

A NEW SPECIES OF *HEMIAUCHENIA* (ARTIODACTYLA, CAMELIDAE) FROM THE LATE BLANCAN OF FLORIDA

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A new species of lamine, *Hemiauchenia gracilis* n. sp., is present at six late Blancan fossil localities in Florida: Inglis 1A and 1F in Citrus County; DeSoto Shell Pits 1 and 5 in DeSoto County; Santa Fe River 1 in Columbia County; and Waccasassa River 9A in Levy County. The fossil deposits at these locations are thought to be between 1.8 and 2.5 million years old. The holotype specimen is a right mandibular fragment including p4 through m3. *Hemiauchenia gracilis* lacks p1 through p3. The teeth of *H. gracilis* are similar to those of *Hemiauchenia macrocephala* and *Hemiauchenia edensis*, with an intermediate crown height and a small degree of crenulation. Postcranial elements of *H. gracilis* are very long and slender, especially the radio-ulna and the phalanges, apparently adaptations for cursoriality. Stable carbon isotope data for *H. gracilis* show a mixed-feeding signature, with more browse than grass. A phalanx with the size and proportions of those of *H. gracilis* was found at the late Pliocene 111 Ranch, Graham County, Arizona. This would potentially extend its range as far west as Arizona, drawing it closer toward Mexico and Central America, and possibly giving insight into the origin of the extant Lamini.

Key Words: *Hemiauchenia gracilis* n. sp.; Florida; Pliocene; Lamini; stable carbon isotopes.

INTRODUCTION

The tribe Lamini (Webb 1965) includes the living llamas, vicuñas, guanacos, and alpacas. The earliest known lamine fossils, represented by the genus *Pleiolama*, occurred in the Great Plains of North America approximately 11 million years ago (Webb & Meachen 2004). The closely related extinct lamine genus *Hemiauchenia* appeared approximately ten million years ago. The extinct genus *Palaeolama* and the modern South American lamines are thought to have evolved from *Hemiauchenia* (Wheeler 1995). Much is known about extinct and extant lamines, but the gap between the two is still a mystery. This gap is confounded by a lack of lamine fossils from Central America. The discovery of this new fossil lamine species helps to fill a gap in the origins of extant Lamini.

In 1962, the late Ben Waller found an unusually small lamine radio-ulna otherwise resembling *Hemiauchenia* at the Santa Fe River site 1 in Columbia County. Subsequently much more material that resembled this initial find was uncovered in Citrus County at Inglis 1A by Florida Museum of Natural History stu-

dents and staff. Additional specimens were later found at DeSoto Shell Pits 1 and 5 by Steve and Suzan Hutchens and Reed and Barbara Toomey. Specimens were also recovered at the Waccasassa River 9A and Inglis 1F sites by the Hutchenses. All material that was found by Ben Waller, the Hutchenses, and the Toomeys was generously donated to the Florida Museum of Natural History. Figure 1 shows the general location of these fossil sites.

Santa Fe River locality 1 is a river bend less than 0.5 km in length. The bottom of the river in this small stretch produces both Rancholabrean and late Blancan fossils (Morgan & Hulbert 1995). Among the species found at Santa Fe River 1 that indicate the presence of late Blancan deposits are *Borophagus diversidens*, *Canis lepophagus*, *Nannippus peninsulatus*, *Platygonus bicalcaratus*, *Hemiauchenia blancoensis*, and *Rhynchotherium praecursor* (Morgan & Hulbert 1995). Although the referred Santa Fe River specimen of *Hemiauchenia gracilis* was not collected in situ with other Blancan taxa, its age can reasonably be inferred to be late Blancan given its chronologic distribution at other Florida vertebrate sites.

The Inglis 1A site is a sinkhole deposit with excellent preservation of a diverse vertebrate fauna. The site is approximately five meters below present sea level,

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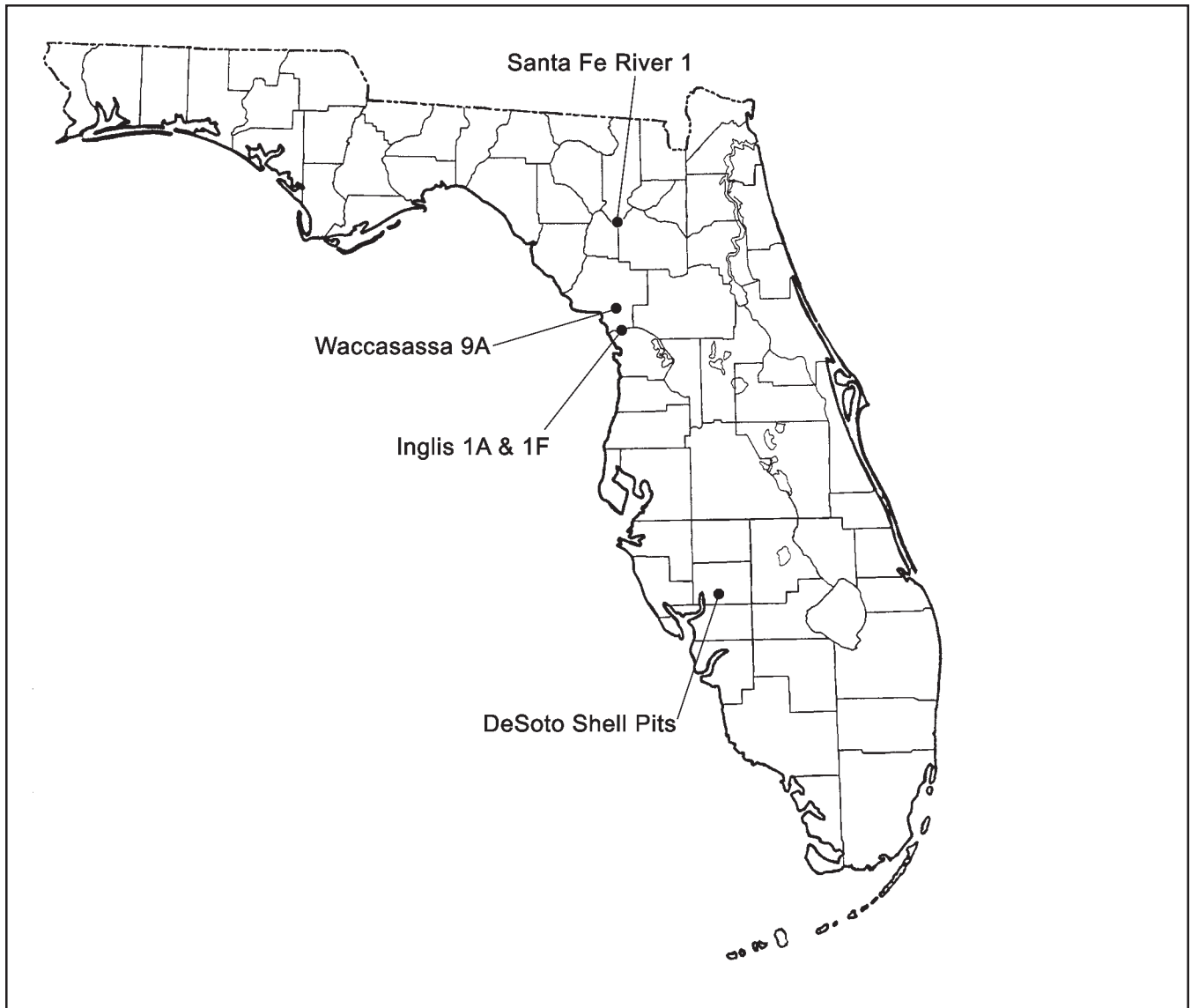


Figure 1. A map of Florida showing the locations of late Pliocene fossil vertebrate localities Inglis 1A and 1F, the DeSoto Shell Pits (1 and 5), Waccasassa River 9A, and Santa Fe River 1.

but lacks any marine fossils. Thus, it would seem that deposition occurred at a time of low sea level (Morgan & Hulbert 1995). Larger animals may have fallen or climbed into the sinkhole and starved to death. The faunal assemblage indicates a slightly cooler, or more open habitat than is present today in Citrus County (Meylan 1982; Webb & Wilkins 1984; Morgan 1991). Abundant ungulates and carnivores have been found at Inglis 1A including both the new lamine and *Hemiauchenia macrocephala* (Morgan & Hulbert 1995; Emslie 1998; Ruez 2001).

Inglis 1A is important because it was deposited closely after the Great American Biotic Interchange and coincides with a surge in native faunal diversity; it also lies along the broad subtropical Gulf Coastal Corridor. As a result, Inglis 1A contains many taxa that give us clues into the Plio-Pleistocene faunal history of Florida as well as the faunal exchange with South America (Webb 1976; Ruez 2001). The presence of Blancan indicators and the absence of *Mammuthus* at Inglis 1A place it in the latest Blancan mammal age with a date of approximately 2.0-1.8 Ma (Morgan & Hulbert 1995; Bell

et al. 2004). No comprehensive study has been done on the much less species-rich Inglis 1F locality, but it shares all of its faunal elements with the much richer Inglis 1A local fauna.

The DeSoto local fauna is the designation for the vertebrate fauna from dark silty beds within the Caloosahatchee Formation from three commercial shell mines in DeSoto County, Florida (Morgan & Hulbert 1995). DeSoto Shell Pit 1 shares at least 23 different species of mammals with the Inglis 1A site and also lacks *Mammuthus* (Ruez 2001). The deposition at Inglis 1A occurred below present-day sea level (possibly during a glacial event), whereas DeSoto site 1 was deposited five to ten meters above present sea level during 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 & Hulbert 1995). Two teeth of *Nannippus peninsulatus* were found at DeSoto Shell Pit 5, but this species was not found at DeSoto Shell Pit 1 or Inglis 1A, suggesting that DeSoto Shell Pit 5 might be slightly older than the other two sites. However, DeSoto site 5 is also thought to be late Blancan (Richard Hulbert pers. commun.).

Waccasassa River site 9A is previously unpublished, but is thought to be Blancan, based on the co-occurrence of *Capromeryx arizonae*, the new lamine, and *Arctodus pristinus* (Richard Hulbert pers. commun.). One phalanx that may belong to the new lamine was discovered in Arizona at the well known late Blancan 111 Ranch locality in Graham County, potentially expanding its range further west (Mary Thompson pers. commun.).

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 & MacFadden 2000) and the photosynthetic pathway utilized by consumed plants is preserved in the carbon compounds. In the Pliocene and 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‰; 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 (Koch et al. 1998). This study includes a stable carbon isotope analysis to estimate the diet of the new Blancan lamine.

MATERIALS AND METHODS

To perform this study, specimens from this new lamine were compared to specimens from: *Pleiolama vera*, *Hemiauchenia macrocephala*, *Hemiauchenia edensis*, *Hemiauchenia blancoensis*, "*Hemiauchenia*" *minima*, *Palaeolama mirifica*, *Lama glama*, and *Lama guanacoe*. Specimens of *Pleiolama vera*, *Hemiauchenia blancoensis* and "*Hemiauchenia*" *minima* were so significantly different from the new *Hemiauchenia* species that they are rarely used as comparisons in this paper. The anatomy of the dromedary by Smuts and Bezuidenhout (1987) was used for muscular attachment comparisons. Original specimens of the new *Hemiauchenia* used in this study are identified in referred specimens. Comparative specimens were not specifically identified by number in most cases except extant species (Zooarchaeology collection, UF Z7333 *Lama glama*, UF Z7839 *Lama sp.*, UF Z8427 *Lama sp.*, UF Z8430 *Lama guanacoe*, UF Z9279 *Lama sp.*) and all are housed at the Florida Museum of Natural History, except two *Hemiauchenia edensis* metapodials which are housed at the Los Angeles County Museum of Natural History, LACM 30235 and LACM 28033. Very few statistical analyses were performed due to the extremely small sample size of the elements of the new lamine. Any statistics performed were averages and simple ratios.

For teeth, uppercase letters denote upper dentition and lowercase letters denote lower dentition. All measurements under 300 mm were taken with digital calipers to the nearest 0.1 mm. All other measurements were taken with manual sliding calipers to the nearest millimeter (Tables 1 and 2). For stable carbon isotope analysis, tooth enamel from the p4 or m2 was sampled for carbon isotopic composition following the methods of Feranec and MacFadden (2000).

ABBREVIATIONS

Institutional Abbreviations.—UF, Vertebrate Paleontology, Florida Museum of Natural History, University of Florida, Gainesville. LACM, Los Angeles County Museum of Natural History, Los Angeles, California.

Table 1. Tooth measurements (in mm) of *Hemiauchenia gracilis* n. sp. from the late Pliocene of Florida.

Catalogue number	Tooth position	Length (anterior-posterior)	Width (lingual-labial)	Crown height
UF 210714	P4	13.8	10.9	14.5
UF 45493	M1	17.8	12.7	7.1
UF 210714	M1	21.8	14.3	11.4
UF 210716	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

Anatomical Abbreviations.—M. denotes Musculus, R denotes right, and L denotes left.

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen 1848

Family CAMELIDAE Gray 1821

Tribe LAMINI Webb 1965

Genus *HEMIAUCHENIA* Gervais and Ameghino
1880

HEMIAUCHENIA GRACILIS n. sp.

Holotype.—UF 210707, R dentary fragment with p4-m3 (Fig. 2A-B). Housed at the Florida Museum of Natural History, University of Florida, Gainesville.

Type Locality.—De Soto Shell Pit 5, De Soto County, Florida, Caloosahatchee Formation, latest Blancan (UF locality DE011).

Other Localities.—Inglis 1A (CI001) and Inglis 1F (CI022), Citrus County, Florida; DeSoto Shell Pit 1 (DE007), DeSoto County, Florida; Santa Fe River 1 (CO003), Columbia County, Florida; and Waccasassa River 9A (LV040), Levy County, Florida, all late Blancan, ca. 2.5-1.8 Ma.

Referred Specimens.—DeSoto Shell Pit 5: UF 210707 R mandibular fragment with p4-m3; UF 210714 R maxillary fragment with P4-M1; UF 210715 L mandibular fragment with m3; UF 210716 L maxillary fragment with DP3-DP4; UF 210717 R m3; UF 210702 R humerus, distal end; UF 210701 L radio-ulna; UF 210706

L astragalus; UF 210709 L calcaneum; 210710 R calcaneum; UF 210711 L metacarpal, proximal; UF 210704, UF 210708, UF 210712, UF 210703 phalanx, proximal; UF 210705 phalanx, medial. DeSoto Shell Pit 1: UF 179636 radio-ulna, distal. Inglis 1A: UF 45493 maxillary fragment with M1-M2; UF 176915 humerus, distal; UF 176925 femur, distal; UF 45275, UF 45276 femur, proximal; UF 176935 metatarsal; UF 210720 R metacarpal, proximal; UF 18230 metacarpal; UF 18236 metapodial, distal; UF 179639, UF 18237, UF 179638 phalanx, proximal; UF 177024 phalanx, distal. Inglis 1F: UF 210721 phalanx, proximal; UF 210722 R astragalus; UF 210723 phalanx, medial; UF 210724 cuneiform; UF 210725 unciform. Waccasassa River 9A: UF 210726 R metacarpal, proximal; UF 210727 tibia, distal. Santa Fe River 1: UF 8917 radio-ulna.

Diagnosis.—*Hemiauchenia gracilis* is placed in the genus *Hemiauchenia* based on the following characters: relative degree of hypsodonty of cheek teeth compared to other lamines, long, slender limbs, and a proximal phalanx with 'W'-shaped suspensory scar not extending onto the shaft. *H. gracilis* shares many homologous character states with *Hemiauchenia macrocephala* and *Hemiauchenia edensis* such as slender postcranial elements, small size, and gracile molars. *H. gracilis* is considerably smaller than *Hemiauchenia blancoensis*, "*Hemiauchenia*" *minima*, and *Pleiolama vera*. The postcranial elements of *Hemiauchenia gra-*

Table 2. Measurements of the postcranial elements of *Hemiauchenia gracilis*, in mm. GL, greatest length; BP, breadth of proximal end; BD, breadth of distal end; SD, smaller diameter of diaphysis; LO, length of olecranon of ulna; SDO, smallest depth of olecranon (ulna only); DPA, depth across processus anconae (ulna only).

Catalog number	Element	GL	BP	BD	SD	LO	SDO	DPA
UF 176915	Humerus			36.8				
UF 210702	Humerus			40.9				
UF 210701	Radio-ulna			44.8	27.4	64.5	38.5	48.4
UF 8917	Radio-ulna	472		49.8	31.5	64.5	40.3	50.7
UF 179636	Radio-ulna			41.4				
UF 45275	Femur		67.0		23.8			
UF 45276	Femur		66.8		23.2			
UF 176935	Metapodial	320	33.0	39.4	19.1			
UF 18236	Metapodial			38.2				
UF 210720	Metapodial		31.1		16.8			
UF 210711	Metapodial		34.9					
UF 210726	Metapodial		34.2					

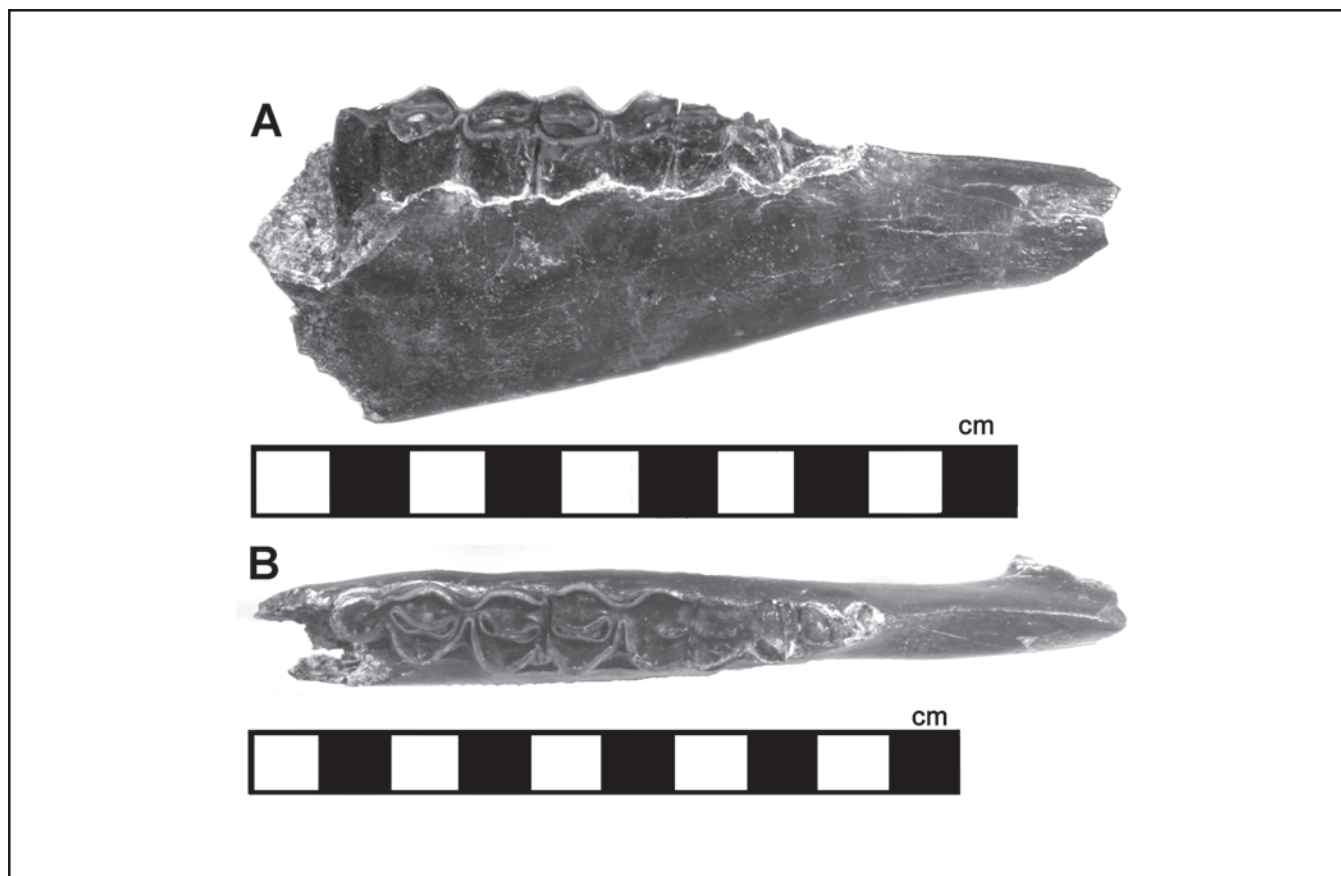


Figure 2. *Hemiauchenia gracilis* n. sp., holotype, right mandible with p4-m3, UF 210707 from DeSoto Shell Pit 5. A. labial view, B. occlusal view.

cilis are consistently more slender than those of *H. macrocephala*. The radio-ulna is longer, but all other postcranial elements are shorter than those of *H. macrocephala*. The postcranial elements of *Hemiauchenia gracilis* are always longer and usually more robust than those of *H. edensis*.

DESCRIPTION

Cranium.—The holotype 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). On the holotype (Figs. 2A-B), the mandible is broken at the midpoint of the mandibular symphysis. *Hemiauchenia gracilis* lacks an alveolus for the p1 at this midpoint, and therefore lacked the p1. When compared to three dentaries of *Hemiauchenia edensis*, the dentary of *Hemiauchenia gracilis* is deeper and more robust. *Hemiauchenia edensis* has a very shallow mandible with an average

depth at the posterior end of the m3 of approximately 34 mm. This measurement is compared with 43 mm in *Hemiauchenia gracilis*. 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 *Hemiauchenia gracilis* (without a p3). When compared with numerous dentaries of *Hemiauchenia macrocephala*, the dentary of *Hemiauchenia gracilis* is always shallower and the tooth row is always shorter (Table 1).

The deciduous teeth, DP3 and DP4, are very molariform (Fig. 3). The DP3 presents the trilobate quality of artiodactyl deciduous premolars, though not as pronounced as those of *Hemiauchenia macrocephala*. It almost appears to be a deformation of an M1. The DP4 is bilobate (molariform) and resembles an M2. They show the root splay common to deciduous premolars.

The P4 has a distinctly rounded and laterally flattened shape with an open ‘U-shaped’ dental cavity (Fig. 4). In my observations, a ‘U-shaped’ dental cavity in

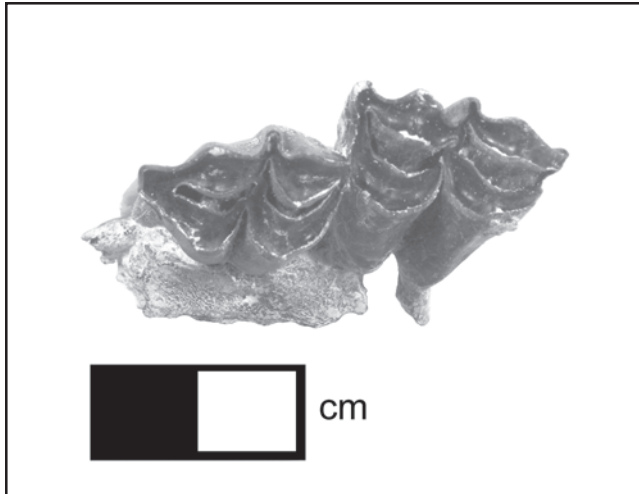


Figure 3. Maxillary fragment of *Hemiauchenia gracilis* n. sp. with DP3 and DP4, UF 210716, occlusal view.

lamines is diagnostic of the genus *Hemiauchenia*. The genus *Palaeolama* has sharply pointed lophes with ‘V-shaped’ crescents. The P4 appears to have little wear, and is in excellent condition. The P4 in *Hemiauchenia edensis* is considerably smaller than those of *Hemiauchenia macrocephala*, with a maximum length of 11.6 mm and a maximum width of 9.3 mm (Table 1). The P4 of *Hemiauchenia gracilis* retains a rounded appearance from labial to lingual sides, whereas the P4 of *H. edensis* tapers toward the lingual side, forming a more ‘V-shaped’ premolar.

The upper molars of *Hemiauchenia gracilis* are less robust in appearance than those of *Hemiauchenia macrocephala*. The enamel on *H. gracilis* molars is thin, but the molars are coated in a complete layer of cementum in all specimens, much like the molars of *H. macrocephala*. The teeth of *H. gracilis* show a minor degree of crenulation. This is also found on teeth of *H. macrocephala* (Webb & Stehli 1995), but *H. edensis* shows no crenulation. In *H. gracilis*, the M1 (Fig. 4) is shorter and smaller than that in *H. macrocephala*, as is the m3 (Fig. 5A). However, it maintains the same shape. Again the ‘U-shaped’ dental cavity is conserved. The shape of the tooth crown, although less hypsodont, also maintains the same pattern. The ribs of the molars (parastyle, mesostyle, and metastyle) are close in height to the cusps of the crescents as in *H. macrocephala*. The anterior and posterior labial crescents are raised, and the anterior and posterior lingual crescents are close in height to the former two structures. The M2 of *H.*

gracilis has a very similar appearance to the M1, except that it is slightly larger with thicker cusps.

The lower dentition of *Hemiauchenia gracilis* is much more transversely compressed than that of *Hemiauchenia macrocephala*, but less so than that of *Hemiauchenia edensis*. *H. gracilis* has very prominent anterior enamel folds on the m3 (Fig. 5B), which are referred to as ‘llama buttresses’ (Frick 1921; Webb et al. in press). These folds help it withstand a great deal of interdental wear in an anteroposterior direction. The four m3s of *H. edensis* are 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 *H. gracilis*. The crown height in the unworn m3 of *H. gracilis* is midway between those of *H. edensis* and *H. macrocephala*. The posterolophid on the m3 is robust in *H. gracilis* and has a completely longitudinal orientation when compared with *H. macrocephala* and *H. edensis*, which have a more anteriorly curved orientation. The hypsodonty indices of the m3 (unworn crown height of the m3 in mm over unworn anteroposterior length of the m3 in mm) in four

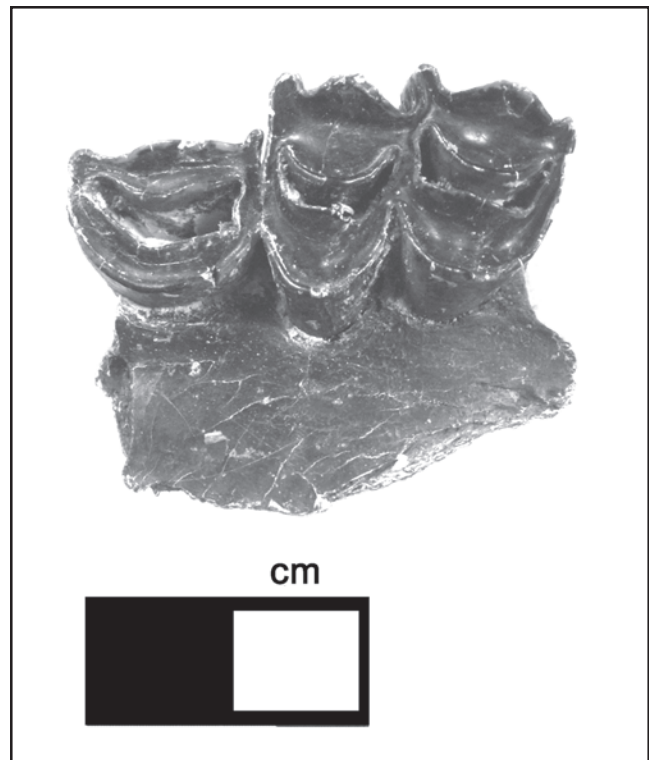


Figure 4. Maxillary fragment of *Hemiauchenia gracilis* n. sp. with P4 and M1, UF 210714, occlusal view.

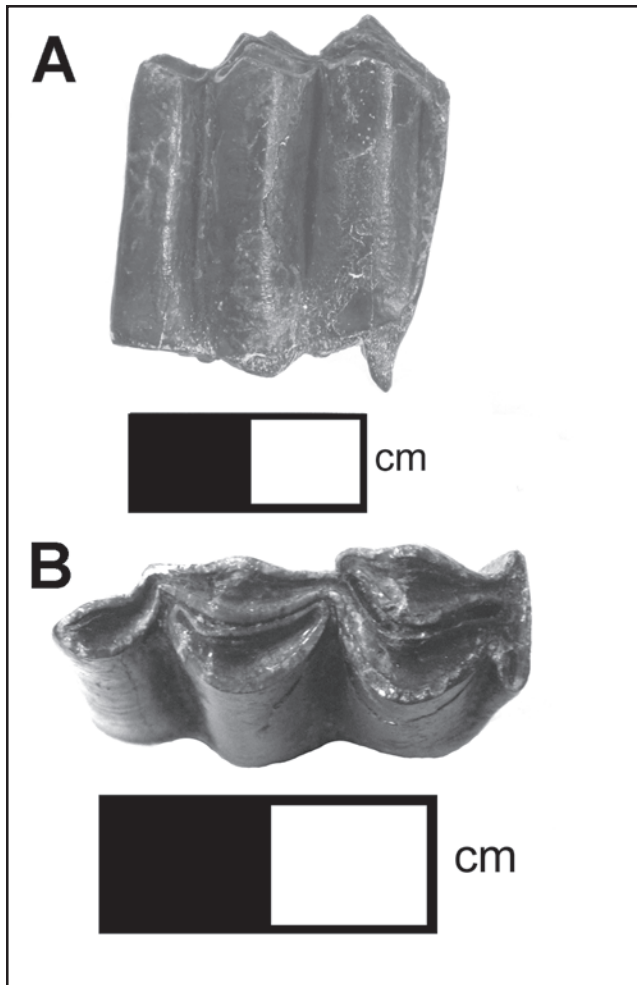


Figure 5. Lower right m3 of *Hemiauchenia gracilis* n. sp., UF 210717, A. labial view, B. occlusal view.

species, are: $27.2/28.2=0.96$ in *Hemiauchenia gracilis* (n=1); $33.2/32.3=1.02$ in *Hemiauchenia macrocephala* (n=3); $22.5/25=0.90$ in *Hemiauchenia edensis* (n=2); and $27/26=1.03$ in *Lama glama* (n=1).

Postcrania.—The postcranial skeleton of *Hemiauchenia gracilis* is well represented (Table 2). The long, slender nature of the limb bones is the most striking feature. Two distal humeri were recovered for *H. gracilis*. The size of the humerus differentiates it from *Hemiauchenia macrocephala*. These distal humeri were approximately one-half the depth, two-thirds the width, and much less robust than those of *H. macrocephala*. The dimensions of the distal humeri of *H. gracilis* were similar to those of extant lamines (*Lama guanicoe* and *Lama glama*) and *Hemiauchenia edensis* (n=2). The humeri of *H. gracilis* were slightly more robust than those of either *H. edensis* or the extant lamines in the olecranon fossa, the fossa radialis,

and the thickness of the humeral shaft, but was more gracile at the extreme distal end (see measurements below). 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 *H. gracilis*. Measurements for the humerus are represented by the breadth of the distal end in mm over the depth of the distal end in mm. For the following four species, the measurements are: $38.8/39=0.99$ in *Hemiauchenia gracilis* (n=2); $65/60=1.08$ in *Hemiauchenia macrocephala* (n=2); $37.5/36=1.04$ in *Hemiauchenia edensis* (n=2); and $45/40=1.12$ in *Lama* (n=2).

The radio-ulna is the most diagnostic postcranial element for *Hemiauchenia gracilis* (Fig. 6A). The most striking feature of the radio-ulna of *H. gracilis* is the great length. It is about 1.2 times longer than the average length for the radio-ulnae of *Hemiauchenia macrocephala*, but is still considerably shorter than those of either *Pleiolama vera* or *Hemiauchenia blancoensis* (see below). Of the two *H. gracilis* radio-ulnae specimens that were available, only one has a usable length. The other has been restored, and there is no visible point of contact to validate the length as accurate. However, the overall shapes of these 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 *Hemiauchenia gracilis* than in any other lamine specimen available for analysis (Fig. 6B). 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 radio-ulnae of *Hemiauchenia gracilis* displays this pattern.

The radio-ulnae of *Hemiauchenia gracilis* can be distinguished from those of *Hemiauchenia edensis* by size. There were no complete specimens of *H. edensis* to compare lengths. However, the average width of the radio-ulnar shaft in *H. edensis* (n=2) was 22 mm, and the average breadth of the distal end was only 32.4 mm as compared to an average width of 29.5 mm and average distal breadth of 45.3 in *H. gracilis*. *H. gracilis* has a limited area for attachment of the *M. triceps brachii* and *M. anconeus*. *Hemiauchenia macro-*

cephala has a large surface area for the attachment of both these muscles. In *H. gracilis* there is complete fusion of the ulna to the radius at the distal portion of the bone. The radio-ulna from the De Soto 5 site appears to articulate with the humerus from that same site. Measurement comparisons, length of the radio-ulna in mm over midshaft width in mm, were made for the following species: $472/31.5=14.9$ in *Hemiauchenia gracilis* (n=1); $392.3/38.6=10.1$ in *Hemiauchenia macrocephala* (n=4); $291.7/23.4=12.4$ in *Lama* (n=1); $544.4/42.8=12.7$ in *Pleiolama vera* (n=1); and $517/38=13.6$ in *Hemiauchenia blancoensis* (n=1). These measurements show that although *H. gracilis* does not have the longest radio-ulna, it does have greatest length to width ratio.

The femora of *Hemiauchenia gracilis* bear a striking resemblance to those of extant lamines. The diameter of the femoral shaft is only slightly greater than that of *Lama*. The distal and proximal ends are also highly

similar in size and shape. The length of the shaft of *H. gracilis* is unknown, because no complete specimens are available. An estimate of length can be made from the proportions of the other elements of the skeleton and it is thought that the femora of *H. gracilis* are considerably longer than those of *Lama*. The femur presents a very rugose lateral supracondylaris tuberosity, which appears to facilitate a large *M. flexor digitorum superficialis* and large *M. adductor femoris brevis et magnus*. The trochanter major in the De Soto 5 specimen is quite rugose, suggesting strong attachments for the *M. gluteus accessorius*, *M. gluteus profundus* and possibly the *M. vastus lateralis*. However, *Hemiauchenia macrocephala* shows stronger *M. vastus lateralis* scars than does *H. gracilis*. The fovea capitis 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 capitis extends from the middle of the caput femoris to the su-



Figure 6. Radio-ulnae of *Hemiauchenia gracilis* n. sp. A, UF 210701 (top), UF 8917 (bottom), anterior view. B, UF 210701 (left), UF 8917 (right), close-up of the proximal end in lateral view.

ture of the epiphysis. The trochanter minor is well worn in both femur specimens; however it appears to have been sharply pointed in life. Although *H. gracilis* has a number of pronounced rugosities where muscle attachments were present, the femora of *H. macrocephala* are more rugose overall. No femora of *Hemiauchenia edensis* were available for comparison. Measurements for the femur consist of breadth of the proximal end in mm over smallest width of the shaft in mm for the following three species: $66.9/23.5=2.8$ in *Hemiauchenia gracilis* (n=2); $96.1/30.4=3.16$ in *Hemiauchenia macrocephala* (n=1); $65.6/20.5=3.2$ in *Lama* (n=2).

The distal end of a tibia was recovered from Waccasassa River 9A that possibly belongs to *Hemiauchenia gracilis*. This specimen is not discussed here because it was too incomplete for comparison.

The astragali of *Hemiauchenia gracilis* are significantly smaller than the astragali of *Hemiauchenia macrocephala*. The astragali of *H. gracilis* possess a very deep notch on the plantar side that articulates with the cuboid and navicular bones. This notch seems to be present in all other lamines, but not all artiodactyls. The flange on the medial surface of the astragalus is greatly reduced in *H. gracilis*, allowing the navicular bone to reach the deep notch. There is also a large concave facet located medially on the dorsal side of the astragalus. The articular facets of the astragalus of *H. gracilis* are well defined, but not as well as those of *H. macrocephala*. The astragalus of this species is also less robust than those of *H. macrocephala*. The astragali of *H. gracilis* are indistinguishable from those of *Hemiauchenia edensis*. Measurements for the astragalus, length in mm over width in mm, for the following four species are: $39/24.6=1.58$ in *Hemiauchenia gracilis* (n=3); $58.8/42.3=1.39$ in *Hemiauchenia macrocephala* (n=4); $39.3/26.6=1.47$ in *Hemiauchenia edensis* (n=1); and $42.8/23.8=1.79$ in *Lama* (n=4).

The calcanea of *Hemiauchenia gracilis* are smaller than other Florida lamine species. The proximal tuber and shaft are transversely narrower than in *Hemiauchenia macrocephala* and the tuber is noticeably more gracile in *H. gracilis*. Articular facets on the calcaneum of *H. gracilis* appear to mirror those on *H. macrocephala*, however, all the facets in *H. gracilis* are less prominent. *Hemiauchenia gracilis* have very similar calcanea to "*Hemiauchenia minima*" from the late Clarendonian Love Bone Bed (Webb et al. 1981) in gracility; however, they are considerably smaller overall than those of "*H. minima*". Like the astragali, the calcanea of *H. gracilis* are indistinguishable from those of

Hemiauchenia edensis. One cuneiform and one unciform were found at Inglis 1F, but they were so well worn that any diagnosis other than their size would be impossible.

The metapodials of *Hemiauchenia gracilis* are absolutely shorter, and have smaller diameters than metapodials of *Hemiauchenia macrocephala*. The metapodials of *H. gracilis* are longer than those of *Hemiauchenia edensis*. Measurements of the metapodials, length in mm over width in mm, for the following six species are: $320/19.1=16.7$ in *Hemiauchenia gracilis* (n=1); $346/24.8=13.9$ in *Hemiauchenia macrocephala* (n=4); $279.5/37=7.55$ in *Hemiauchenia edensis* (n=2); $211.2/80.9=2.61$ in *Lama* (n=5); $420/25.1=16.7$ in *Pleiolama vera* (n=1); and $470/33.5=14.0$ in *Hemiauchenia blancoensis*. These measurements show that although *H. gracilis* does not have the longest metapodials, it does have very gracile (high length to width ratio) metapodials when compared with other lamines.

Several proximal phalanges were found for *Hemiauchenia gracilis* (Fig. 7). These phalanges are characterized by being shorter and more gracile than those of *Hemiauchenia macrocephala*. The proximal phalanges have a triangular shaft shape with a wide posterior side and a tapering anterior side. These also



Figure 7: Proximal phalanges of *Hemiauchenia gracilis* n. sp., posterior view, highlighting the W-shaped suspensory ligament scar on the first two phalanges. From left to right, UF 210708, UF 210712, and UF 210703.

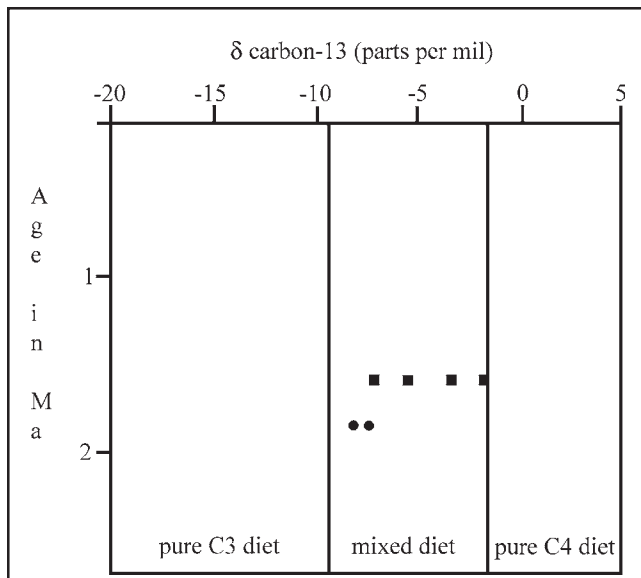


Figure 8: Stable carbon isotope data for *Hemiauchenia macrocephala* (squares) and *Hemiauchenia gracilis* n. sp. (circles). *H. macrocephala* data taken from Feranec and MacFadden (2000); diagram modeled after MacFadden and Cerling (1996).

have a very high length to width ratio (length/width ~ 7.1 for *H. gracilis*, compared to 5.4 for *H. macrocephala*, 6.1 in *Hemiauchenia edensis* and 6.0 for 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 those of *H. macrocephala*. The proximal phalanges of *H. gracilis* have the W-shaped suspensory ligament scar that is diagnostic of the genus *Hemiauchenia* (Honey et al. 1998).

ISOTOPE RESULTS

Tooth enamel of the new *Hemiauchenia* species had a mean $\delta^{13}\text{C}$ of -8‰ . This is consistent with a mixed-feeding strategy including both C_3 and C_4 plant materials, but slightly more C_3 plant material. See Figure 8 for a summary of isotopic results.

DISCUSSION

Hemiauchenia gracilis is a gracile lamine that lived in Florida during the late Blancan. Finds of this species are relatively rare, although there is evidence it existed in at least six fossil localities in Florida and possibly as far west as Arizona and it is a good indicator species of late Blancan faunas. It may be a sister species to *Hemiauchenia macrocephala*, with which it shares many morphological synapomorphies. Alternatively, it

may be a sister species to *Hemiauchenia edensis* (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 similar dentition. Until a more detailed cladistic analysis is completed, the new gracile lamine species may be considered closely related to both.

Preliminary isotope data from *Hemiauchenia gracilis* suggest that it was mainly a browser with a small amount of grass in the diet ($\delta^{13}\text{C}$ of -8‰). *Hemiauchenia macrocephala* from the Irvingtonian appears to be a mixed feeder, with $\delta^{13}\text{C}$ values of -2 to -7‰ (Feranec & MacFadden 2000). Feranec (2003) found that *H. macrocephala* was predominantly a browser to mixed feeder in the latest Blancan ($\delta^{13}\text{C}$ of -8.1 to -14.7‰). If this was the case, then it would seem that *H. macrocephala* and the new *Hemiauchenia* species would be in direct competition for food sources. However, these two species were found together at two sites in the late Blancan (Morgan & Hulbert 1995), arguing that these two animals do not have highly overlapping diets. Further isotopic and ecomorphological analyses could resolve whether *H. macrocephala* and *H. gracilis* competed for, or partitioned food resources.

The limb proportions and the muscle scars of *H. gracilis* give insight into its functional morphology and paleoecology. The lengthening and narrowing of the distal limb elements in this species seems to be an adaptation for greater cursoriality (Hildebrand & Goslow 2001). The metapodials are not as long as those in *Hemiauchenia macrocephala* and this may indicate that *H. macrocephala* had a more cursorial ecology (Scott 1985). This would complement the carbon isotope signatures from the Irvingtonian of *H. macrocephala*, as *H. macrocephala* incorporated more graze into its diet and therefore would be more likely to dwell in open plains or a habitat that would foster a cursorial lifestyle. *H. gracilis* appears to have large scars for its flexor and extensor digitorum muscles. These muscles may have facilitated the animal's cursorial locomotion, providing stability for its particularly long, gracile limbs. The small attachment surfaces for the triceps and anconeus muscles suggest that the animal may have had relatively weaker forelimb retraction. This may have very well been the case if the forelimbs were gracile. However, the gluteus muscles, and vastus lateralis muscles appear to be large on this animal, implying that the retraction of the hind limb was powerful. Yet, the muscle scars corresponding to the vastus lateralis were still more pronounced on the larger, more robust *H. macrocephala*.

The phalanx from Arizona indicates that *Hemiauchenia gracilis* may have ranged out of the Florida peninsula and into the tropical latitudes of Mesoamerica. *H. gracilis* may have had an affiliation with the true (extant) llamas that crossed the Isthmus of Panama in the late Pliocene, as did *Palaeolama* (Webb 1976). 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.

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