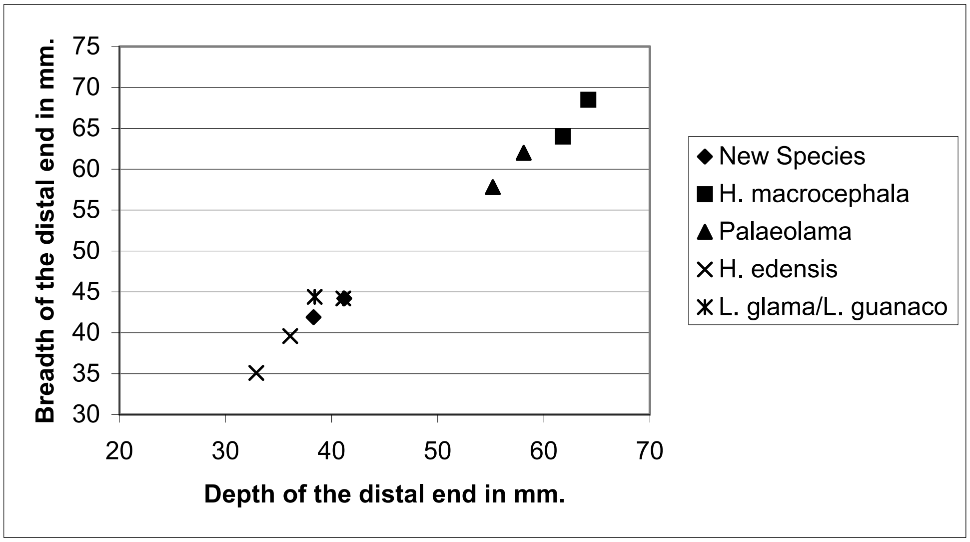


Figure 13: Comparison of the breadth of the distal end against the depth of the distal end of the humerus in several species of lamines. Only distal ends were compared because that was the only available complete measurement for the new species.

Table 4: Measurements of the new species' radio-ulnae in mm.

Catalog number	Greatest Length (GL)	Length of Olecranon (LO)	Smallest depth of olecranon (SDO)	Depth across the Processus Anconaeus (DPA)	Smallest diameter of the diaphysis (SD)	Depth of distal end (DD)	Breadth of distal end (BD)
UF 210701	No contact	64.5	38.5	48.4	27.4	38.9	44.8
UF 8917	472	64.5	40.3	50.7	31.5	42.2	49.8
UF 179636	N/A	N/A	N/A	N/A	N/A	35.9	41.4

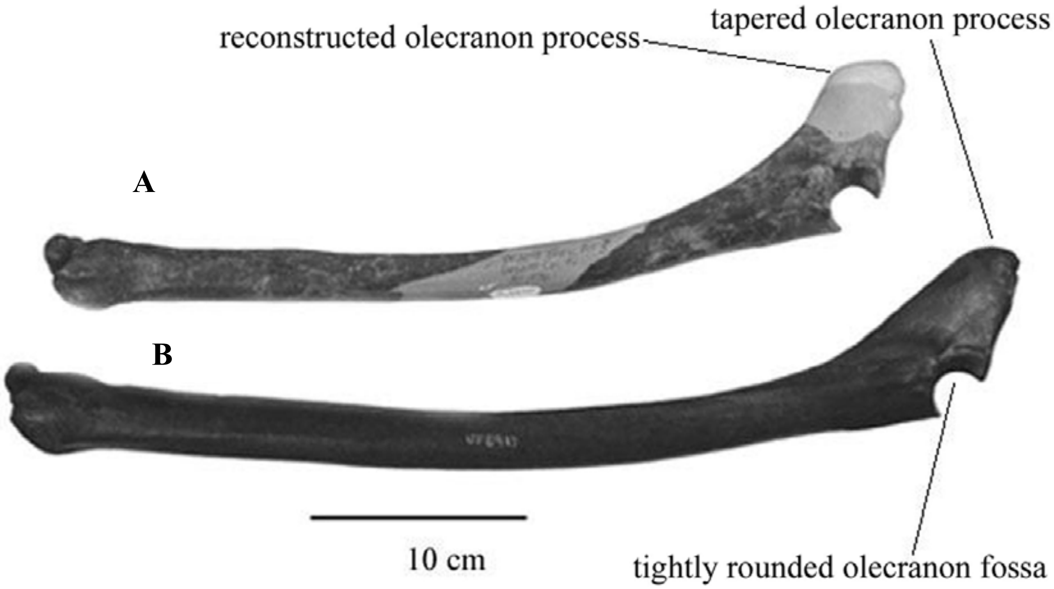


Figure 14: Radio-ulnae of new *Hemiauchenia* species, A. UF 210701, B. UF 8917, lateral view.

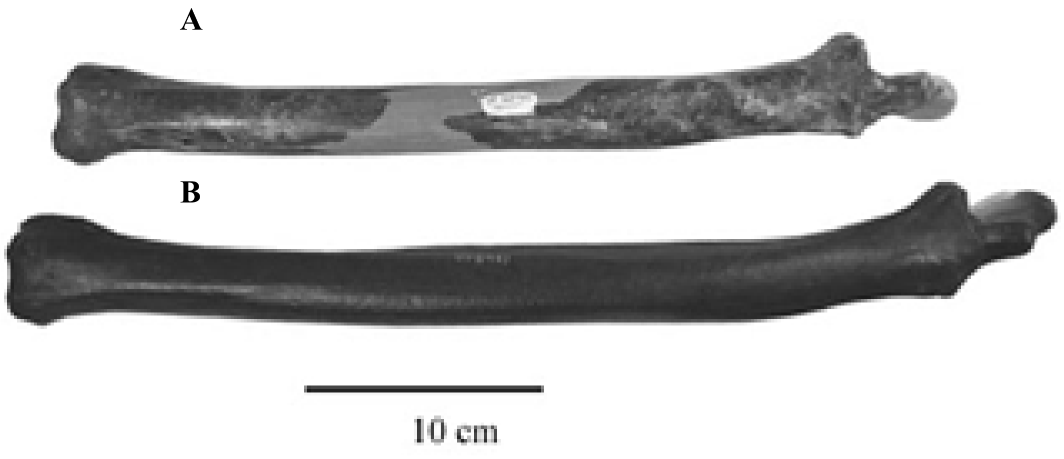


Figure 15: Radio-ulnae of the new species, A. UF 210701, B. UF 8917, anterior view.

The most striking feature of the radio-ulna of the new species is the length. It is about 1.2 times longer than the radio-ulnae of *H. macrocephala* and 1.3 times longer than that of *Palaeolama* (Figure 16). Out of the two radio-ulna specimens that were available, only one has a usable length. One has been restored, and there is no visible point of contact to validate the length as accurate. However, the overall shape of the specimens are identical and there is no doubt that they belong to the same species.

The radio-ulna is long and slender with small proximal ends and a short olecranon process with a tapered appearance. The trochlear incisure of the radio-ulna where it articulates with the humerus is more tightly curved and neatly rounded in the new species than in any other lamine specimen avaliable for analysis. This feature distinguished the radio-ulna of this species from other possible species matches in the Frick collection at the American Museum of Natural History.

In *Hemiauchenia* the shaft of the radio-ulna remains thin and functionally uniform all the way down to the styloideus process where the radio-ulnae has an abrupt thickening to facilitate articulation with the carpals. The new species displays this pattern. In *Palaeolama*, the distal end of the radio-ulnar shaft gradually thickens toward the medial styloid process, and produces a very robust appearance in the distal half of the radio-ulna.

The radio-ulna of the new species can be distinguished from *H. edensis* by size. There were no whole bone specimens of *H. edensis* to compare lengths. However, the smallest width of the radio-ulnar shaft in *H. edensis* was 22 mm, and the breadth of the distal end was only 32.4 mm (compare to the new species measurements in Table 4).

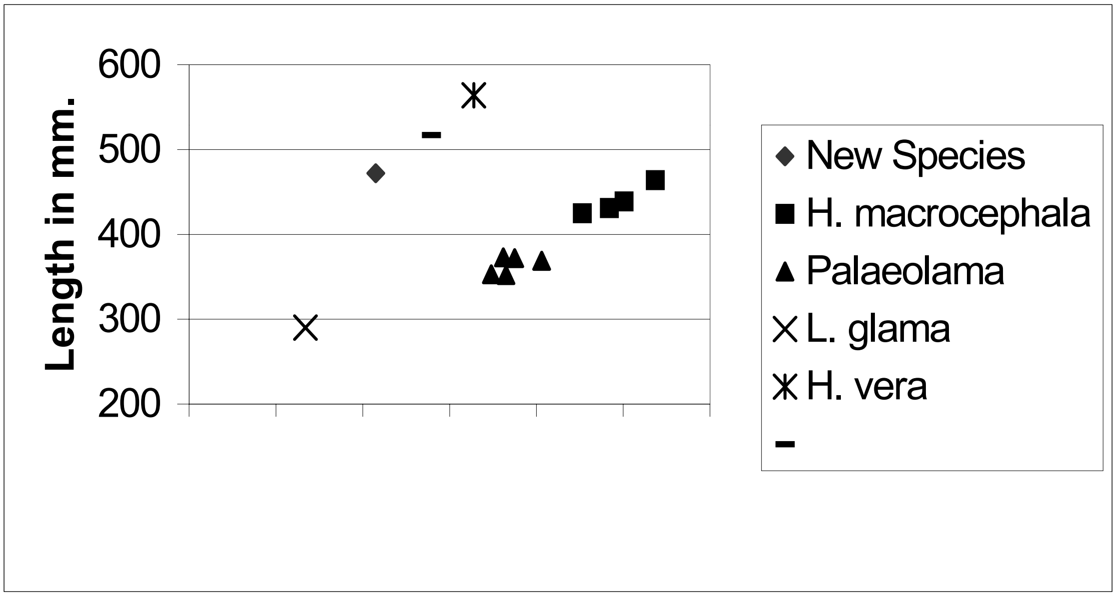


Figure 16: Comparison of lengths and widths of radio-ulnae in six species of lamines. *H. vera* and *H. blancoensis* specimens are from the F:AM. No complete radio-ulna specimens were available from *H. edensis*.

In the new species there is limited area for attachment of the *M. triceps brachii* and *M. anconeus*. In both *H. macrocephala* and *Palaeolama* there is a large surface area for the attachment of both these muscles. Since these muscles extend the elbow joint and flex the shoulder joint, this reduction would have given the new species a very gracile appearance in the leg and shoulder and may have compromised power for agility.

One very interesting character of the radio-ulna of the new species is the complete fusion of the ulna to the radius at the distal portion of the bone. In *H. macrocephala* and *Palaeolama* as well as extant lamines, there is a small aperture where the ulna has not completely fused to the radius. Neither of the two whole bone specimens of the new species show this aperture and a portion of the distal end of a third radio-ulna does not show it either. This complete fusion of the radius and ulna appears to be present in some earlier species of *Hemiauchenia*, such as *H. vera* and *H. blancoensis*. This complete fusion is present to a degree in *H. edensis* where a pin-sized aperture is present. The purpose of this complete fusion could possibly be an adaptation to cursory. The reduction of apertures in the bone could have strengthened the radio-ulna, making it more amenable to the impacts of cursorial activity. The radio-ulna from the De Soto site appears to articulate with the humerus from that same site.

The femora of the new species bear a striking resemblance to those of extant lamines (Table 5 and Figure 17). The diameter of the femoral shaft is only slightly greater than that of *Lama* (Figure 18). The distal and proximal ends are also highly comparable in size and shape. The length of the shaft of the new species is unknown because there are no complete femora available. A good estimate of length can be made from the proportions of the other elements of the skeleton and it is thought that the femora of the new species are considerably longer than those of *Lama*.

Table 5: Measurements of the new species' femora in mm.

Catalog number	Breadth of proximal end (BP)	Smallest circumference of the diaphysis (CD)	Smallest diameter of the diaphysis (SD)
UF 45275	67.0	28.8	23.8
UF 45276	66.8	30.3	23.2

The femur presents a very rugose lateral supracondylaris tuberosity, which appears to facilitate a large *M. flexor digitorum superficialis* and to some extent a large *M. adductor*. The trochanter major in the De Soto specimen is quite rugose, suggesting strong attachments for the *M. gluteus accessorius, M. gluteus profundus* and possibly the *M. vastus lateralis*. However, both *H. macrocephala* and *Palaeolama* show stronger *M. vastus lateralis* scars than does the new species. The fovea capitus is only a small notch in the middle of the caput femoris, this is a shared character state with *H. macrocephala*. In the extant lamines, the fovea capitus extends from the middle of the caput femoris to the suture of the epiphysis. *Palaeolama* shares this modern condition. The trochanter minor is well worn in both femur specimens, however it appears to have been sharply pointed in life. Although the new species has a number of pronounced rugosities where muscle attachments were present, the femora of both *H. macrocephala* and *Palaeolama* are more rugose overall. No femora of *H. edensis* were available for comparison. No tibia material was recovered for the new species.

The astragali (Table 6 and Figures 19 and 20) of the new species are significantly smaller than the astragali of *H. macrocephala* or *Palaeolama* (Figure 21). In fact, the astragali of the new species are approximately the same size as deer (*Odocoileus virginianus*) astragali (Table 6 and Figure 21), and are sometimes confused with the latter. However, there are a few very important features on the astragali of the new species that diagnose them as lamine. One feature is a very deep notch, on the plantar side that articulates with the cuboid and navicular bones. This notch is present in all other lamines, but not deer. This notch is possibly a locking mechanism in lamines, and most likely other camelids, that facilitates standing upright for extended periods of time. The flange on the medial surface of the astragalus is greatly reduced in the new species, allowing the navicular bone to reach the deep notch. The large concave facet located medially on the dorsal side of the astragalus also seems to help facilitate the locking mechanism in the lamine astragalus. The articular facets of the astragalus of the new species are well defined, but not as well as those of *H. macrocephala* or *Palaeolama*. The astragalus of this species is also less robust than either of the other two species. The astragali of the new species are indistinguishable from those of *H. edensis*.

Figure 17: Femora of new *Hemiauchenia* species, A. UF 45276, B. UF 45275, posterior view.

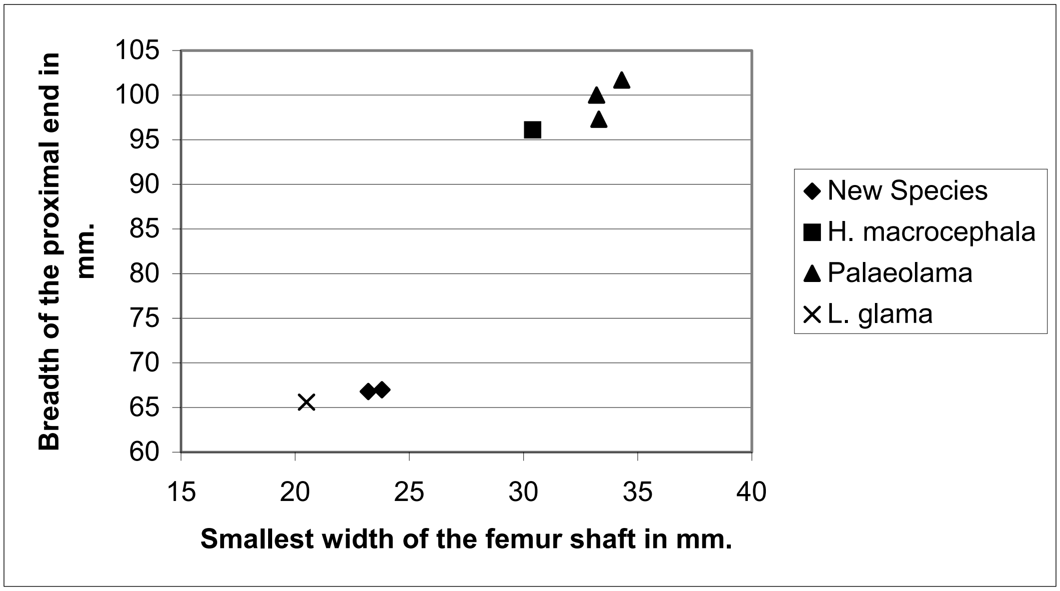


Figure 18: Comparison of breadth of the proximal end to minimum shaft width of femora in four lamine species. These measurements were chosen due to limited specimen availability in the new species.

Table 6: Measurements of the new species' astragali in mm.

Catalog number	Length of astragali	Width of astragali
UF 210722	38.0	24.1
UF 10281	40.4	25.4
UF 210706	38.6	24.3
Deer astragalus UF 210713	37.3	23.4

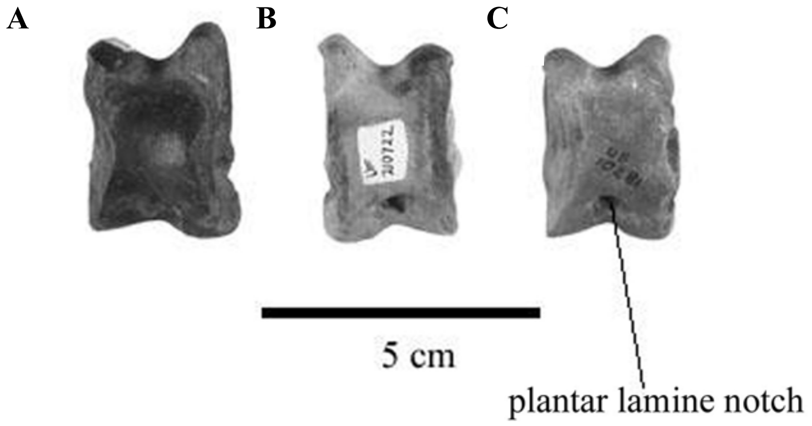


Figure 19: Astragali of new *Hemiauchenia* species, A. UF 210706, B. UF 210722, C. UF 10281, plantar view.

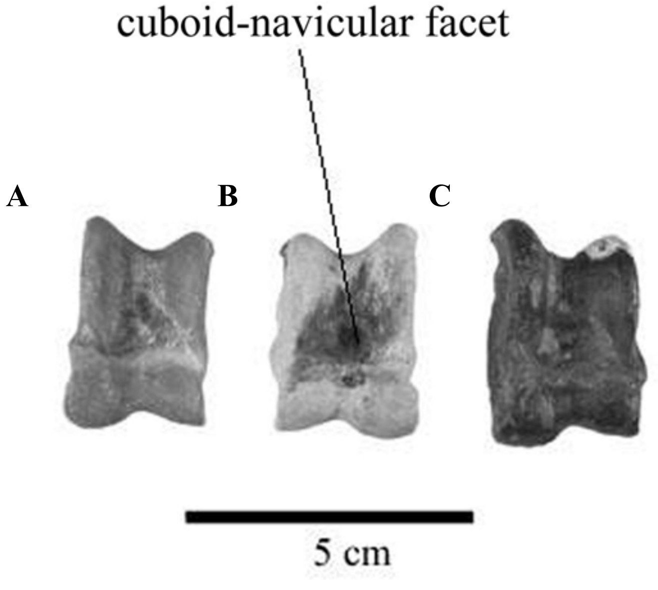


Figure 20: Astragali of new species, A. UF 10281, B. UF 210722, C. UF 210706, dorsal view.

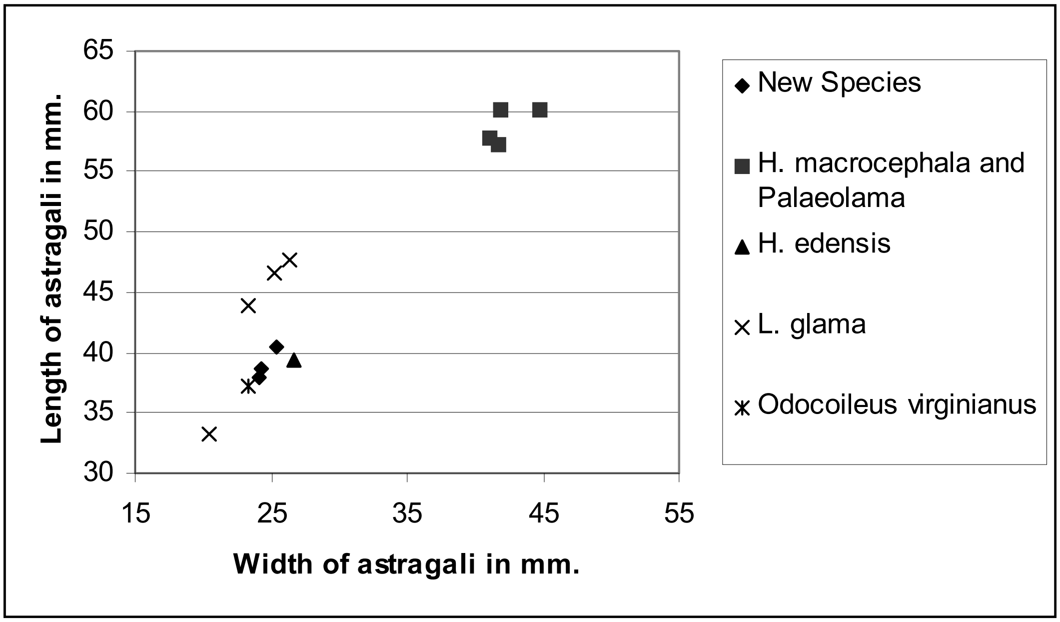


Figure 21: Size comparisons of the astragali of the new *Hemiauchenia* species to other lamine species and deer, *Odocoileus virginianus*. *H. macrocephala* and *Palaeolama* astragali are indistinguishable.

The calcanea (Table 7 and Figures 22 and 23) of the new species are smaller than other Florida lamine species. The proximal tuber and shaft are transversely narrower than in *H. macrocephala* or *Palaeolama*, and the tuber is noticeably more gracile in the new species. Articular facets on the calcaneum of the new species appear to mirror those on *H. macrocephala*, however, all the facets in the new species are less prominent. The new species has very similar calcanea to “*Hemiauchenia” minima* in gracility, however, they are considerably smaller overall than those of “*H.” minima*. Like the astragali, the calcanea of the new species are indistinguishable from those of *H. edensis*.

Table 7: Measurements of the new species' calcanea in mm.

Catalog number	Greatest length (GL)	Length across the Coracoid process	Length across the Sustentaculum tali
UF 210709	broken	26.8	39.8
UF 210710	89.2	27.8	37.2

One cuneiform and one unciform were recovered from the Inglis 1A site. However, these elements were so badly worn that there is little information to be gleaned from them besides their small size.

The most remarkable aspect of the metapodials is their gracility as is indicated in Figure 24 and Table 8. The metapodials of the new species were absolutely shorter than those of *H. macrocephala*, longer than those of *Palaeolama*, and had a smaller diameter than metapodials of either of the other species (Figure 25). The metapodials of the new species are longer than those of *H. edensis*, but approximately the same width, making the metapodials of the new species appear more gracile. This intermediate length and extremely narrow width are distinctive features of this new lamine.

Several proximal phalanges were found for the new species, as shown in Table 9 and Figure 26. These phalanges are characterized by being shorter and more gracile than the phalanges of *H. macrocephala*. The proximal phalanges have a triangular shaft shape with a wide posterior side and a tapering anterior side. They have the greatest length to width ratio (length/width ≈ 7.1, compared to 5.4 in *H. macrocephala*, 6.1 in *H. edensis* and 6.0 in extant lamines) out of all fossil Florida lamines and extant lamines, so the phalanges have a very gracile appearance. One medial phalanx and one distal phalanx were also recovered, they too, were smaller than either *H. macrocephala* or *Palaeolama*. The proximal phalanges of the new species have the W-shaped suspensory ligament scar that is diagnostic of the genus *Hemiauchenia* (Figure 26).

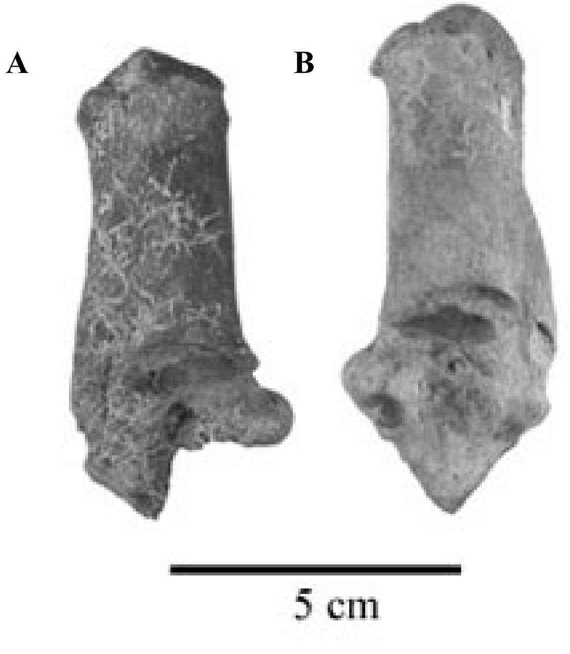


Figure 22: Calcanea of new *Hemiauchenia* species, A. UF 210709, B. UF 210710, medial view.

Figure 23: Calcanea of new species, A. UF 210710, B. UF 210709, anterior view.

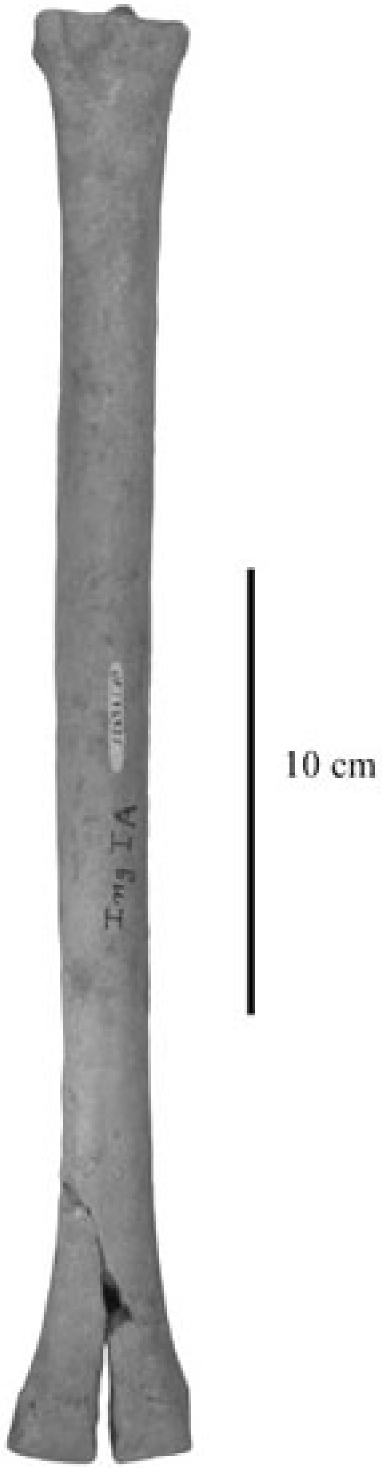


Figure 24: Metatarsal of new *Hemiauchenia* species, UF 176935, anterior view.

Table 8: Measurements of the new species' metapodials in mm.

Catalog number	Greatest length (GL)	Breadth of proximal end (BP)	Breadth of distal end (BD)	Smallest diameter of diaphysis (SD)
UF 176935	320	33.0	39.4	19.1
UF 18236	N/A	N/A	38.2	N/A
UF 210720	N/A	31.1	N/A	16.8
UF 210711	N/A	34.9	N/A	N/A
UF 210726	N/A	34.2	N/A	N/A

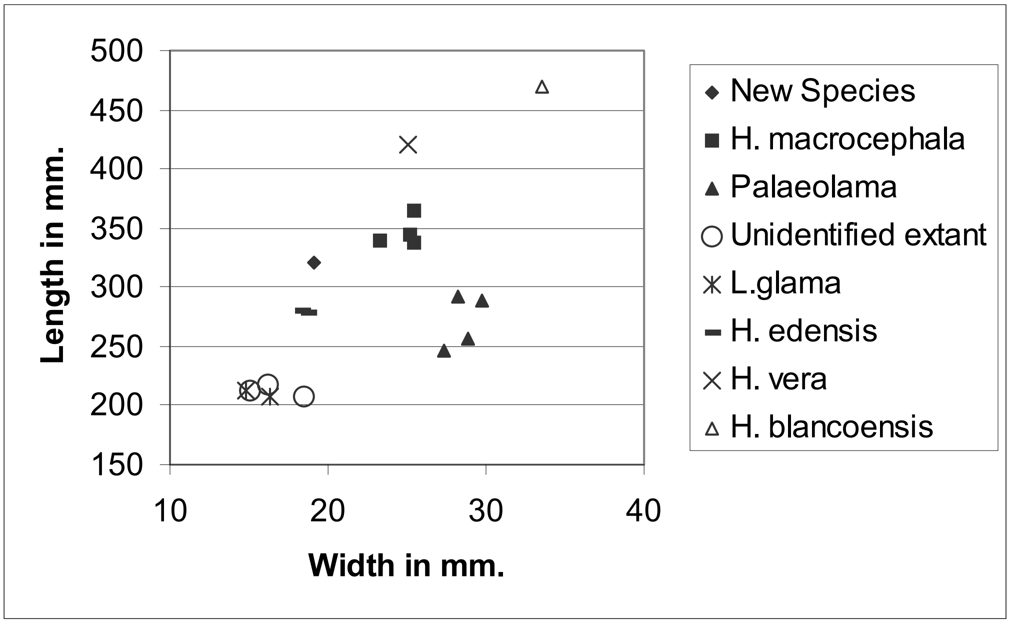


Figure 25: Comparison of metapodial lengths and widths in several species of lamines. *H. vera* and *H. blancoensis* specimens are from the F:AM. Unidentified extant lamines may be *L. glama* or *L. guanicoe*.

Table 9: Measurements of the new species' proximal phalanges in mm. See abbreviations from Table 8.

Catalog number	GL	BP	BD	SD
UF 97203	74.5	17.8	14.9	11.3
UF 179638	82.6	18.5	16.0	10.7
UF 179639	84.2	19.6	14.6	11.1
UF 18237	71.2	17.8	14.4	10.8
UF 210704	66.2	17.7	14.1	10.4
UF 210708	78.5	18.3	15.8	10.3
UF 210712	67.9	18.1	14.9	10.6
UF 210703	67.7	18.1	14.5	10.4

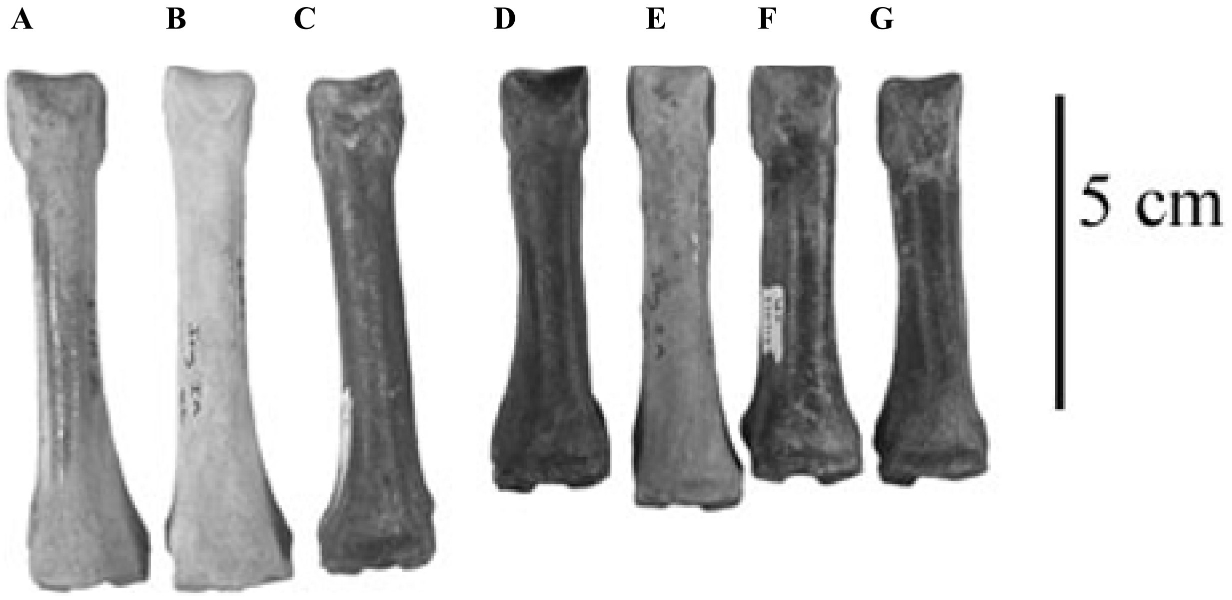


Figure 26: Proximal phalanges of new *Hemiauchenia* species, anterior view, A-C manus phalanges, D-G pes phalanges.
A. UF 179638, B. UF 179639, C. UF 210708, D. UF 210703, E. UF 18237, F. UF 210712, G. UF 210704

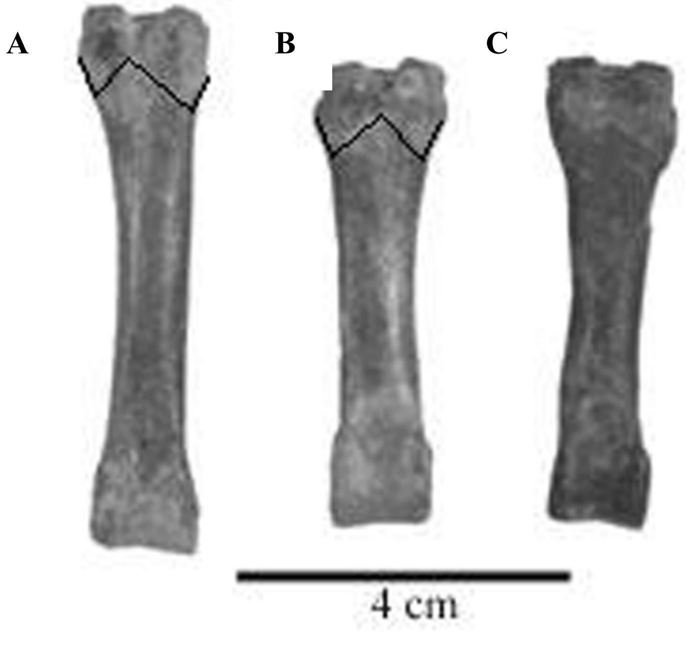


Figure 27: Proximal phalanges, posterior view highlighting the W-shaped suspensory ligament scar on phalanges A and B, All 6 proximal phalanges display this scar. A. UF 210708, B. UF 210712, C. UF 210703

CHAPTER 4
PALEOECOLOGY OF THE NEW SPECIES

The new species is found as a part of a rich mammalian fauna. At the same two Florida fossil localities lived other terrestrial mammalian species including a wide range of carnivorans: Canidae, Ursidae, Procyonidae, Mustelidae, Felidae and Hyaenidae; other mammalian orders including Xenarthra, Insectivora, Chiroptera, and Lagomorpha; at least three families of Rodentia: Castoridae, Geomyidae, Muridae; and many other ungulates including families: Equidae, Tapiridae, Tayassuidae, Cervidae, Antilocapridae, Bovidae, Mammutidae and other similar sized artiodactyls (see Table 10 for a complete species listing of concurrent fauna at both Inglis 1A and DeSoto Shell Pits). Other artiodactyls that coexisted with the new species include: *Hemiauchenia macrocephala*, *Odocoileus virginianus*, and *Capromeryx arizonensis* (Ruez 2001).

Body size can be a very useful indicator of the habitat in which an animal lives and its role in that habitat (MacFadden and Hulbert 1990). Some good skeletal indicators that have been used to assess approximate body mass in ungulates are long bone elements, especially the diameter of the femur (Scott 1985), and certain dental characters (Janis 1990; MacFadden and Hulbert 1990). Estimated body mass, used in conjunction with postcranial proportions, can give an accurate assessment of a species preferred habitat. However, using long bone lengths to estimate body mass in camelids can be problematic, and therefore should be avoided (Scott 1985).

Table 10: Concurrent species at the Inglis 1A and DeSoto Shell Pits fossil localities.

- Xenarthra
  - Dasypodidae
    - *Dasypus bellus*
  - Pampatheriidae
    - *Holmesina floridanus*
  - Glyptodontidae
    - *Glyptotherium arizonae*
  - Megalonychidae
    - *Megalonyx leptostomus*
  - Megatheridae
    - *Eremotherium eomigrans*

- Insectivora
  - Soricidae
    - *Blarina carolinensis*

- Carnivora
  - Canidae
    - *Canis edwardii*
  - Procyonidae
    - *Procyon,* sp. nov.
  - Mustelidae
    - *Trigonictis macrodon*
  - Hyaenidae
    - *Chasmaporthetes ossifragus*

- Lagomorpha
  - Leporidae
    - *Sylvilagus webbi*

- Rodentia
  - Sciuridae
    - *Sciurus* sp.
  - Geomyidae
    - *Orthogeomys propinetis*
  - Muridae
    - *Sigmodon curtisi*
    - *Reithrodontomys* sp.
    - *Ondatra idahoensis*

Table 10: continued.

Artiodactyla
  Camelidae
    Hemiauchenia macrocephala
    Hemiauchenia (sp. nov.)
  Antilocapridae
    Capromeryx arizonensis
  Cervidae
    Odocoileus virginianus

Perissodactyla
  Tapiridae
    Tapirus, sp. nov.
  Equus
    Equus sp.

Proboscidea
  Mammutidae
    Mammut americanum

Table adapted from Ruez (2001).

Dentition

Dentition is often the best indicator for determining the type of diet to which a mammal is best adapted. In ungulates, it is possible to differentiate between a browsing and grazing diet by the morphology of the teeth. A grazing diet generally consists of ≥ 90% grasses. A browsing diet consists of ≥ 90% leaves and soft foliage. Mixed feeders fall in between these two extremes (Janis 1990). A dentition suitable for a grazing diet usually consists of hypsodont molars, with reinforcements of enamel or cementum, and broad incisor breadth. A dentition that is more indicative of a browsing diet has a narrow mandibular symphysis and brachydont molars with crenulated enamel that have little to no cementum. They also have narrower incisors that may be "feathered" for dexterity in stripping leaves from branches. Mixed feeders tend to share a suite of traits from both groups (Perez-Barberia and Gordon 2001;Webb and Stehli 1995).

It is known from direct observation that *Odocoileus virginianus* is a browser, whereas, the teeth of *H. macrocephala* suggest that it was probably a grazer to a mixed feeder. The teeth of the new species show properties of both browsers and grazers. The new species has teeth that are more hypsodont than a deer, but less hypsodont than *H. macrocephala*. They also have a complete coating of cementum, which tends to correlate with a grazing diet (Webb and Stehli 1995).

Mesowear

Analyzing mesowear patterns in ungulate teeth is a new method to determine paleodiet in conjunction with hypsodonty indices. Mesowear patterns refer to the combined result of tooth attrition and abrasion (tooth on tooth and tooth on food wear) (Butler 1972; Fortelius 1985). Cusp relief and cusp shape are the two major attributes that are analyzed in mesowear analyses. Cusp relief is the difference in height between cusp tips and inter-cusp valleys. In pure grazers, there is little difference in these heights. Browsers have a large discrepancy between these heights. Cusp shape refers to the apex of the paracone or metacone in ungulates. The shape is described as sharp, rounded or blunt. These analyses seem to be based on qualitative characters and can be performed with the naked eye, or only with a hand lens (Fortelius and Solounias 2000).

In both *Hemiauchenia macrocephala* and the new species of *Hemiauchenia* the cusp relief could be referred to as high, as it is in all extant camelids. Likewise, the cusp shape could be referred to as rounded or blunt in most cases. This combination of mesowear characters suggests a mixed feeder, as are extant lamines. In *Palaeolama* and *H. edensis*, on the other hand the cusp relief is high, but the cusp shape is sharp, indicating a browser (Fortelius and Solounias 2000) (Figures 7 and 8 for new species, Figure 10 for *H. macrocephala* and *Palaeolama*, Figure 9 for *H. edensis*).

Stable Carbon Isotope Analysis

Stable carbon isotope analysis is a useful tool for reconstructing herbivore paleodiet (Koch et al. 1998). It is useful because the carbonate apatite found in tooth enamel maintains high isotopic fidelity during fossilization (Feranec and MacFadden 2000) and the photosynthetic pathway utilized by consumed plants is preserved in the carbon compounds (Figure 28). In the Pleistocene of Florida, plants that utilize the C_4 pathway are drier grasses and shrubs and when ingested, produce tooth enamel signatures with $\delta^{13}C$ values of approximately -2 to 5‰, whereas, plants that use the C_3 pathway are leaves and softer foliage and when ingested, produce tooth enamel signatures with $\delta^{13}C$ values of approximately -20 to -10‰. Therefore, grazers will have a C_4 signature in their tooth enamel and browsers will have a C_3 signature in their tooth enamel; whereas, mixed feeders will have intermediate isotopic values (Hallman and Meachen in review; Koch et al. 1998).

H. macrocephala from the Irvingtonian, appear to be mixed feeders, with $\delta^{13}C$ values of -2 to -7 ‰ (Feranec and MacFadden 2000; Hallman and Meachen in review). Feranec (2003) found that *H. macrocephala* was predominantly a browser to mixed feeder in the latest Blancan, however, the tooth morphology suggests these animals were mixed feeders to grazers, and warrants further analyses on this issue. The new *Hemiauchenia* species appears to be mainly a browser with a small amount of grass in the diet ($\delta^{13}C$ of -8‰). It should also be noted that at all sites where *Palaeolama mirifica* is present, the new species is absent and vice versa (Morgan and Hulbert 1995; Ruez 2001).

This could possibly be due to direct competition for food, however, the δ^{13}C values found for *P. mirifica* are between -10 and -14 ‰, which have sufficiently more of a browsing signature than that of the new species (Figure 29)(Hallman and Meachen in review).

This feeding strategy would have been effective for the new species, because it would avoid sharing a complete food source with either *Odocoileus virginianus* or *H. macrocephala*. The δ^{13}C values for the new species fall in between the δ^{13}C values for *H. macrocephala* and a pure browser.

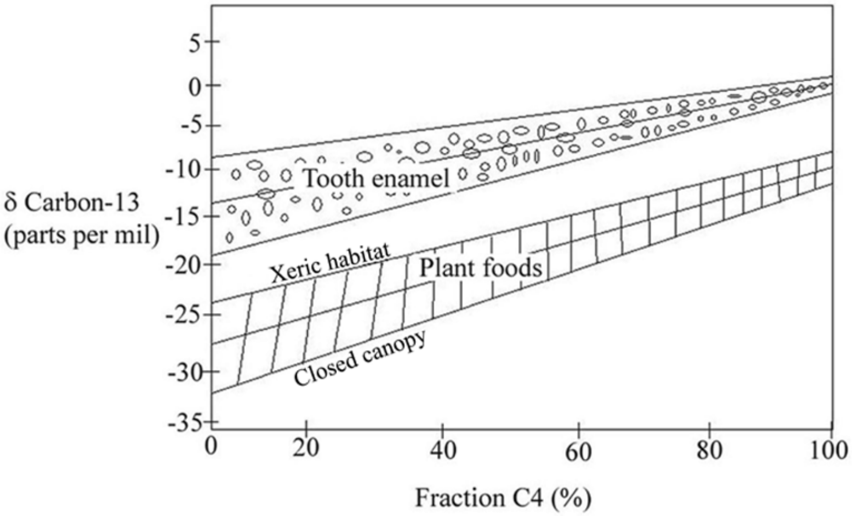


Figure 28: Plot of δ^{13}C values versus fraction C4 contained in varied kinds of plant communities, and the corresponding enriched values of tooth enamel. From MacFadden and Cerling (1996).

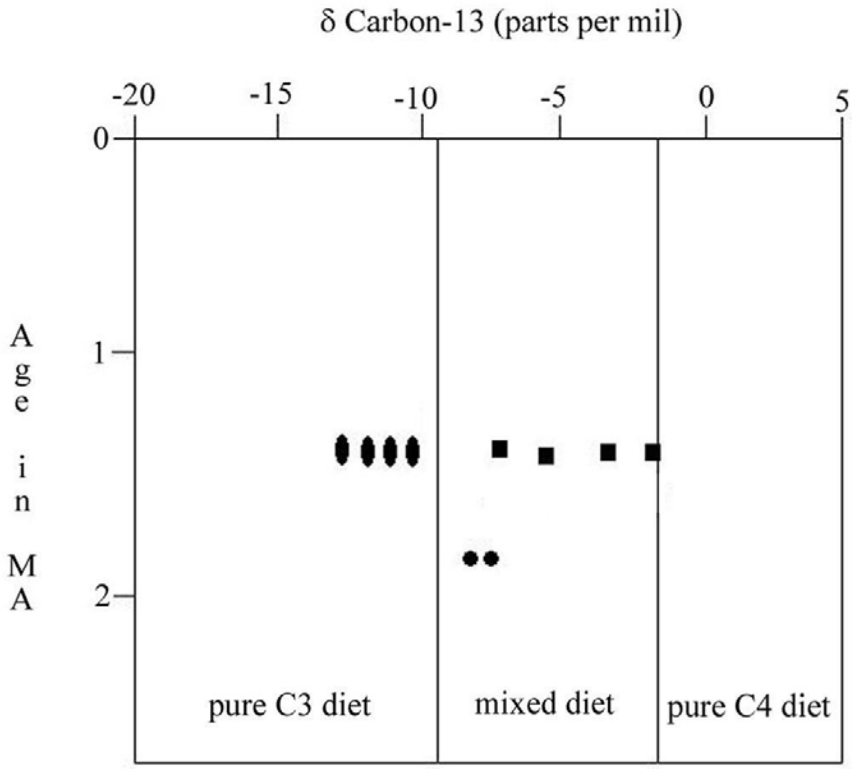


Figure 29: Stable carbon isotope data for three species of lamines, circles represent the new *Hemiauchenia* species, squares represent *Hemiauchenia macrocephala* and ovals represent *Palaeolama mirifica*. Data were taken from Hallman and Meachen (in review) and Feranec and MacFadden (2000). Diagram modeled after MacFadden and Cerling (1996).

Limb Proportions

According to Scott (1985), the limb proportions of extant ungulates will sort them in to five habitat categories: Flat, open grasslands or arid areas; mixed woodland and open areas; heavy forest; true mountainous habitat; or rolling hill country. This may hold true for extinct ungulates. Although metapodials are not a good indicator of body mass, they are an accurate indicator of habitat adaptation. The extant ungulates that live in open country have long metapodials (≈23-27 cm long); the ungulates from mountainous regions or thick forests have shorter metapodials (≈14-22 cm long); and the species living in scattered woodland or hilly habitats have intermediate length metapodials (Scott 1985). Based on the metapodial lengths of this new species and the comparison of the metapodial lengths of species concurrent in time span (*H. macrocephala* and *Palaeolama*) and the data in appendices 1 and 2 of Scott (1985), it seems that this new species was a scattered woodland dweller. The length of the metapodials of the new species fell in between those of *H. macrocephala* and *Palaeolama*, this suggests that it would be more likely to dwell in open habitat than *Palaeolama*, but less likely than *H. macrocephala*. Based on stable carbon isotope data this animal would be more likely to dwell in a forested habitat. The validity of either prediction can be assessed when the proposed habitats that this animal lived in are examined.

Inglis 1A was thought to be a scrubby savanna habitat. Inglis 1C was thought to be a heavily forested neighboring habitat, but the new species was only present at Inglis 1A. One might expect to find this species in forested habitats as well, considering the amount of browse in its diet, the fact that it is absent from these forested sites suggests that it preferred scrubby savanna or open environments. The almost identical faunal composition at the DeSoto Shell Pits indicates a very similar type of environment (Morgan and Hulbert 1995). The reason for this open habitat preference may have stemmed from its mode of predator evasion.

Scott (1985) separated artiodactyls by their distinct modes of predator evasion. Long-limbed artiodactyls generally have heightened cursorial ability and use a cursorial evasion technique, whereas short-limbed artiodactyls prefer to take cover and freeze. The extremely long limbs of the new species suggest that it may have had heightened cursorial ability. This heightened cursorial ability would have made it more efficient for the new species to evade predators by running from them in an open habitat. Running in a forested habitat would be clumsy and the new species' height would have made it difficult to hide from predators. For animals with shorter legs and smaller body sizes it is more efficient to use the hide and freeze mode of predator evasion, thereby necessitating that they dwell in a forested area where they could take cover (Scott 1985).

This new species, perhaps dwelled in a location where a forested habitat bordered a scrubby habitat so it could take advantage of both forest and open environments. It probably preferred a savanna type habitat with scattered trees. The length of its limbs may also have facilitated the type of feeding used by the gracile African gerenuks, which stand on their hind legs to reach otherwise inaccessible leaves.

CHAPTER 5
CONCLUSIONS

The new species of *Hemiauchenia* is a gracile lamine that lived in Florida during the late Pliocene and early Pleistocene. It is relatively rare and appears to have been sparsely distributed along the west coast of Florida. It may be a sister species to *Hemiauchenia macrocephala*, with which it was originally mistaken and with which it shares many morphological synapomorphies. Alternatively it may be a sister species to *Hemiauchenia edensis*, a little known fossil lamine species from the early Pliocene of Florida and the southwestern United States, with which it also shares many morphological synapomorphies, such as gracile limb bones and a very similar dentition. Until a more detailed cladistic analysis is completed, the new gracile lamine species may be considered closely related to both.

This new species ate mainly browse with occasional grass mixed in, and preferred to dwell in a savanna type environment. It was probably an agile cursor, using its running and leaping abilities to avoid predators. It coexisted with *Hemiauchenia macrocephala,* but has never been found at the same site with another Florida lamine, possibly to avoid competition for a food source.

The fossil sites at Inglis 1A and 1C were closed long ago, but the De Soto Shell Pit site is still active. More material of the new species from De Soto would help augment our understanding of the form and function of this animal.

Placing new species on record will help future discoveries. It would also seem worthwhile to investigate Blancan/Irvingtonian fossil sites north and south of Inglis 1A and DeSoto to see if the range of this lamine expanded farther than we now know. The possible astragalus found in the F:AM collection from Texas and the phalanx from Arizona hint that this species may have ranged into the tropical latitudes of Mesoamerica. This new species may have had an affiliation with the true (extant) llamas that crossed the isthmus of Panama in the early Pleistocene, as did *Palaeolama*. The morphological similarities it shares with extant lamine species (e.g. small body size and reduced dental formula) may not be a coincidence, but a true insight into the ancestral nature of the extant lamines. Although this lamine has at present a limited fossil record, it may be a closer ancestor than any other known species. It would also be worthwhile to investigate further the Texas site from which the F:AM astragalus was found, to determine whether the new species was actually there or whether the astragalus belonged to the similar species, *Hemiauchenia edensis*.

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BIOGRAPHICAL SKETCH

Julie Anna Meachen was born in Cleveland, Ohio, on August 28, 1978 to Sarah Elizabeth Mulé Meachen and Edward Willis Meachen. She lived in many states across the U.S. until the age of 11 when she moved to Tampa, Florida. She completed her bachelor's degree in zoology at the University of Florida, where she decided that she wanted to become a mammalian paleontologist. She worked and volunteered in the vertebrate paleontology collection at the Florida Museum of Natural History until her matriculation into the master's program in zoology at the University of Florida in 2001. In September of 2003, she will move to Los Angeles, California, to begin her Ph.D. studies at UCLA, where she will work on fossil Carnivorans under the guidance of Dr. Blaire Van Valkenburgh.