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Article

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Abstract: A newly discovered deposit on the bed of the Steinhatchee River produced a moderately diverse assemblage of 15 vertebrate taxa herein designated the Steinhatchee River 2A (STR 2A) local fauna. Mammalian taxa isotopically shown from other sites to be either grazers or grazing-dominated mixed-feeders numerically dominate the fauna, especially a species of *Equus*. About 75% of the 552 identifiable fossils from STR 2A, representing a minimum of nine individuals, are referred to the informally named *Equus* (*Equus*) sp. A. The site produced the first known examples of associated upper and lower cheekteeth and lower incisors for this species, and also one of just two records outside of central and southern peninsular Florida. Like most Pleistocene sites in Florida, xenarthrans are diverse, with two cingulates, *Dasypus* and *Holmesina*, and two pilosans, *Paramylodon* and *Megalonyx*. An astragalus and several metatarsals of *Holmesina* are within the size range of *H. septentrionalis*, but also have some characteristics found in the older species *H. floridanus*. These finds corroborate that an evolutionary transition between these two species occurred in Florida during the Irvingtonian. The age of STR 2A is most likely middle Irvingtonian, ca. 0.5–0.7 Ma, an interval poorly known in Florida and the rest of the southeastern USA.

Keywords: Florida; Pleistocene; paleontology; *Holmesina*; *Equus*; *Tapirus*; *Hemiauchenia*

1. Introduction

On 22 June 2022, R. Sinibaldi and J. Branin discovered a concentration of unusually well-preserved vertebrate fossils in the Steinhatchee River (STR; Figure 1). As of that date in 2022, the Division of Vertebrate Paleontology of the Florida Museum of Natural History (FLMNH) housed less than 200 late Pleistocene or Eocene specimens from the STR, all obtained since 1977 by donations from avocational fossil hunters. Especially during the 1960s and 1970s, FLMNH crews using scuba gear recovered thousands of vertebrate fossils from numerous sites in northcentral Florida rivers, but they never collected in the STR. No reference to vertebrate fossils from the STR were published prior to 2001 [1–5]. The first, and so far, only, fossil vertebrate specimen from the STR to be found in a scientific publication is an Eocene basilosaurid cetacean tooth, UF/VP 21221 [6]. It is not known when recreational fossil collecting began in the STR. In a popular fossil guidebook published in 1988 [7], the STR is noted as a good place to collect fossils of Pleistocene land vertebrates and Eocene marine vertebrates and invertebrates.

Vertebrate fossils in the FLMNH collection have been found in over 100 rivers, streams, and spring runs from Florida. Most are collected in modern alluvium, having been eroded, transported, and redeposited, sometimes repeatedly. More rarely, in situ deposits with fossils are found either in the bank or on the beds of waterways. Examples from Florida include skeletons of the oreodont *Mesoreodon floridensis* and other fossils from the late Oligocene White Springs 3B locality in the bed of the Suwannee River [8], a nearly complete skeleton of the late Miocene dugong *Metaxytherium floridanum* (UF/VP 11579) from a creek

bank in northwestern Gainesville [9], well-preserved early Pleistocene skulls of the sloth *Megalonyx leptostomus* (UF/VP 216900) and the raccoon *Procyon megalokolos* (UF/VP 275500) along with a diverse fauna at the Withlacoochee River 1A locality [10–12], and an associated complete skull and mandible of *Panthera atrox* found in the bed of the Ichetucknee River (UF/VP 9076) [13].

Figure 1. Map of the Steinhatchee River (STR) in the Big Bend Region of northcentral Florida showing the general location of the STR 2A vertebrate fossil locality and the boundaries of the STR 1, STR 2, STR 3, and STR 4 subdivisions of the river indicated by lines drawn across the river.

The Irvingtonian North American Land Mammal Age (NALMA) was proposed in 1951 [14] and its boundaries were revised in 2005 [15]. The Irvingtonian falls between the Blancan and Rancholabrean NALMAs, and it correlates with the later part of the early Pleistocene and most of the middle Pleistocene (ca. 1.6–0.25 Ma). The first publications of fossil sites from Florida that were designated as Irvingtonian did not occur until 1974 [4,16]. But some collecting in the first half of the 20th century did recover fossils later recognized as Irvingtonian.

The first, but long unrecognized, source for Irvingtonian fossils in Florida were the open-pit phosphate mines of southwestern Polk and adjacent counties in southcentral Florida. These mines are well known for their early Pliocene (latest Hemphillian NALMA) fossils, collectively known as the Palmetto Fauna [17,18], and middle Miocene sirenians and cetaceans [9,19]. Fossils of the Pleistocene mammals *Mammuthus* and *Equus* were

collected in these mines during the early 1900s [1], as was a distal phalanx of a megatheriid sloth [20]. It was not until stratigraphically controlled collecting in the phosphate mines by S. D. Webb and J. S. Waldrop in the 1960s and 1970s resulted in many specimens with sufficient taxonomic diversity to show that almost all the Pleistocene vertebrate fossils from these phosphate mines were from the Irvingtonian [21].

In 1941, Ted Galusha and associates working for Childs Frick collected vertebrate fossils from two fissure fill deposits in the McLeod Limerock Mine, Levy County, north-central Florida. No published research was conducted on the McLeod fossils until after Frick's collection was integrated into the American Museum of Natural History after his death [22–25], and most taxa from McLeod remain unstudied. Personal communication from Galusha was cited as the basis for a Irvingtonian age for the McLeod fossils [22], but no additional data were provided to support this claim. The relatively large size and derived morphology of the McLeod specimens of *Smilodon gracilis* suggested an age younger than early Irvingtonian [23]. In the first detailed discussion of the biochronology of the McLeod local fauna [21], it was placed in the middle Irvingtonian, the first and, until the present, only locality of this age from Florida.

Several Irvingtonian localities were discovered in Florida in the middle and late 1960s (Table 1, Figure 2). Four of these, Inglis 1A, Punta Gorda, Pool Branch, and Coleman 2A, were the first to be published [4,26,27]. The mammals from the latter were comprehensively studied [16], and the mammals present for all four of these sites were listed in a table in [4]. Updated mammalian faunal lists for Inglis 1A and Colemen 2A appeared in [28]. Additional Irvingtonian sites were discovered in Florida during the 1970s and 1980s (Table 1), most notably those from Leisey Shell Pit (Figure 2). They led to a more detailed chronology of Pleistocene fauna and mammalian species ranges in Florida, and a division of the Irvingtonian in Florida into four subintervals [21,24]. The oldest of these subintervals, best characterized by the Inglis 1A, Inglis 1C, and De Soto Shell Pit localities, is now regarded as latest Blancan following revision of the Blancan–Irvingtonian boundary from about 2 Ma to about 1.6 Ma [12,15]. Thus, the Irvingtonian in Florida is currently divided into three subintervals, named the Irvingtonian 1, 2, and 3 (Ir1, Ir2, and Ir3) from oldest to youngest. For the ages of these subintervals, we accept the values presented by [29]—Ir1, 1.6–1.0 Ma; Ir2, 1.0–0.4 Ma; and Ir3, 0.4–0.25 Ma—although their boundaries are not well calibrated. The number of significant Irvingtonian localities in Florida has substantially increased since 1995, most importantly being the addition of more Ir3 sites (Table 1). This has allowed better characterization of this subinterval. The Ir2 is still the most poorly known of the Florida Irvingtonian subintervals.

## 2. Geographical and Geological Settings

The Steinhatchee is a relatively short (ca. 60 km long), blackwater river in the Big Bend region of northcentral Florida ([30]; Figure 1). It originates in southwestern Lafayette County, then courses in a generally south-southwestern direction forming the boundary between Dixie and Taylor counties, and finally turns west just before reaching the Gulf of Mexico. Its banks and bed are largely Eocene limestone. Limestone is present at or near the surface over much of the Florida platform, and, given the area's hot and humid climate, karst features are common today, particularly sinkholes, caves, and springs [31,32]. Karstification in northcentral Florida has been ongoing since the late Oligocene, as evidenced by fossils of this age recovered from ancient paleokarst deposits [33] such as the SB-1A, Buda, and Brooksville localities [34–37]. In all, over 160 paleokarst deposits with vertebrate fossils are known from Florida, including some of the richest localities known from the state such as Thomas Farm, Inglis 1A, and Reddick [33,38–44]. Most of these have been exposed by open-pit mining of limestone, but a few have been discovered in banks or beds of rivers. Examples of the latter are the Miller Site in the lower Suwannee River [45,46] and the Withlacoochee River 1A and 4A localities [12,47,48].

Table 1. Major Irvingtonian vertebrate fossil localities from Florida. Date is the year that fossils were first collected at that locality. MSR (mammal species richness) is the number of known mammalian taxa. Numerals in MAP NO. are used to identify sites on the map in Figure 2. Inglis 1A, long considered to be Irvingtonian, is now regarded as the latest Blancan [12,15].

Locality	County	Site Code	Date	MSR	Subage	Map No.
McLeod Limerock Mine	Levy	LV003	1941	14	Ir2	1
Punta Gorda	Charlotte	CH002	1964	8	Ir1	2
Pool Branch Site	Polk	PO014	1964	13	Ir1	3
Coleman 2A	Sumter	SM001	1965	36	Ir3	4
Sebastian Canal	Brevard	BR009	1967	12	Ir3	5
Payne Creek Mine	Polk	PO069	1969	22	Ir1	6
Palmetto Mine	Polk	PO097	1969	22	Ir1	6
Crystal River Power Plant	Citrus	CI011	1969	16	Ir1	7
Haile 16A	Alachua	AL033	1973	33	Ir1	8
Leisey Shell Pit 2	Hillsborough	HI010	1978	9	Ir1	9
Rigby Shell Pit	Sarasota	SA001	1982	12	Ir1	10
Phosphoria Mine	Polk	PO128 and PO131	1982	9	Ir1	6
Pareners Branch	Alachua	AL058	1982	10	Ir1	11
Leisey Shell Pit 1A	Hillsborough	HI007	1983	34	Ir1	9
Haile 21A	Alachua	AL043	1983	17	Ir1	8
Leisey Shell Pit 3A	Hillsborough	HI015	1986	17	Ir1	9
Leisey Shell Pit 3B	Hillsborough	HI019	1987	13	Ir1	9
Fort Green Mine	Hardee/Polk	PO094 and HR052	1988	9	Ir1	6
Tucker Borrow Pit	Brevard	BR011	1993	13	Ir1	12
Tri-Britton Site	Hendry	HN011	2001	18	Ir3	13
La Belle Highway Pit	Hendry	HN012	2001	16	Ir3	14
Dickerson Coquina Pit	St. Lucie	SL002	2002	16	Ir3	15
Haile 16B	Alachua	AL124	2005	9	Ir1	8
Steinhatchee River 2A	Dixie	DI012	2022	11	Ir2	16

The FLMNH naming convention for vertebrate fossil sites in rivers is to divide a river into sections which are assigned numbers. Individual sites within a section are assigned letters, starting with A. When the river forms the boundary between two counties, for cataloging and databasing purposes the site is assigned to the county to the east or north of the boundary. The Steinhatchee River (STR) is divided into four sections by the FLMNH VP division (Figure 1), with STR 1 extending from its mouth at the Gulf of Mexico to the point of its confluence with Boggy Creek at ca. 29.718° N, 83.347° W. STR 2 extends from there to the Steinhatchee River Rise at ca. 29.770° N, 83.325° W. STR 3 begins where the river exits Lafayette County, ca. 29.823° N, 83.313° W and ends at its southern terminus at the Steinhatchee Sink at 29.777° N, 83.316° W. The river flows underground between the sink and rise for about 1.1 km. STR 4 includes that portion of the river within Lafayette County.

The Steinhatchee River 2A Locality—The fossil site discovered by Sinibaldi and Branin in June 2022 lies within the lower third of STR 2 as defined above (Figure 1, exact location on file at FLMNH). In the FLMNH database, its locality code is DI012. The site's dimensions are about 23.5 m parallel to the bank by about 5.6 m; its thickness has not been determined. Sediments consist of a mixture of medium- to large-sized limestone boulders and light gray clay. These sediments match those of the adjacent bank, leading us to conclude that STR 2A represents a large slump from a paleosinkhole now exposed on the bank. Given the freshness of the exposed fossil bones, the minimal amount of covering of vegetation and sandy debris, and that the site was not found by any previous fossil collectors, the slump is likely to be relatively recent. The STR experienced severe flooding during August 2019 when local rainfall amounts of 60 to 80 cm occurred within a few days, and this may have been the triggering event of the slumping.
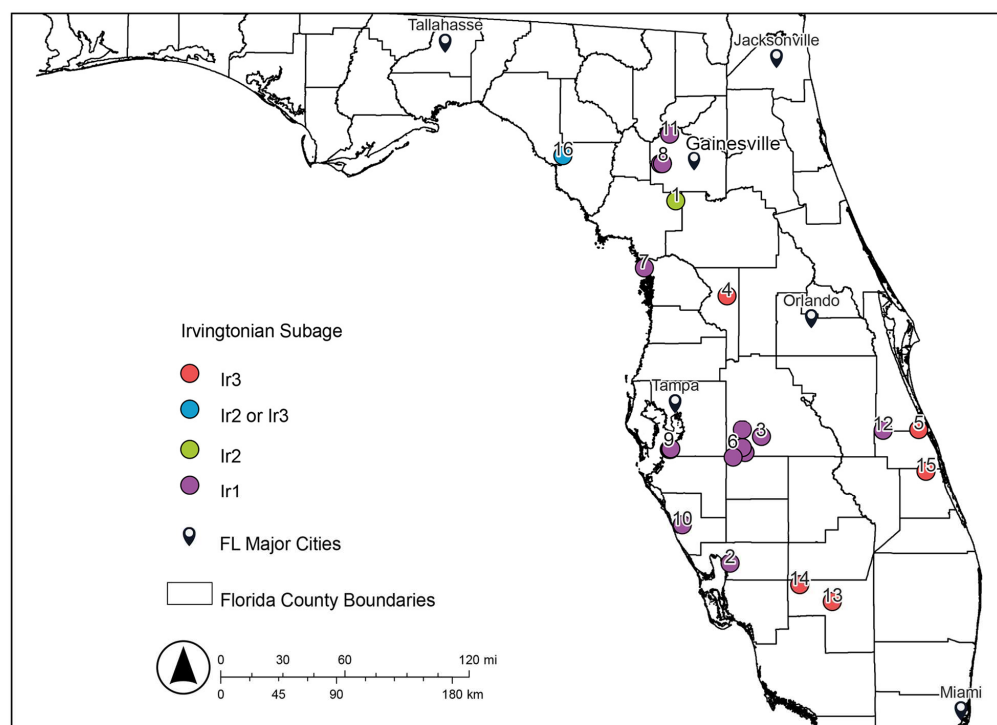
Figure 2. Location of major Irvingtonian vertebrate fossil localities in Florida. Numerals match sites as shown in Table 1. Numbers 6, 8, and 9 refer to multiple sites within a relatively small aera.

The top of the fossil-bearing sediments of STR 2A during average water levels varies from 1 to 3 m below the river's surface. The discovery on 22 June 2022 occurred when water levels were unusually low due to a drought combined with a lower-than-normal tide, thus the highest portions of the site were exposed above the water. On all subsequent collecting trips, water levels were much higher, and the entire site was submerged. Collecting was carried out using scuba gear and lights because of the murky dark water. The last collecting trip was on 8 August 2023, just before the area was impacted by Hurricane Idalia. On that day, about 26 kg of sediment (dry weight) was collected for later screenwashing at the FLMNH. No fossils of small mammals were found in the washed matrix, but it did produce two teeth from large mammals (UF/VP 556641 and 559767), two partial armadillo osteoderms (UF/VP 559765–559766), and the five fish vertebrae described below. The STR 2A fossils were collected legally under the aegis of Florida's Program of Vertebrate Paleontology and duly reported to the FLMNH.

3. Materials and Methods

The STR 2A fossils are housed in the UF/VP research collection of the Division of Vertebrate Paleontology, Florida Museum of Natural History (FLMNH), Gainesville (USA). They were identified by comparison with previously cataloged Pleistocene fossils in the collection, as well as skeletons of modern vertebrates in collections of the FLNMH. The catalog records of all the specimens can be downloaded from https://specifyportal.floridamuseum.ufl.edu/vp with a search for Site Key equal to DI012 (first two letters must be capitalized). Linear measurements were taken with digital calipers to the nearest 0.1 mm. Digital images of specimens were taken with a Nikon D5100 camera and an AF-S Micro NIKKOR 60 mm F2.8G ED lens. The images were edited with Adobe Photoshop to remove backgrounds, add scale bars, and when necessary to lighten or darken images to improve visibility of features.

Abbreviations used for mammalian teeth are I and i for upper and lower incisors, C and c for upper and lower canines, P and p for upper and lower premolars, and M and m for upper and lower molars. Deciduous teeth are identified using D or d. A

numeral following one of these abbreviations indicates tooth position. For example, DI2 is a deciduous upper second incisor and p3 is a permanent lower third premolar. Dental measurement abbreviations are AW, anterior width; L, length; and PW, posterior width. Equid and camelid cheekteeth are measured both on the occlusal surface and at the base of the crown; these are differentiated using the abbreviations O and B, respectively, e.g., BPW.

Institutional collection abbreviations used are AMNH FM, fossil mammals, American Museum of Natural History, New York (USA); MCZ VPM, mammalian vertebrate paleontology, Museum of Comparative Zoology, Harvard University, Massachusetts (USA); UF/VP, vertebrate paleontology, Florida Museum of Natural History, University of Florida, Gainesville (USA); UF/TRO, former Timberlane Research Organization fossil collection, now housed at the FLMNH; UF/FGS, former Florida Geological Survey vertebrate fossil collection, now housed at the FLMNH.

4. Results

Systematic Paleontology

Class ACTINOPTERYGII Klein, 1885
Subclass NEOPTERYGII Regan, 1923
Infraclass TELEOSTEI Müller, 1845
Referred specimens: UF/VP 559768, atlas vertebra; UF/VP 559769–559772, four vertebrae.

Description: Three of the vertebrae, UF/VP 559768–559770, are distinctly smaller than the other two (Figure 3D,E). The length and width dimensions of the former group are in the range of 1.0 to 1.5 mm, while those of the latter are 3.3–4.5 mm. This, plus different morphologies, suggest multiple taxa are represented.

Comments: No attempt has been made to identify this small sample to lower taxonomic levels. Future collecting trips to the site will bring back much larger quantities of matrix for screenwashing that should produce diagnostic cranial bones of bony fish as well as additional vertebrae. The fossils of fish from STR 2A may have resulted from dissolution of Eocene marine limestone in the paleokarst feature. If they belong to marine taxa, then an Eocene age is most likely, while if they belong to freshwater taxa, then they are probably from the Pleistocene.

Class REPTILIA Laurenti, 1768
Order TESTUDINES Batsch, 1788
Family EMYDIDAE Rafinesque, 1815
Genus *Terrapene* Merrem, 1820
Terrapene cf. *putnami* Hay, 1906
Referred specimens: UF/VP 548213, fused neural 1 and 2; UF/VP 548214, two fused peripherals.

Comments: Although fragmentary, the two referred specimens display typical features of the carapace of *Terrapene* but are much larger than extant *T. carolina*. Box turtles substantially larger than extant individuals are known from the Blancan, Irvingtonian, and Rancholabrean of Florida [49]. Complete or nearly complete carapaces of large-sized *Terrapene* from the Blancan and early Irvingtonian are morphologically distinct from those of the Rancholabrean specimens, including the neotype UF/VP 3066, and likely represent an undescribed new species [49]. The fossils of *Terrapene* are known from all major Ir2 and Ir3 sites in Florida (Table 1). Specimens of similar size as those from STR 2A are present at Tri-Britton, LaBelle Highway Pit, and Dickerson Coquina Pit. More study is needed to determine if the affinities of large *Terrapene* from the Ir2 and Ir3 of Florida are closer to *T. putnami* of the Rancholabrean or the undescribed species from the Blancan and Ir1.

Figure 3. Osteichthyes and Reptilia from Steinhatchee River 2A, middle Pleistocene, Florida. (**A**) UF/VP 548212, *Alligator mississippiensis*, dorsal view of osteoderm. (**B**,**C**) UF/VP 548472, *A. mississippiensis*, dorsal and lateral views of partial left dentary. (**D**) UF/VP 559771, indeterminate teleost, lateral view of trunk vertebra. (**E**) UF/VP 559768, indeterminate teleost, anterior view of atlas vertebra. (**F**,**G**) UF/VP 548215, *Caudochelys* cf. *crassiscutata*, posterior and dorsal views of right peripheral 11.

Family TESTUDINIDAE Batsch, 1788
Genus *Caudochelys* Auffenberg, 1963
Caudochelys cf. *crassiscutata* (Leidy, 1889)
Referred Specimen: UF/VP 548215, subadult right peripheral 10 and 11 (P10 and P11), associated.

Description: When compared to UF/VP 3151, a subadult shell of *Caudochelys cras-siscutata* from the Rancholabrean Haile 8A locality [50], the morphology of the associated pair of peripherals of UF/VP 548215 closely match only those of the right P10 and P11 (Figure 3F,G). The length of the proximal end of the P11 (ca. 24 mm) is about half that of its distal end (ca.

47 mm). In UF/VP 3151, those dimensions are 21.2 and 39.2 mm, respectively. The posterior border of the P11 that articulates with the pygal is generally straight while the anterior side is slightly convex (Figure 3F). The posterior border of the P10 of UF/VP 548215 is correspondingly concave, while its anterior side is convex. The dorsal surfaces of both peripherals in UF/VP 548215 are proximodistally concave, while those of UF/VP 3151 are flat.

Comments: Medium- to large-sized tortoises persisted in Florida from the early Miocene to the late Pleistocene [50–52]. Thus, their presence at STR 2A is unsurprising. Use of the name *Caudochelys* for this lineage at the genus-level follows [52]; previously, it was used first as a subgenus of *Geochelone*, and later *Hesperotestudo*.

Order CROCODYLIA Owen, 1842
Family ALLIGATORIDAE Gray, 1844
Genus *Alligator* Cuvier, 1807
Alligator mississippiensis (Daudin, 1802)

Referred Specimens: UF/VP 548209, left premaxilla with fifth tooth; UF/VP 548472, anterior portion of left dentary (Figure 3B,C); UF/VP 548473, trunk vertebra; UF/VP 548476, left proximal femur; UF/VP 54876, adult osteoderm; UF/VP 548210–548212, 3 subadult osteoderms, possibly associated (Figure 3A).

Comments: The premaxilla is from a much larger individual than the femur or dentary. All referred specimens are morphologically indistinguishable from those of extant *Alligator mississippiensis*. Fossils of *A. mississippiensis*, especially isolated teeth, osteoderms, and vertebrae, are found at most Ir sites in Florida, including Leisey Shell Pit 1A, Haile 16A, Haile 21A, Tri-Britton, and LaBelle Highway Pit.

Class MAMMALIA Linnaeus, 1758
Superorder XENARTHRA Cope, 1889
Order CINGULATA Illiger, 1811
Family PAMPATHERIIDAE Paula Couto, 1954
Genus *Holmesina* Simpson, 1930
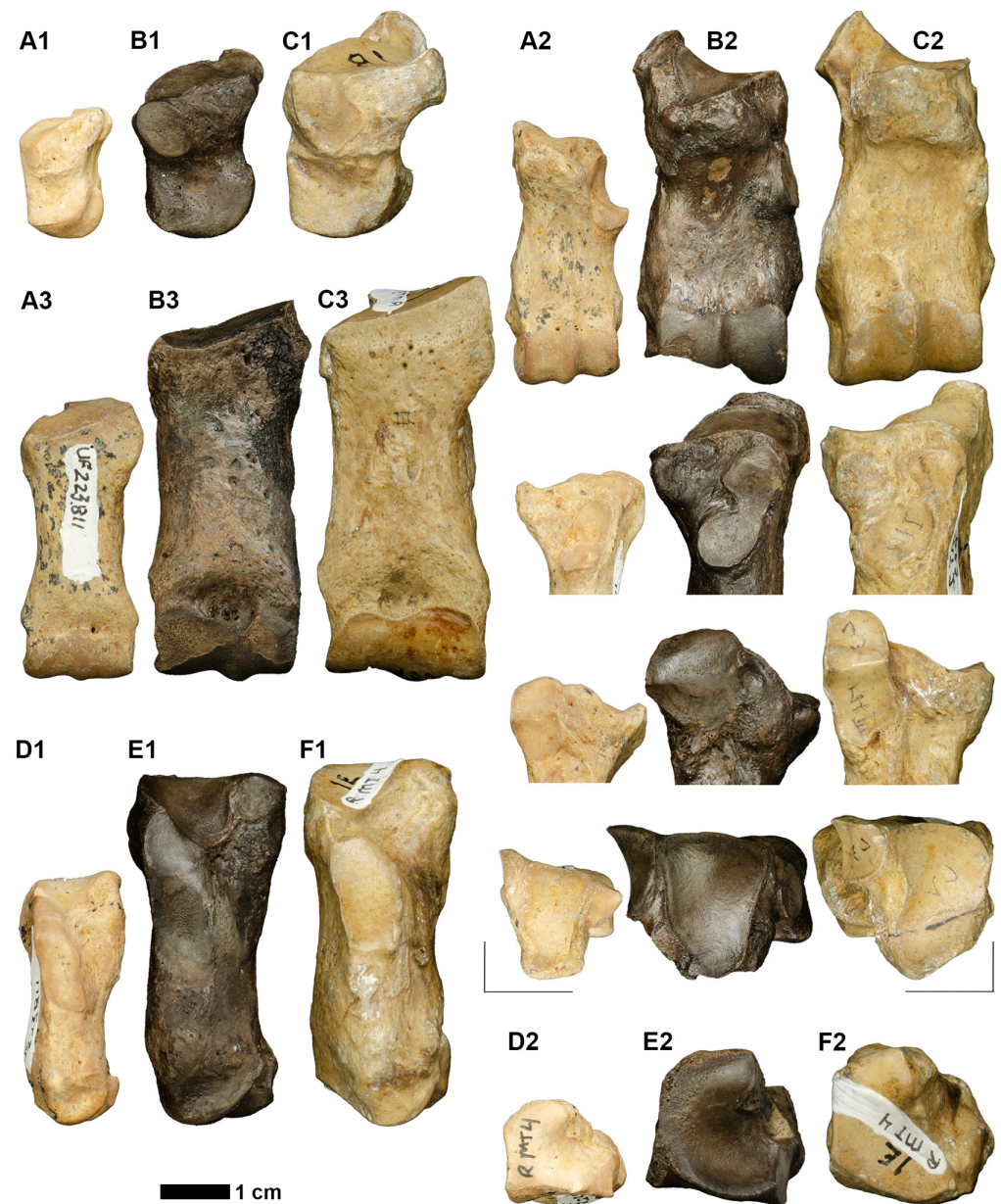*Holmesina* cf. *septentrionalis* (Leidy, 1889)

Referred Specimens: UF/VP 548221, 548222, two cephalic osteoderms; UF/VP 546749, diaphysis of left ulna; UF/VP 548219, 560009, 560010, three immovable carapacial osteoderms; UF/VP 548223, 560007, two immovable carapacial osteoderms of the first row from the pelvic buckler; UF/VP 560008, immovable carapacial osteoderm of the second row from the pelvic buckler; UF/VP 548218, marginal carapacial osteoderm; UF/VP 548220, caudal osteoderm; UF/VP 560011, right metatarsal (MT) 4; UF/VP 560012, associated left pes including MTs 1, 2, and 3, the distal phalanx of digit 2, and the proximal, medial and distal phalanges of digit 3; UF/VP 548224, left astragalus.

Description: Both cephalic osteoderms are complete with the position of UF/VP 548221 towards the anterior portion of the cephalic shield and UF/VP 548222 near the postorbital margin based on thickness and dorsal ornamentation (Figure 4G,H). The diaphysis of the left ulna (UF/VP 546749) is complete but the proximal and distal epiphyseal plates were not recovered (Figure 4A). UF/VP 548219 is missing only a fragment of the anterior portion of the immovable carapacial osteoderm, while UF/VP 560009 and UF/VP 560010 are complete. One immovable carapacial osteoderm of the first row from the pelvic buckler is within the typical size range while the other is notably wide; approximately the width of two imbricating osteoderms fused together. (Figure 4L,M). The immovable carapacial osteoderm from the second row of the pelvic buckler (UF/VP 560008) is complete and does not articulate with either of those from the first row of the pelvic buckler (Figure 4K). UF/VP 548218 is a complete marginal osteoderm which would have been laterally oriented on either the left pectoral buckler or right pelvic buckler of the carapace due to the placement of the two suture zones versus the marginal edges with no suture (Figure 4J). UF/VP 548220 is a relatively small caudal osteoderm presumably from the distal portion of the tail in life (Figure 4I).

Figure 4. *Holmesina* cf. *septentrionalis* (**A**,**G**–**M**) and *Dasypus bellus* (**B**–**F**) fossils recovered from STR 2A. (**A**) UF/VP 546749, diaphysis of left ulna, anterior view. (**B**) UF/VP 548216, distal right humerus; upper, anterior view, medial right; lower, posterior view, medial left. (**C**) UF/VP 548469, subadult right calcaneum, left, medial view, right, dorsal view. (**D**) UF/VP 548483, carapacial osteoderm. (**E**) UF/VP 548217, imbricating osteoderm. (**F**) UF/VP 559766, rostral portion of imbricating osteoderm. (**G**) UF/VP 548222, postorbital cephalic osteoderm. (**H**) UF/VP 548221, anterior cephalic osteoderm. (**I**) UF/VP 548220, caudal osteoderm. (**J**) UF/VP 548218, marginal osteoderm. (**K**) UF/VP 560008, osteoderm from second row pelvic buckler. (**L**) UF/VP 560007, immovable osteoderm first row pelvic buckler. (**M**) UF/VP 548223, large immovable osteoderm first row pelvic buckler. (**A**–**C**) postcranials, proximal end up. (**D**–**M**) osteoderms, dorsal view, proximal left.

UF/VP 560012 includes several associated elements from the left pes, including MTs 1, 2, and 3, the distal phalanx of digit 2, and the proximal, medial, and distal phalanges of digit 3 (Figure 5B1–B3). A left astragalus (UF/VP 548224; Figure 6C) was also recovered from the site and may be associated with the other left pes elements. All of these pes elements are complete except for minor breakage on the distal portion of MT2 and proximal portion of MT3. UF/VP 560011, a right MT4, is similar in size and may be associated with the left pes elements (UF/VP 560012; Figure 5E1–E2).

Figure 5. *Holmesina* metatarsals (MT) from the Pleistocene of Florida. (**B**) (UF/VP 560012) and (**E**) (UF/VP 560011), *H*. cf. *septentrionalis* MTs from Steinhatchee River 2A compared to those of (**A**,**D**), UF/VP 223811, *Holmesina floridanus* from Haile 7G, late Blancan and (**C**,**F**), UF/VP 9336, *H. septentrionalis* from Branford 1A, late Rancholabrean. (**A1**–**A3**) Left MT1–3. (**B1**–**B3**) Left MT1–3. (**C1**–**C3**) Right MT1–3 mirrored for comparison to left MTs. (**A1**–**C1**) Left lateral view, proximal up, anterior left. (**A2**–**C2**) First row, posterior view, anteromedial concavity with articular facet for MT1 right; second row, right lateral view, anterior right; third row, left lateral view, anterior left; fourth row, proximal view, anterior up. (**A3**–**C3**) Anterior view, articulation with MT2 right. (**D**–**F**) Right MT4s. (**D1**–**F1**) Left lateral view, anterior left. (**D2**–**F2**) Proximal view, articulation with MT 3 right. Proximal up, scale 1 cm.
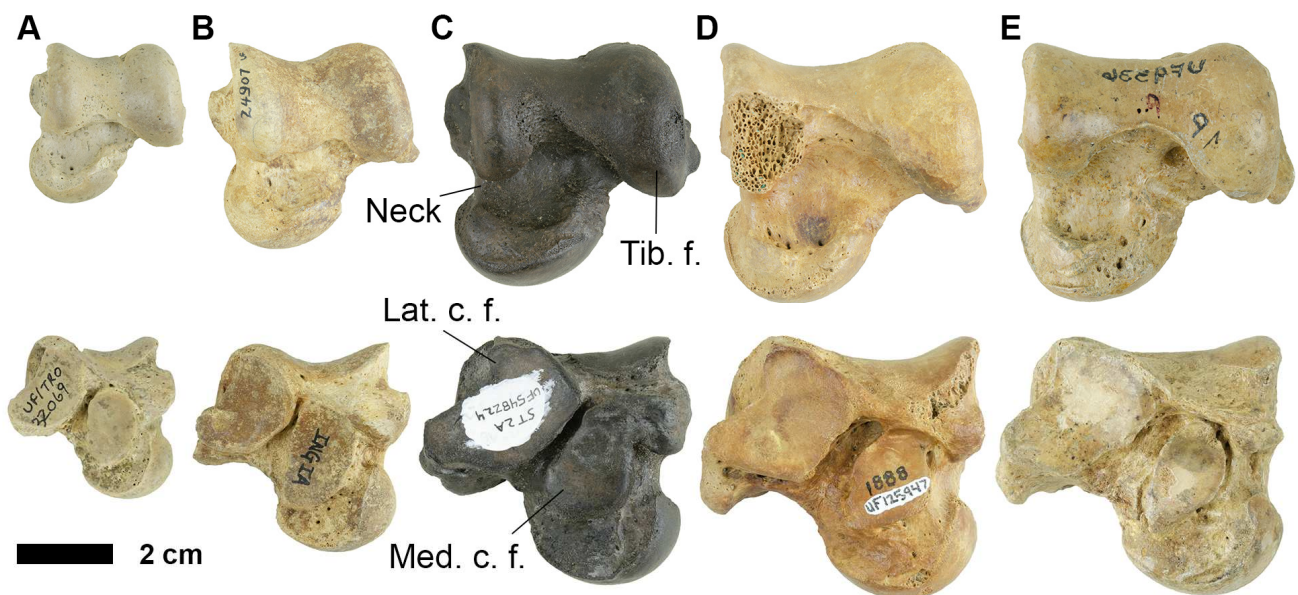
Figure 6. Range of size and morphology in *Holmesina floridanus* and *H. septentrionalis* astragali through time (early Blancan to late Rancholabrean). (**A**) UF/TRO, 32069 *H. floridanus*, Haile 15A, ~2.5 Ma, early late Blancan. (**B**) UF/VP 24907, *H. floridanus*, Inglis 1A, ~1.8 Ma, latest Blancan. (**C**) UF/VP 548224, *H.* cf. *septentrionalis*, STR 2A, middle Irvingtonian. (**D**) UF/VP 125997, *H. septentrionalis*, Rock Springs, ~125 ka, early Rancholabrean. (**E**) UF/VP 9336, *H. septentrionalis*, Branford 1A, ~20 ka, latest Rancholabrean. Upper is anterior/dorsal view, lower is posterior/ventral view, proximal up. Features labeled to indicate where measurements were taken from the neck, astragular neck; Tib. f., tibial facet; Lat. c. f., lateral calcaneal facet; Med. c. f., medial calcaneal facet.

Comments: Pampathere fossils recovered from Florida have been identified as either *Holmesina floridanus* or *H. septentrionalis*. These taxa have been considered an unbranching chronocline by some authors, with *H. floridanus* the smaller representative recovered from the Blancan and early Irvingtonian, and *H. septentrionalis* the larger, more widespread representative recovered from the middle Irvingtonian through Rancholabrean [24,53]. The skeletal anatomy of both *Holmesina* species is similar, but *H. septentrionalis* has greater weight-bearing features [24,53]. A body mass of 44 to 91 kg has been estimated for *H. floridanus* (for late Blancan and early Irvingtonian specimens, respectively), whereas that of *H. septentrionalis* is 216 kg, more than twice the mass of *H. floridanus* [54].

Teeth, osteoderms, and limb elements of *Holmesina* fossils from Florida ranging from the early to latest Pleistocene were analyzed quantitatively and qualitatively in [24] to observe evolutionary patterns and rates and to determine whether the sample was most appropriately regarded as one, two, or three species. The greatest change in size occurred between fossils recovered from the late Blancan and Ir1 but with few morphological differences. However, at least 11 postcranial character differences were found between individuals from the Ir1 and those appearing after the Ir1, along with a substantial increase in size. This was recommended to be the separation between *H. floridanus* and *H. septentrionalis* [24]. We use many of the characters used by [24] to assess the conditions observed in the STR 2A specimens.

The pampathere skeletal elements recovered from STR 2A are tentatively attributed to *Holmesina septentrionalis* based on their relatively large size (Figures 5 and 6; Tables 2 and S1), but they do retain several primitive characteristics found in *H. floridanus*. In addition to their larger size, the STR 2A carapacial osteoderms have a pronounced sagittal keel on their dorsal surfaces as in those of *H. septentrionalis* (Figure 4K–M). The STR 2A pes elements are more variable with size and characteristics intermediate between those of *H. floridanus* and *H. septentrionalis* (Figures 5 and 6).

Table 2. Measurements recorded from astragali of *Holmesina floridanus* (n = 52) and *H. septentrionalis* (n = 14) for comparison to that of the Steinhatchee River 2A *Holmesina* (UF/VP 548224). Measurements were taken with digital calipers and ranges are reported in millimeters. All measurements are listed in Table S1.

Measurement	*H. floridanus*	UF/VP 548224	*H. septentrionalis*
Greatest length, observed range (OR)	30.5–44.8	50.4	45.4–54.4
Proximal articular width, (OR)	24.4–38.8	43.5	42.0–53.0
Depth of tibial facet, medial side, (OR)	17.4–27.8	28.9	25.1–32.1
Distal articular width, (OR)	17.4–26.1	30.1	27.3–31.7
Width of astragular neck range (mm)	15.8–26.7	27.3	28.1–34.8
Greatest diameter of lateral calcaneal facet, (OR)	13.7–24.5	30.6	27.2–32.3
Greatest diameter of medial calcaneal facet, (OR)	11.7–20.6	24.3	17.1–24.7
Minimum distance between calcaneal facets, (OR)	0–3.7	1.9	1.85–6.1
Ratio of gr. diameters of medial and lateral facets, median	84.9%	79.5%	72.6%

The STR 2A astragalus (UF/VP 548224) is within the size range of those of *H. septentrionalis* but intermediate in morphology between *H. floridanus* and *H. septentrionalis* (Figure 6; Table 2). Morphological characteristics shared between UF/VP 548224 and those of *H. floridanus* include an outward extension of the medial process, narrow separation between the medial and lateral facets for articulation with the calcaneum, and similar surface areas of those facets (Figure 6A–C), whereas the medial facet is much smaller than the lateral in *H. septentrionalis* (Figure 6D,E). The astragalus of UF/VP 548224 shares with those of *H. septentrionalis* a strong trochlear indentation on the anterior border of the facet for articulation with the tibia, a concavity on the astragular neck in dorsal view, and some projection of a distolateral process (Figure 6C–E).

Eight measurements were taken on *H. floridanus* and *H. septentrionalis* astragali for comparisons to that of the STR 2A *Holmesina* (UF/VP 548224; Tables 2 and S1). All STR 2A measurements fall within the range of *H. septentrionalis* except for the width of the astragular neck (27.3 mm), which is between the recorded ranges of *H. floridanus* and *H. septentrionalis* (Table 2). The minimum distance between the calcaneal facets in the STR 2A astragalus falls just within the lower end of the range for *H. septentrionalis* and is much closer to the mean value of *H. floridanus*.

Average variation in proportions of certain features, as captured by the coefficient of variation, is greater in *H. floridanus* than *H. septentrionalis*, which is likely due to the known size differences between early late Blancan and early Irvingtonian individuals [24]. Apart from the greater variation in *H. floridanus*, the overall measurement variation for specific astragular features is not significant except for a recorded coefficient of variation notably greater in the measurement capturing the minimum distance between calcaneal facets (44.86% in *H. floridanus* and 32.98% in *H. septentrionalis*), indicating major individual variation in this feature for both species.

The MT1 of UF/VP 560012 is noticeably larger than those of *H. floridanus* and slightly smaller than those of *H. septentrionalis* (Figure 5A1–C1). The medial facet for articulation with MT2 is smallest and continuous with the facet for articulation with the entocuneiform in *H. floridanus* (Figure 5A1). The facet for articulation with MT2 is larger and less continuous with the facet for articulation with the entocuneiform in UF/VP 560012 and even more so in *H. septentrionalis* (Figure 5B1,C1).

The STR 2A MT2 is morphologically similar to those of *H. septentrionalis* in lacking the anteromedial concavity with the articular facet for MT1 as found in *H. floridanus* [24] (Figure 5B2,C2). However, the proximal end of the STR 2A MT2 shares several features with *H. floridanus*, including a posteriorly sloping facet for articulation with the mesocuneiform, continuous facets for articulation with MT1 and entocuneiform and with the MT3 and ectocuneiform, and less separation between the facets for the mesocuneiform and ectocuneiform (Figure 5A2,B2).

Apart from size, the morphology of MT3 does not differ much between *H. floridanus* and *H. septentrionalis*. Differences were found in the proximal articulation with the ecto-

cuneiform in *H. floridanus* and *H. septentrionalis*, but this feature cannot be observed in UF/VP 560012 due to breakage. An additional difference previously unreported in the anterior view of MT3 is an indentation above the distal facet for articulation with the proximal phalanx of digit 3 in both *H. septentrionalis* and that of STR 2A UF/VP 560012, but absent in *H. floridanus* (Figure 5A3–C3).

Along with MT1 and MT2, MT4 has more morphological differences between *Holmesina* taxa than in MT3. Interestingly, the proximal articular surface with the cuboid of MT4 is narrowest in *Holmesina* from the Irvingtonian, broader in those from the Blancan, and broadest in those from the Rancholabrean, indicating a narrowing during the Irvingtonian [24]. This pattern is seen in the STR 2A specimen with a proximal articular surface narrower than those of *H. floridanus* and *H. septentrionalis* (Figure 5D2–F2). In anterior view, the proximal portion of UF/VP 560011 is broader than those of *H. floridanus* and *H. septentrionalis*. The medial facet for articulation with the MT3 is similar in UF/VP 560011 and those of *H. floridanus* in having continuity with the cuboid facet, while these two facets are not continuous in MT4 of *H. septentrionalis* (Figure 5D1–F1).

Family DASYPODIDAE Gray, 1821
Genus *Dasypus* Linnaeus, 1758
Dasypus bellus (Simpson, 1929)

Referred Specimens: UF/VP 548216, distal right humerus; UF/VP 548483, 559765, two immovable carapacial osteoderms; UF/VP 548217, 559766, two partial imbricating osteoderms; UF/VP 548469, partial right calcaneum.

Description: The distal right humerus (UF/VP 548216; Figure 4B) is preserved proximal to the deltoid tuberosity and shows more post-mortem surface wear than the other *D. bellus* specimens from STR 2A (Figure 4B). Two complete osteoderms of *D. bellus* were recovered from STR 2A, an immovable carapacial osteoderm (UF/VP 548483; Figure 4D) and an imbricating osteoderm (UF/VP 548217; Figure 4E). Additionally, two partial osteoderms were recovered during screenwashing efforts including half of an immovable carapacial osteoderm and the rostral portion of an imbricating osteoderm (Figure 4F). The partial right calcaneum of UF/VP 548469 is nearly complete but missing the medial astragular facet and the distal epiphysis (Figure 4C). The rugose epiphyseal surface of the calcaneal process indicates that the epiphysis was not fused in life and therefore the bone is from an immature individual.

Comments: At least two individuals of *D. bellus* are represented from STR 2A based on the presence of adult and subadult remains. The fossils recovered are within the size range of Irvingtonian *D. bellus*, although the humerus is smaller than average while the calcaneum is larger (Figure 4B,C). Preliminary comparative measurements of *D. bellus* humeri indicate that the STR 2A distal humerus (UF/VP 548216) is even smaller than those from the late Blancan Inglis 1A and Withlacoochee 1A localities. Not surprisingly, it is also distinctly smaller than humeri from the Rancholabrean. Contrarily, preliminary quantitative analysis of *D. bellus* calcanea reveal a larger size for the STR 2A calcaneum than those from the late Blancan Inglis 1A and Withlacoochee 1A, early Irvingtonian Haile 16A, and even late Rancholabrean Monkey Jungle Hammock localities. These findings are peculiar because the STR 2A distal humerus is from an adult individual while the calcaneum is from a subadult based on the unfused distal epiphysis. Typically, xenarthrans, including *D. bellus*, increased in size over the course of the Pleistocene and show little if any sexual dimorphism [54].

The *D. bellus* osteoderms from STR 2A are within the expected size range for Irvingtonian individuals, except for the partial imbricating osteoderm (UF/VP 559766; Figure 4F), which is more similar in size to those from Rancholabrean localities. An exhaustive study of *D. bellus* from Florida is needed to better understand the size disparity more broadly and investigate any potential sexual dimorphism along with geographic and chronologic trends.

Order PILOSA Flower, 1883
Family MEGALONYCHIDAE Ameghino, 1889
Genus *Megalonyx* Harlan, 1825

Megalonyx sp.

Referred Specimen: UF/VP 548405, right upper molariform 3.

Description: UF/VP 548405 is preserved from the occlusal surface to the base of the internal dentine, with the thin ever-growing proximal portion not preserved (Figure 7D). The tooth was recovered as two separate pieces during excavation and reunited with adhesive along a longitudinal crack. UF/VP 548405 is identified as a right upper molariform 3 of *Megalonyx* based on comparisons to those in *Megalonyx* spp. skulls recovered from other Florida fossil localities and housed in the FLMNH.
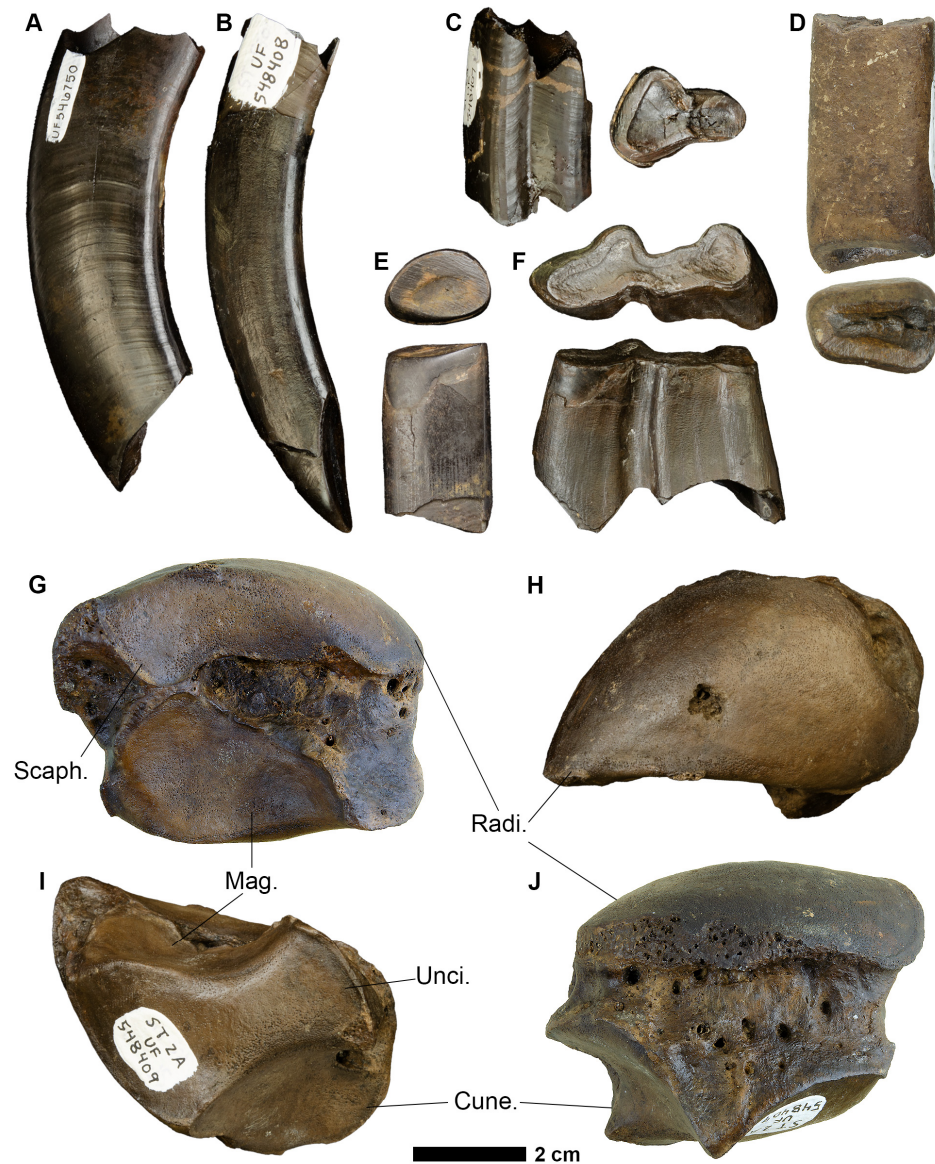
Figure 7. Fossils of *Paramylodon harlani* (**A–C,E–J**) and *Megalonyx* sp. (**D**) from Steinhatchee River 2A, middle Pleistocene, Florida. (**A**) UF/VP 546750, upper left caniniform, left lateral view, occlusal down. (**B**) UF/VP 548408, upper right caniniform, left lateral view, occlusal down. (**C**) UF/VP 548407, right upper juvenile molariform 2, buccal view, occlusal down. (**D**) UF/VP 548405, right upper molariform 3; upper buccal view, occlusal down; lower occlusal view, rostral right. (**E**) UF/VP 559767, partial lower molariform 1; upper occlusal view; lower lingual view. (**F**) UF/VP 548406, left lower juvenile molariform 4; upper occlusal view, lingual down; lower lingual view, occlusal up. (**G–J**) UF/VP 548409, right lunar; (**G**) laterodorsal view; (**H**) proximal view; (**I**) distal view; (**J**) lateroventral view. Abbreviations: Scaph., scaphoid facet; Mag., magnum facet; Radi., radius articular surface; Unci., unciform facet; Cune., cuneiform facet. Scale 2 cm.

Comments. *Megalonyx* of Florida are represented by *M. leptostomus* during the Blancan, *M. wheatleyi* during the Irvingtonian, and *M. jeffersonii* during the Rancholabrean NALMAs. The genus increased in body size through time with an estimated body mass of ~440 kg for *M. leptostomus*, ~600 kg for *M. wheatleyi*, and ~1090 kg for *M. jeffersonii* [54]. Preliminary maximum dimensions of the occlusal surface in several *Megalonyx* molariforms, housed in the FLMNH, were measured for size comparisons (Table S2). UF/VP 548405 has maximum occlusal dimensions of 24.3 mm and 17.2 mm and is noticeably larger than those from the Blancan (average 17.7 by 12.1 mm) and is also slightly larger than those of the Irvingtonian (22.2 by 14.6 mm) (Table S2). The STR 2A *Megalonyx* molariform falls within the size range (average 24.4 by 16.8 mm) of Rancholabrean *M. jeffersonii* with additional measurements needed or more specimens discovered before identifying the STR 2A *Megalonyx* to the species level.

Additionally, UF/VP 548405 is identified as *Megalonyx*, rather than the more commonly recovered *Paramylodon*, because of the wear pattern on the occlusal surface; the softer vasodentine wears more than the surrounding harder orthodentine in *Megalonyx*, causing a ridged surface rather than a flat surface as in those of *Paramylodon*. *Megalonyx* are ecologically interpreted as browsers and often co-occur with the grazing/mixed feeding *Paramylodon* [54,55]. These taxa may have co-existed at STR 2A, with *Megalonyx* less abundant than *Paramylodon*. Alternately, UF/VP 548405 may have been fluvially transported from a Rancholabrean deposit upstream of STR 2A and not collected in situ. The latter is possible because the preservation of UF/VP 548405 differs from most other STR 2A fossils with a lighter brown coloration and greater degree of damage to its external surfaces (Figure 7D).

Family MYLODONTIDAE Ameghino, 1889
Genus *Paramylodon* Brown, 1903
Paramylodon harlani (Owen, 1840)

Referred Specimens: UF/VP 548461, medial fragment of right palate; UF/VP 546750, upper left caniniform tooth; UF/VP 548408, upper right caniniform tooth; UF/VP 548407, right upper juvenile molariform tooth 2; UF/VP 559767, partial lower molariform tooth 1; UF/VP 548406, left lower juvenile molariform tooth 4; UF/VP 548463, right proximal scapula; UF/VP 548464, fragment of proximal humerus; UF/VP 548409, right lunar; UF/VP 548410, right juvenile lunar; UF/VP 548462, right trapezoid; UF/VP 548412, right proximal metacarpal 4; UF/VP 548413, left proximal metacarpal 5; UF/VP 548484, proximal ribs (3); UF/VP 548460, associated left tibia fragments (4); UF/VP 548459, juvenile right calcaneum fragments (2); UF/VP 548425, right lateral astragalus; UF/VP 548411, left juvenile ectocuneiform.

Description: The medial palate fragment (UF/VP 548461) may be from a subadult individual based on the relatively small size and porous texture. Both caniniform teeth are well preserved with most of the ever-growing roots intact (Figure 7A,B). UF/VP 546750 (left caniniform) is approximately twice the diameter of UF/VP 548408 (right caniniform), indicating the presence of at least two adult individuals due to the difference in size. The occlusal surfaces of both juvenile molariform teeth (UF/VP 548406, 548407) and the adult molariform (UF/VP 559767) are well preserved but the ever-growing root portions are broken away (Figure 7C,E,F).

As is typical of scapula preservation in the fossil record, only the glenoid fossa is preserved in UF/VP 548463 with the remainder of the scapula not recovered. The humeral head fragment of UF/VP 548464 could be associated with the proximal scapula. Manus elements preserved for the STR 2A *P. harlani* include right lunars of an adult (UF/VP 548409; Figure 7G) and juvenile (UF/VP 548410), right trapezoid (UF/VP 548462), right proximal metacarpal (MC) 4 (UF/VP 548412), and left proximal MC5 (UF/VP 548413). The lunar, trapezoid, and MC4 of the right manus are more similar in preservation than the MC5 of the left manus and may be associated.

Three proximal rib heads of *P. harlani* are preserved, each also with the proximal portion of the shaft; their lengths (as preserved) are each about 145 mm. Most of the fossils

recovered from STR 2A are varying shades of brown with consistent coloration. One of the proximal ribs has splotches of orange along with dark brown coloration which is indicative of a slightly different preservational environment. All three associated left tibial fragments (UF/VP 548460) preserve part of a facet with one encompassing a portion of the proximal surface and the other two from the distal end.

The right juvenile calcaneum (UF/VP 548459) is fragmented in two parts, one preserving the portion distal to the epiphyseal surface for articulation with the astragalus and the other preserving a portion of the calcaneal process. The lateral portion of the right astragalus (UF/VP 548425) is preserved with at least half of the facet for the articulation with the tibia. A complete left ectocuneiform (UF/VP 548411) from a juvenile was also recovered but is smaller and likely not associated with the right juvenile calcaneum.

Several additional folivoran elements were recovered from STR 2A and while identification cannot be confirmed with the presence of two sloth genera, *Megalonyx* and *Paramylodon*, these likely belong to the more common *Paramylodon*. Additional folivoran elements include the centrum of a thoracic vertebra, two caudal vertebrae, a partial hemal arch, the proximal portion of a rib, a proximal phalanx, and a medial phalanx.

Comments: The *Paramylodon* fossils recovered from STR 2A indicate the presence of at least two adults and, likely, two juveniles. As discussed in the *Megalonyx* section, *Paramylodon* and *Megalonyx* often co-occur with occlusal tooth morphology, indicating a predominately grazing diet for *Paramylodon* and a browsing diet for *Megalonyx*. The abundance of *Paramylodon* remains at STR 2A, along with the single and questionable *Megalonyx* fossil, are indicative of a paleoenvironment with greater grazing potential (i.e., savanna or grassland). This agrees with the large numbers of fossils recovered at STR 2A belonging to grazing ungulates.

Only three *P. harlani* carpals were recovered and yet two of them are right lunars: one juvenile and one adult (Figure 7G–J). The right lunar from an adult individual is complete and compares favorably with the morphology of the juvenile lunar. None of the manus elements would have articulated in life so their associations are unclear.

Three measurements were taken to capture the maximum dimensions of several *Paramylodon* lunars collected from Pleistocene deposits (Table 3). A line drawing of a *P. harlani* right lunar (UCMP 24262) was used to capture the size and morphology of one of the two Rancholabrean specimens [56] (p. 149, Figure 71). Maximum measurements, used to calculate volume, include the maximum length of the radial condyle, maximum height of the facet for articulation with the unciform, and maximum width of the combined facets for articulation with the scaphoid and magnum. An additional measurement was collected to capture morphological variation in the minimum distance between the facets for articulation with the scaphoid and magnum (Tables 3 and S3).

Table 3. Measurements recorded from lunars of *Paramylodon harlani* from Blancan (n = 3), Irvingtonian (n = 7), and Rancholabrean (n = 2; UCMP 24262; [56]) deposits for comparison to that of the STR 2A specimen (UF/VP 548409). Measurements were taken with digital calipers and are reported in millimeters. See Table S3 for a complete list of the measurements.

Measurement	Blancan	Irvingtonian	UF/VP 548409	Rancholabrean
Maximum length of radial condyle, OR	42.9–58.9	59.2–66.0	73.6	71.0–72.4
Maximum height of facet for articulation with unciform, OR	30.3–39.9	43.4–49.3	50.8	50.1–62.6
Maximum width of combined facets for articulation with scaphoid and magnum, OR	39.1–46.0	39.3–50.9	52.3	59.6–60.0
Average volume of combined maximum measurements (mm^3)	85,156	135,303	195,490	241,312
Minimum distance between facets for articulation with the scaphoid and magnum, OR	4.9–6.3	0–7.4	1.6	4.0–6.6

As previously reported and based on lunar measurements recorded here, *P. harlani* increased in size through time [54]. The STR 2A right lunar (UF/VP 548409 is larger than those collected from Blancan and Irvingtonian localities in Florida and smaller than the Rancholabrean specimen from California [56] (p. 149, Figure 71). A larger sample size of Rancholabrean *P. harlani* lunars are needed to improve this analysis. Interestingly, the minimum distance between the facets for articulation with the scaphoid and magnum is on average narrowest in Irvingtonian *P. harlani* with no separation in several specimens, as opposed to the Blancan and Rancholabrean specimens (Tables 3 and S3). The minimum distance recorded for UF/VP 548409 is from the lower end of the range at 1.6 mm.

Superorder LAURASIATHERIA Waddell, Okada, and Hasegawa, 1999
Order CARNIVORA Bowdich, 1821
Family CANIDAE Bonaparte, 1845
Genus *Urocyon* Gray, 1837
Urocyon cf. *minicephalus* Martin, 1974
Referred Specimen: UF/VP 548427, distal right tibia.

Description: As preserved, this specimen is 78.5 mm long, with a minimum shaft width of 7.5 mm. Maximum distal width is 13.7 mm; distal depth, 9.6 mm. Comparisons of the distal end with those of similar-sized modern procyonids, mustelids, mephitids, and felids showed significant differences, while those of canids were most similar. Among canids, the morphology and size match that of the gray fox *Urocyon*, in particular the Ir3 species *U. minicephalus* (Figure 8; Table 4). On the articular surface for the astragalus, the medial groove is deeper and better defined than the lateral groove (Figure 8D). The medial malleolus is prominent.

Figure 8. Right distal tibiae from middle Pleistocene *Urocyon* from Florida. (**A,C**) UF/VP 559678, *Urocyon minicephalus* from Coleman 2A, Sumter County, anterior and distal views. (**B,D**) UF/VP 548427, *Urocyon* cf. *minicephalus* from Steinhatchee River 2A, Dixie County, anterior and distal views.

Table 4. Measurements (in mm) on the distal end of the tibiae of *Urocyon* from the Irvingtonian of Florida. UF/VP 548427 is from the Steinhatchee River 2A locality and identified as *U.* cf. *minicephalus*. UF/VP 559671–559685 are from Coleman 2A (Table 1), the type locality of *U. minicephalus* [16]. The statistics are for the Coleman 2A sample only.

Catalog Number	Maximum Distal Width	Maximum Distal Depth
UF/VP 548427	13.7	9.6
UF/VP 559671	14.2	8.7
UF/VP 559672	13.9	9.1
UF/VP 559673	13.8	9.2
UF/VP 559674	13.1	8.3
UF/VP 559675	13.7	9.2
UF/VP 559676	14.3	9.8
UF/VP 559677	12.9	8.7
UF/VP 559678	14.3	9.5
UF/VP 559679	13.8	9.1
UF/VP 559680	13.7	9.0
UF/VP 559681	12.5	8.5
UF/VP 559682	13.3	8.8
UF/VP 559683	14.0	9.3
UF/VP 559684	13.2	9.4
UF/VP 559685	12.6	8.8
Mean	13.55	9.03
Standard Dev.	0.59	0.40
CV	4.35	4.42

Comments: Three species of *Urocyon* are currently recognized from the Pleistocene of Florida: *U. citrinus*, *U. minicephalus*, and the extant species *U. cinereoargenteus* [16,57]. *Urocyon citrinus* is only known from a relatively small number of specimens from the latest Blancan Inglis 1A locality, and the distal end of a tibia is not represented [57]. The Ir3 Coleman 2A locality produced a large sample of *U. minicephalus* from multiple individuals, including many complete and distal tibiae (Table 4). Nine specimens from the Ir2 McLeod Limerock Pit Pocket A site were referred to *U. minicephalus* [57], but no tibia was recovered. *Urocyon cinereoargenteus* has been identified from several Rancholabrean sites in Florida, but diagnostic cranial and dental fossils have only been found at Seminole Field, Arredondo 2A, Reddick, and Devils Den [28,58,59]. A new species of *Urocyon* was named based on specimens from Seminole Field [58], but it was synonymized with *U. cinereoargenteus* [59]. *Urocyon minicephalus* was sometimes also considered a synonym of *U. cinereoargenteus*, e.g., [26,60], but its validity was reestablished by [57].

The partial tibia UF/VP 548427 firmly establishes the presence of *Urocyon* at the STR 2A locality, but such a specimen is not fully diagnostic at the species level. A tentative identification to *U. minicephalus* is based on the estimated age of the site and the close resemblance to the *Urocyon* tibiae from Coleman 2A.

Family Indeterminate

Referred Specimens: UF/VP 548457, thoracic vertebra; UF/VP 548458, juvenile thoracic vertebra.

Comments: These two specimens belong to a medium-sized carnivore but lack diagnostic features to identify them to the family level. It is possible that they belong to *Urocyon*.

Order PERISSODACTYLA Owen, 1848

Family TAPIRIDAE Gray, 1821

Genus *Tapirus* Brisson, 1762

Tapirus sp.

Referred Specimens: UF/VP 553071, palate right I3, P2–M3 and left I3, C, P1–M3; UF/VP 546753, left p3; UF/VP 548429, edentulous left dentary fragment; UF/VP 548428 right proximal metacarpal 5; UF/VP 548430, proximal phalanx, digit 2 or 4; UF/VP 546754, juvenile left astragalus.

Description: On UF/VP 553071 (Figure 9), the P1–P3 are fully erupted and slightly worn with only small areas of visible dentine on the occlusal surface; the M1 has more wear with dentine exposed along the entire length of the protoloph but only a small area on the metaloph;

the M2 is fully erupted and with very slight wear to the crests of the lophs; and the crown of the M3 has formed but this tooth has not begun to erupt. The right and left P4 are at slightly different stages of eruption, with the right P4 nearly fully erupted with polishing of the crown indicating it had emerged from the gum; however, distinct wear facets are not present on its lophs. The left P4 remains in the crypt, and the left DP4 was likely still in place (although not preserved with the specimen); unlike the right P4, the surface of the crown of the left P4 is not polished. The only bones preserved in UF/VP 553071 are the nearly complete premaxillae and the ventral portions of the maxilla. Crushing has broken all the bones and some of the teeth on the left side, leading to varying amounts of distortion throughout the specimen.

The general size of the STR 2A tapirid is within the range of medium-sized species of the genus *Tapirus*, such as *Tapirus terrestris*, *T. pinchaque*, *T. veroensis*, or *T. lundeliusi* (Table 5; Figure 10). Like other members of this group, the cheekteeth of the STR 2A tapirid are much larger than small species such as *T. polkensis* and much smaller than larger species such as *T. indicus*, *T. haysii*, *T. merriami*, and *T. webbi* [12,61–63].

Table 5. Comparison of dental measurements of Steinhatchee River 2A *Tapirus* with those of other species. Statistics are mean ± standard deviation in top line; observed range in bottom line. The parentheses around values for M3 of UF/VP 553071 reflect that it is not fully mineralized. Specimen data in Table S4.

Tooth ID	UF/VP 553071 Left Side	UF/VP 553071 Right Side	*Tapirus veroensis*	*Tapirus lundeliusi*	*Tapirus haysii*	*Tapirus polkensis*
P1 L	17.8		18.70 ± 1.08, 45 15.7–20.6	18.56 ± 0.86, 16 17.0–19.8	21.19 ± 1.35, 7 19.7–23.3	14.39 ± 0.92, 30 12.3–16.5
P2 L		19.4	19.74 ± 1.02, 4 16.7–21.9	19.44 ± 0.84, 18 18.0–21.6	22.07 ± 1.20, 10 20.6–24.3	15.39 ± 0.67, 35 14.0–17.0
P2 AW		20.5	21.17 ± 1.18, 46 17.2–23.3	21.45 ± 0.90, 18 19.7–22.9	23.87 ± 1.14, 11 22.0–25.4	16.78 ± 0.97, 36 15.1–19.1
P2 PW		22.6	23.40 ± 1.24, 42 21.1–25.8	23.51 ± 0.87, 18 22.2–25.1	26.23 ± 1.39, 11 23.8–28.0	18.98 ± 0.72, 35 17.8–20.8
P3 L		19.9	20.31 ± 1.10, 43 17.4–22.6	19.97 ± 0.55, 18 18.6–21.6	22.89 ± 1.08, 11 21.6–24.5	16.09 ± 0.64, 38 14.5–17.0
P3 AW		22.6	24.55 ± 1.22, 42 21.5–26.6	24.64 ± 0.77, 15 23.7–26.1	27.26 ± 1.01, 11 25.7–29.0	20.36 ± 1.00, 35 16.6–22.0
P3 PW		23.6	24.52 ± 1.20, 40 22.1–26.7	24.08 ± 0.89, 16 22.7–25.7	26.96 ± 1.20, 12 25.4–29.3	20.04 ± 0.75, 36 18.5–21.9
P4 L		21.0	21.63 ± 1.21, 52 18.7–23.6	21.25 ± 0.73, 18 19.5–22.2	23.71 ± 0.97, 7 22.6–25.0	16.78 ± 0.77, 37 15.0–18.3
P4 AW		24.1	26.93 ± 1.35, 50 24.0–29.3	26.51 ± 0.91, 16 24.3–27.5	29.69 ± 1.59, 7 28.0–31.9	21.74 ± 1.11, 36 19.4–23.4
P4 PW		24.4	26.26 ± 1.39, 51 23.0–28.9	25.22 ± 0.89, 17 23.6–26.9	28.88 ± 1.59, 7 27.2–30.8	20.57 ± 1.03, 36 19.0–22.6
M1 L		21.7	22.79 ± 1.11, 59 20.2–25.5	22.19 ± 1.01, 19 19.3–23.9	25.01 ± 0.77, 13 23.9–26.1	17.94 ± 0.98, 50 15.4–20.1
M1 AW		24.7	26.48 ± 1.10, 55 24.1–28.8	26.49 ± 0.62, 19 25.3–27.7	29.12 ± 1.02, 12 26.9–30.7	20.96 ± 0.88, 51 19.4–22.9
M1 PW		22.8	24.09 ± 0.98, 55 22.2–26.3	23.33 ± 0.68, 18 22.1–24.9	26.28 ± 1.16, 12 24.5–28.5	18.30 ± 0.79, 49 16.7–20.0
M2 L	24.4	24.5	24.93 ± 1.13, 59 22.8–27.6	24.46 ± 1.15, 18 21.7–26.2	27.73 ± 1.15, 15 25.5–29.4	19.78 ± 0.93, 41 17.9–21.7
M2 AW	27.5	27.5	28.88 ± 1.38, 56 25.0–31.9	28.34 ± 0.93, 18 25.8–29.6	32.80 ± 1.63, 15 30.8–36.1	22.84 ± 0.70, 42 21.4–24.1
M2 PW	24.9	24.8	25.88 ± 1.16, 54 23.1–28.3	24.34 ± 0.99, 16 22.2–26.0	29.07 ± 1.58, 13 27.4–33.0	19.70 ± 0.84, 42 17.4–21.3
M3 L	(24.3)		24.71 ± 1.18, 66 22.0–27.9	25.06 ± 1.07, 17 22.5–27.0	28.41 ± 0.83, 12 27.1–29.9	20.19 ± 0.91, 37 18.8–23.4
M3 AW	(26.4)		28.40 ± 1.60, 60 24.7–31.7	27.72 ± 1.04, 16 26.0–29.2	33.17 ± 1.14, 12 31.5–35.9	22.65 ± 0.78, 38 21.4–24.2
M3 PW	(23.8)		24.01 ± 1.43, 60 20.3–27.0	22.72 ± 1.26, 16 2 0.6–25.8	28.05 ± 1.78, 12 25.1–31.3	18.36 ± 0.94, 37 16.1–20.5
		UF/VP 546753				
p3 L	22.0		21.46 ± 1.22, 51 18.0–24.6	21.00 ± 1.10, 15 19.1–23.2	23.88 ± 1.03, 10 22.5–25.4	16.40 ± 0.96, 34 14.4–18.2
p3 AW	15.8		16.00 ± 1.25, 52 14.1–19.4	15.33 ± 0.66, 14 14.3–16.4	17.43 ± 0.41, 10 16.7–17.9	12.24 ± 0.62, 32 10.7–13.8
p3 PW	17.8		18.02 ± 1.42, 52 15.1–20.9	16.80 ± 0.57, 14 16.0–17.7	19.35 ± 1.09, 9 18.1–21.5	13.81 ± 0.78, 35 11.7–15.3
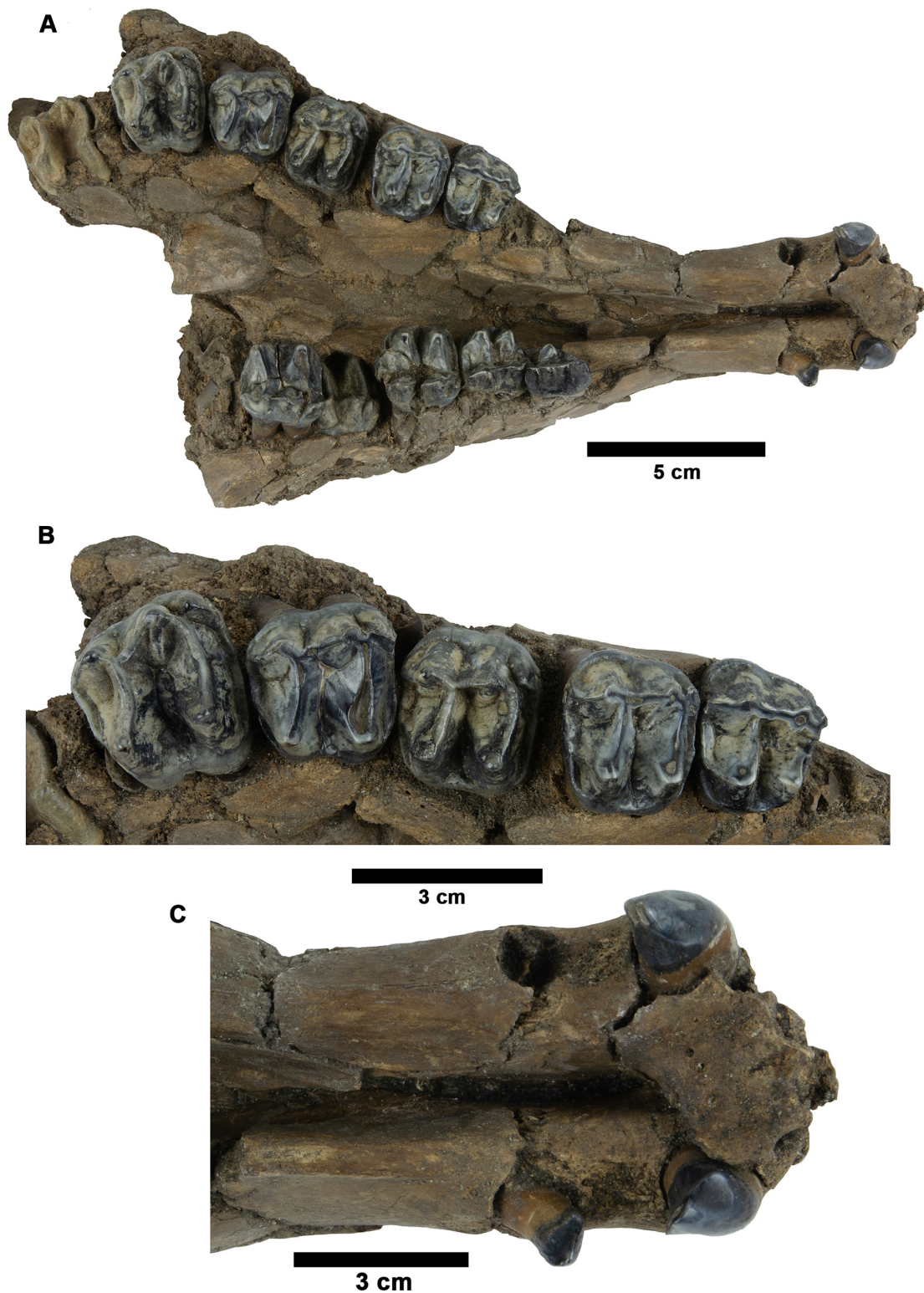
Figure 9. UF/VP 553071, palate of *Tapirus* sp. from Steinhatchee River 2A, middle Pleistocene, Florida. (**A**) Ventral view of entire specimen (except left M2 and M3 that were found adjacent to the remainder of the specimen, without surrounding bone). (**B**) Close-up of the right P2–M2. (**C**) Close-up of the anterior region of the rostrum with right and left I3 and left C.
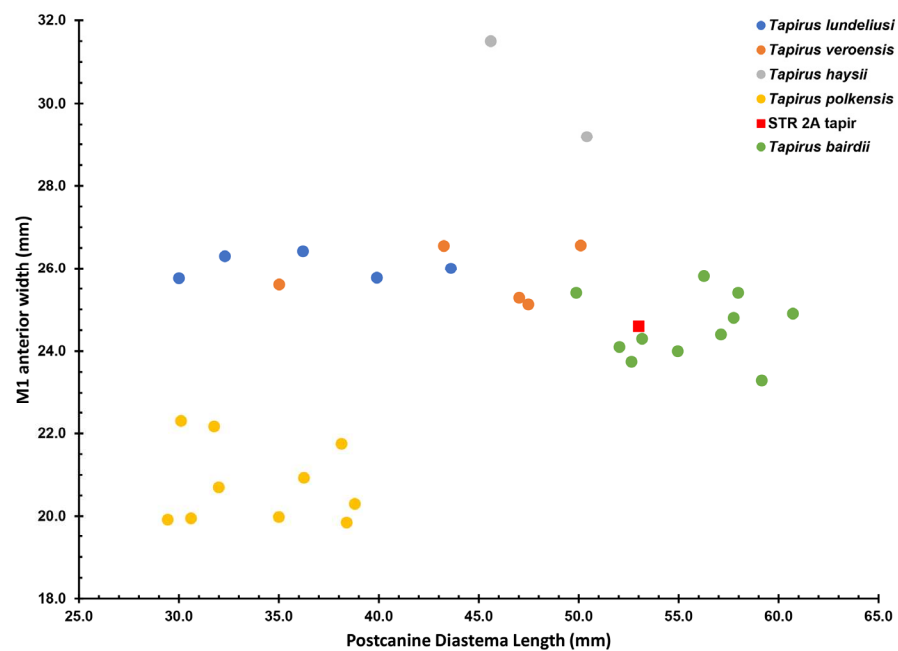
Figure 10. Relationship between muzzle length and body size (represented by M1 basal anterior width, BAW) in *Tapirus*. Among medium-sized species, those with M1 BAW 23–26.5 mm, diastema length is shortest in *T. lundeliusi* from the early Pleistocene of Florida and greatest in extant *T. bairdii*. Values for *Tapirus* sp. from the middle Pleistocene Steinhatchee River 2A lie within those of *T. bairdii* and outside those of fossil species from the southeastern USA. Data listed in Supplemental Table S5.

The premaxillae of UF/VP 553071 (Figure 9C) preserve the alveoli for the I1–I2, whose diameters are approximately equal in size and about half that of the I3. The incisor arcade is semicircular without any diastema. The diastema length between the I3 and C is 9.7 mm. Crown dimensions of the caniniform I3 are mesiodistal length 10.6, transverse width 10.8, and height 14.8 mm. There are sharp mesial and distal ridges on the I3. Laterally, the posterior process of the premaxilla terminates in an acute point approximately 20 mm anterior to the P1 on the better-preserved left side. The anteromedial process of the maxilla articulates with the posterior process of the premaxilla for a length of ca. 30 mm and is visible in lateral view. In lateral view, the descending maxillary-premaxillary suture ends at the anterior margin of the canine alveolus. A very low (<2 mm), short vertical flange is present on the dorsal edge of the anteromedial process of the maxilla. Although its outer wall is broken, the infraorbital foramen is otherwise well preserved on the right side of UF/VP 553071 and is located dorsal to the anterior half of the P3.

The C has a simple conical crown with faint mesial and distal ridges (Figure 9C). The crown dimensions are mesiodistal length 6.7, transverse width 5.4, and height 8.2 mm. The true value of the postcanine diastema cannot be measured accurately due to crushing, but as preserved they are approximately 53 mm on the left side and 55 mm on the right.

The P1 has a sharp ectoloph with three cusps whose heights decrease posteriorly. The lingual portion of its crown has a large, posteriorly located conical cusp with a wear facet on its posterior side from occlusion with the p2. There are other faint bumps and ridges on the lingual shelf of the P1, but no distinct transverse crests. The P1 lacks a buccal cingulum.

The general morphology of the P2–M3 in UF/VP 553071 (Figure 9B) resembles those of *Tapirus* species from the late Miocene to the recent of North and South America in having a tall ectoloph formed by the parastyle, paracone, and metacone; transverse protoloph and metaloph that in unworn or slightly worn teeth appear as sharp ridges that connect with the ectoloph labially and the intervening valley between them is open lingually; and well-developed anterior and posterior cingula. On the P2–P4 of UF/VP 553071, the posterior cingula continue around the buccal sides to terminate midway between the paracone and

metacone. The upper molars bear less well-developed posterobuccal cingula. On only the P2, a faint buccal cingulum extends posteriorly from the parastyle, but it fades away before it can connect to the posterobuccal cingulum. The heights of the protoloph and metaloph on the P2 rapidly decrease buccally, such that they end at the base of the ectoloph. On the slightly worn or unworn P4, M2, and M3, they connect at or near the top of the ectoloph (this feature cannot be seen on the more worn P3 and M1). The protocone and hypocone are taller than the paracone and metacone, slightly so in the premolars, greatly so in the molars. The parastyles on the P3–M3 of UF/VP 553071 are large and just slightly lower than the paracones when unworn but are not greatly enlarged as in *T. veroensis* and *T. haysii*.

The isolated lower premolar, UF/VP 546753 (Table 5), is identified as a p3 rather than a p4 based on comparison of ratios of BPW/L and BAW/BPW in samples of these teeth from Pleistocene species of *Tapirus* from Florida, and by the presence of a cristid obliqua. The latter is short and low, such that it does not block the interlophid valley labially. Wear on the protolophid and hypolophid is minor, but dentine is exposed on all four major conids. UF/VP 546753 occludes well with the posterior half of the P2 and the anterior half of the P3 of UF/VP 553071, such that it may belong to the same individual as the palate.

The postcranial elements match those of moderate-sized *Tapirus* in morphology. The astragalus, UF/VP 546754, is from a young juvenile, while the other two are from subadults or adults based on the degree of ossification of the surface bone and fusion of epiphyses. Thus, together they demonstrate that the minimum number of individuals of *Tapirus* from the site is two.

Comments: The degree of tooth eruption and wear on the cheekteeth of UF/VP 553071 differs from that observed in other species of *Tapirus*, including *Tapirus polkensis* [63], *Tapirus lundeliusi* [12], or *Tapirus veroensis* [64,65]. The degree of eruption and wear on the P1–P3, the left P4, and M3 fit the subadult stage [63], while those of the right P4 and both M2s are at the young adult stage. Since only one specimen is known, it is not possible to determine if this is a taxonomically significant difference with other species of *Tapirus*, or just an individual with a somewhat unusual eruption sequence for its cheekteeth.

A phylogenetic analysis of 10 species of *Tapirus*, including all five known species from Florida, determined that the Pleistocene species *T. lundeliusi*, *T. haysii*, and *T. veroensis* formed a monophyletic clade that was named the subgenus *Helicotapirus* [12]. Within *Helicotapirus*, *T. lundeliusi* was found to be the sister taxon to *T. haysii* plus *T. veroensis*. It also showed that the closest relatives to *Helicotapirus* were the extant *Tapirus bairdii* and the Hemphillian *T. polkensis*.

Of the 39 characters used in the cladistic analysis [12], 15 can be scored using UF/VP 546753 and 553071 (Table 6). Of these, seven are relatively uninformative as they are the same state as observed in all three species of *Helicotapirus* plus *T. bairdii*, and *T. polkensis*: infraorbital foramen located dorsal to the P3 or P2 (Character 22, state 1 of [12]); anteromedial process of maxilla exposed in lateral view dorsal to premaxilla (25:0); unworn crown height of the cheekteeth is tall compared to outgroups (41:1); P2 ratio is greater than 0.85 (45:1); transverse lophs and lophids on premolars are well separated (47:1); P2 protoloph extends lingually just to the base of the ectoloph (48:1, polymorphic in *T. haysii*); and the P3 protoloph merges half way or higher onto the ectoloph (49:2). This is conclusive evidence to place the STR tapirid in the genus *Tapirus*, but at this point it cannot be unambiguously referred to the subgenus *Helicotapirus*.

Two characters unambiguously support a sister group relationship between the STR 2A *Tapirus* with *T. haysii* and *T. veroensis* to the exclusion of *T. lundeliusi* (Figure 11B): dorsal maxillary flange is absent or very slight (26:0); and the p3 crista obliqua is weak or absent, such that is does not block the interlophid valley (73:1). However, there are two characters which conflict with this arrangement as *T. lundeliusi*, *T. haysii*, and *T. veroensis* shared the derived state and the Steinhatchee River 2A *Tapirus* has the primitive state (Figure 11A): parastyle development on the P3–M3 is strong (55:1); and posterolabial cingulum is present on the P2–M3 (56:0). There is a single character for which the STR 2A *Tapirus* and *T. lundeliusi* share the plesiomorphic state while *T. haysii* and *T. veroensis* share the derived

state: P2 metaloph just reaches the base of the ectoloph (51:1). There is a single character for which the STR 2A *Tapirus*, *T. lundeliusi*, and *T. veroensis* share the plesiomorphic state while *T. haysii* is polymorphic (Table 6): the P1 with large posterolingual cusp (43:1). Also, there is a single character which *T. haysii*, *T. lundeliusi*, and *T. veroensis* share the plesiomorphic state while the STR 2A *Tapirus* has the derived state: the relatively long postcanine diastema (37:2). These last three characters are equally compatible with either of the phylogenetic arrangements suggested by the first two pairs of characters (Figure 11). Surprisingly, no synapomorphies are present, supporting an exclusive sister group arrangement between the STR 2A *Tapirus* and *T. veroensis*, as might be expected on chronologic grounds. There is a single character that supports a sister group relationship between the STR 2A *Tapirus* and *T. haysii*; the posterior process of premaxilla ends about midway over the C–P1 diastema (27:2). Recovery of more complete skulls of the STR 2A *Tapirus* with lacrimal, nasal, frontals, and/or parietal bones or dentaries with lower dentitions would add additional informative characters that could potentially determine which of the phylogenetic arrangements in Figure 11 is more likely, or even support a different hypothesis. Additional specimens would also increase sample sizes, allowing better understanding of intraspecific variation. At the present time, the STR 2A *Tapirus* cannot be confidently assigned to any of the named species in the genus.

Table 6. Character states for species of *Tapirus*. Character numbers and states as in [12].

Character Number	ST 2A *Tapirus*	*Tapirus lundeliusi*	*Tapirus veroensis*	*Tapirus haysii*	*Tapirus polkensis*	*Tapirus bairdii*
22	1	1	1	1	1	1
25	0	0	0	0	0	0
26	0	1	0	0	1	1
27	2	1	1	2	1	3
37	2	0	0	0	0	2
41	1	1	1	1	1	1
43	1	1	1	1, 2	0, 1	1
45	1	1	1	1	1	1
47	1	1	1	1	1	1
48	1	1	1	1, 2	1	1
49	2	2	2	2	2	2
51	1	1	2	2	1	1
55	1	2	2	2	1	1
56	0	1	1	1	0	0
73	1	0	1	1	0	0

Following the publication of a series of papers [12,62–66], the systematics of *Tapirus* in Florida during the Irvingtonian and Rancholabrean NALMAs appeared relatively straightforward. During the preceding late Hemphillian and Blancan intervals, two or three species of *Tapirus* coexisted in Florida at any point in time [12,61,63]. Only a single species from the Blancan, *Tapirus haysii*, survived into the early Irvingtonian. This large species is not present at localities younger than Ir1, being replaced by medium-sized specimens which were referred to *Tapirus veroensis* [64–66]. The first records of late Pleistocene fossils of *Tapirus* in North America consisted of isolated teeth and other fragmentary remains and were initially referred to the extant Brazilian tapir [67]. The first late Pleistocene tapir skull found in North America was recovered from the Vero locality in 1916. It proved to be quite different from those of any of the extant species of *Tapirus*, and was accordingly described as a new species, *T. veroensis* [64,68]. Over the past century, a few skeletons, additional skulls, numerous mandibles, and hundreds of isolated teeth have been collected at Rancholabrean sites in the southeastern USA, and, after accounting for ontogenetic variation, all fall within the range of a single species [64,65,69].
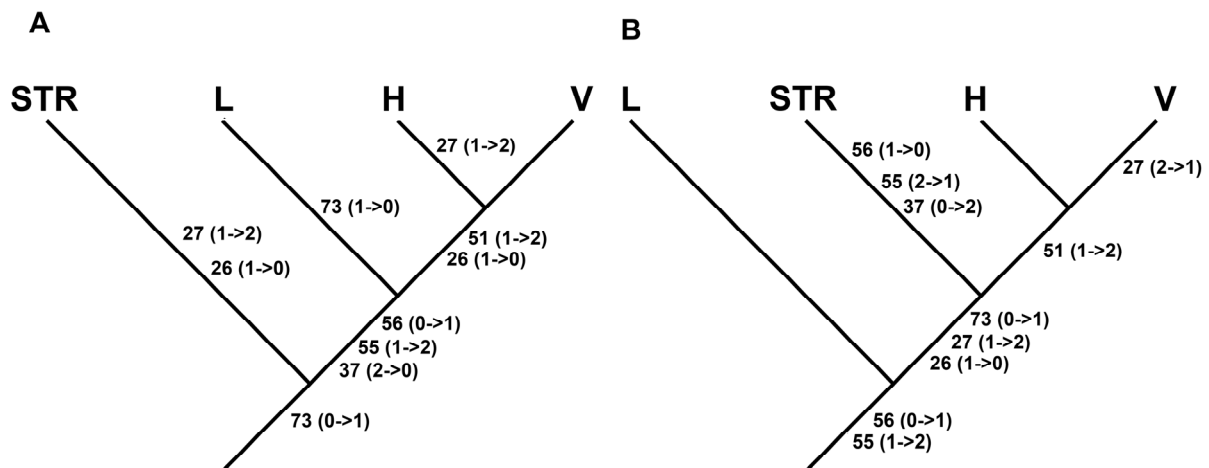
Figure 11. Two equally most parsimonious relationships of *Tapirus* sp. from the Steinhatchee River 2A (STR) with the three Pleistocene species known from Florida: *Tapirus lundeliusi* (L), *Tapirus haysii* (H) and *Tapirus veroensis* (L). (**A**) STR is sister taxon to L+H+V. (**B**) L is sister taxon to STR+H+V. Numbers for characters and character states from [12]. Only characters that can be observed on the STR *Tapirus* sp. are shown. The sister group relationship between *T. haysii* and *T. veroensis* relative to *T. lundeliusi* is supported by other characters [12]. The mixture of derived and primitive character states observed in the STR *Tapirus* results in several reversals or parallelisms (see text for discussion).

The fossil record of *Tapirus* in Florida during the Ir2 and Ir3 is much poorer than either the Ir1 or Rancholabrean. Searching the FLMNH VP collections using https:// specifyportal.floridamuseum.ufl.edu/vp/ on 9 September 2024 returned 377 specimen records of *Tapirus* from the Ir1 from Florida, 1220 records from the Rancholabrean, but just 89 from the Ir2 and I3 combined. The genus was originally not listed as present at the Coleman 2A locality [4,16,28]. A distal tibia of *Tapirus* (UF/VP 125414) was collected at Coleman 2A during the original major excavation in 1965 but was misidentified as an equid and remained unnoticed in the FLMNH VP collection for about 25 years. Its presence along with a metacarpal collected at the site after 1965 was first reported by [66]. Although the sample was very limited, the significance was that they were the only known Ir3 *Tapirus* from Florida at the time and that their size fell within the range of *T. veroensis* rather than that of *T. haysii*. In the past 30 years, the number of specimens of Ir3 *Tapirus* from Florida has increased modestly, most notably about 60 fossils from the Tri-Britton locality, including three isolated nasal bones and some partial dentitions [65]. Also, two previously unpublished maxillae from Ir3 sites, UF/VP 237848 from Dickerson Coquina Pit and UF/VP 217399 from Handi-Fill Shell Pit, increased sample sizes of upper cheekteeth from this interval. Collectively, it can now be stated with confidence that the species of *Tapirus* in Florida during the Ir3 was *T. veroensis*. Even stronger support for this comes from the Ir3 Camelot site in South Carolina, which produced skulls and mandibles referable to *T. veroensis* [70,71].

The status of *Tapirus* during the Ir2 in Florida is even more poorly known than the Ir3. The only Ir2 specimens previously known from Florida were AMNH FM 37410 and 37411, a partial juvenile maxilla with the DP3–DP4 and dentary with the dp2–dp3, respectively. Their size falls within the limited range of overlap between *T. haysii* and *T. veroensis*. These two were first referred to *T. haysii* [66] and later *T. veroensis* [12]. They cannot be directly compared to any of the STR 2A tapirids, and are probably best regarded at this point as *Tapirus* sp. Given the chronologic ranges of *T. haysii* and *T. veroensis*, discovery of a partial skull of *Tapirus* from the Ir2 would be expected to be one of these two species. Even an intermediate form showing an evolutionary transition from *T. haysii* to *T. veroensis* would not have been surprising, as suggested by [66]. Instead, the mixture of derived and primitive character states found on UF/VP 553071 from the STR 2A suggests a more

complex history for middle Pleistocene *Tapirus* in Florida. Additional specimens from this interval are needed to determine the details of this history.

Family EQUIDAE Gray, 1821
Genus *Equus* Linnaeus, 1758
Subgenus *Equus* (*Equus*) Linnaeus, 1758
Equus sp. "A" sensu Hulbert, 1995

Referred Specimens: UF/VP 546768, associated premaxillae with left I2–I3 and C, partial right and left maxillae with P2–M3; UF/VP 547378, associated left maxilla with P2–M3, isolated left I2–I3 and C, and isolated right P2–M2; UF/VP 547456, associated right premaxilla with I1; UF/VP 546757, 547473–547476, five left petrosals; UF/VP 547464–547472, nine right petrosals; UF/VP 547407, associated right I1–I3, P2–P3, left I2, P2–P3, mandibular symphysis with left and right i1–c, p2–m3; UF/VP 546777, associated right I2–I3; UF/VP 546766, associated right DP2–DP3 and left DP2–DP4; UF/VP 547409, associated left and right M2; UF/VP 547433, left DP3; UF/VP 546767, 547431, two right DP4s; UF/VP 547434–547435, two left DP3s or DP4s; UF/VP 547432, right DP3 or DP4; UF/VP 547422, left P2; 547410, 547412, two right P2s; UF/VP 546769, 547424, two left P3s; UF/VP 547411, 547414 two right P3s; UF/VP 546770, left P4; UF/VP 546771, left right P4; UF/VP 547423, slightly worn left P3s or P4; UF/VP 546772, 546774, 547415–547418, six right M1s; UF/VP 547425–547427, three left M2s; UF/VP 546773, 547419, two right M2s; UF/VP 546774, 547428, two heavily worn left M1s or M2s; UF/VP 547429, left M3; UF/VP 547421, right M3; UF/VP 546780, 547457–547460, five I1s or I2s; UF/VP 546856, right I3; UF/VP 546857 isolated canine; UF/VP 547379, associated partial left and right dentaries with p2–m3; UF/VP 547408, associated mandibular symphysis with left i1–c and right i1–i2, right p2–m3, and left p2–m1; UF/VP 546758, associated right i2–i3 and left and right p2–m3; UF/VP 546779, left i1; UF/VP 546778, 547461–547462, three right i2s; UF/VP 547463, right i3; UF/VP 547437, left dp2; UF/VP 547436, right dp2; UF/VP 547438, left dp3; UF/VP 547439, right dp4; UF/VP 547440, worn right dp3 or dp4; UF/VP 547455, left p2; UF/VP 547441, right p2; UF/VP 547454, left p4; UF/VP 546761–456762, 546776, 547442–547443, five right p4s; UF/VP 546759–546770, two heavily worn p3s or p4s; UF/VP 547451, 547453, 547997, three left m1s; UF/VP 546763, right m1; UF/VP 547444, 547452, associated left and right m2; UF/VP 547445–547446, two right m2s; UF/VP 546765, heavily worn left m1 or m2; UF/VP 546764, heavily worn right m1 or m2; UF/VP 547449–547450, two left m3s; UF/VP 547447–547448, two right m3s. Postcranial elements and fragmentary cranial specimens of *Equus* from STR 2A are listed in Supplemental Table S6.

Description: Both upper and lower incisors have coronal cementum that wears off on the labial side near the occlusal surface. All three upper incisors have complete infundibula (Figure 12C) until the feature wears off. The bottom of the infundibulum is visible inside UF/VP 547460, an unworn I2, and its total depth is about 22 mm. The infundibula of the lower incisors are more variable. A complete infundibulum is present on two of three i1s (Figure 12A; UF/VP 547407 and 546779), but there is small gap in the lingual wall of the infundibulum on each of the right and left i1s of UF/VP 547408. In all i2s that preserve an infundibulum on the occlusal surface, its lingual wall has a 1.5 to 5.5 mm wide gap (Figure 12A,B). On all four known examples, the i3 lacks an infundibulum and has a linguolabially compressed crown that is slightly curved in occlusal view. There is a small hook-like feature at the mesial end of the i3 (Figure 12A,B).

Large canine teeth are associated with the two upper dentitions, UF/VP 546768 and 547378, and two of the lower dentitions, UF/VP 547407 and 547408 (Figure 12A,C). The latter two specimens have much less worn cheekteeth than the two uppers, so these represent four different individuals, all regarded as males due to the large size of the canines. Additionally, a large canine was found near the two partial dentaries that make up UF/VP 547379. The cheekteeth of UF/VP 547379 are worn to the same degree as those of UF/VP 546768 and 547378. The diastema between the I3 and C on UF/VP 546768 is about 21 mm, much longer than the i3-c diastema in either of the dentaries, about 3 mm in UF/VP 547407 and 5 mm in UF/VP 547408. All premaxillae or mandibular symphyses

that were recovered at STR 2A had either large canines or large empty alveoli for them; none lacked canines or had small vestigial ones, the two states usually found in females of *Equus*. The upper and lower canines are very similar in size and crown morphology, a central conical cusp flanked by thin, lingually curved, mesial and distal carinae.
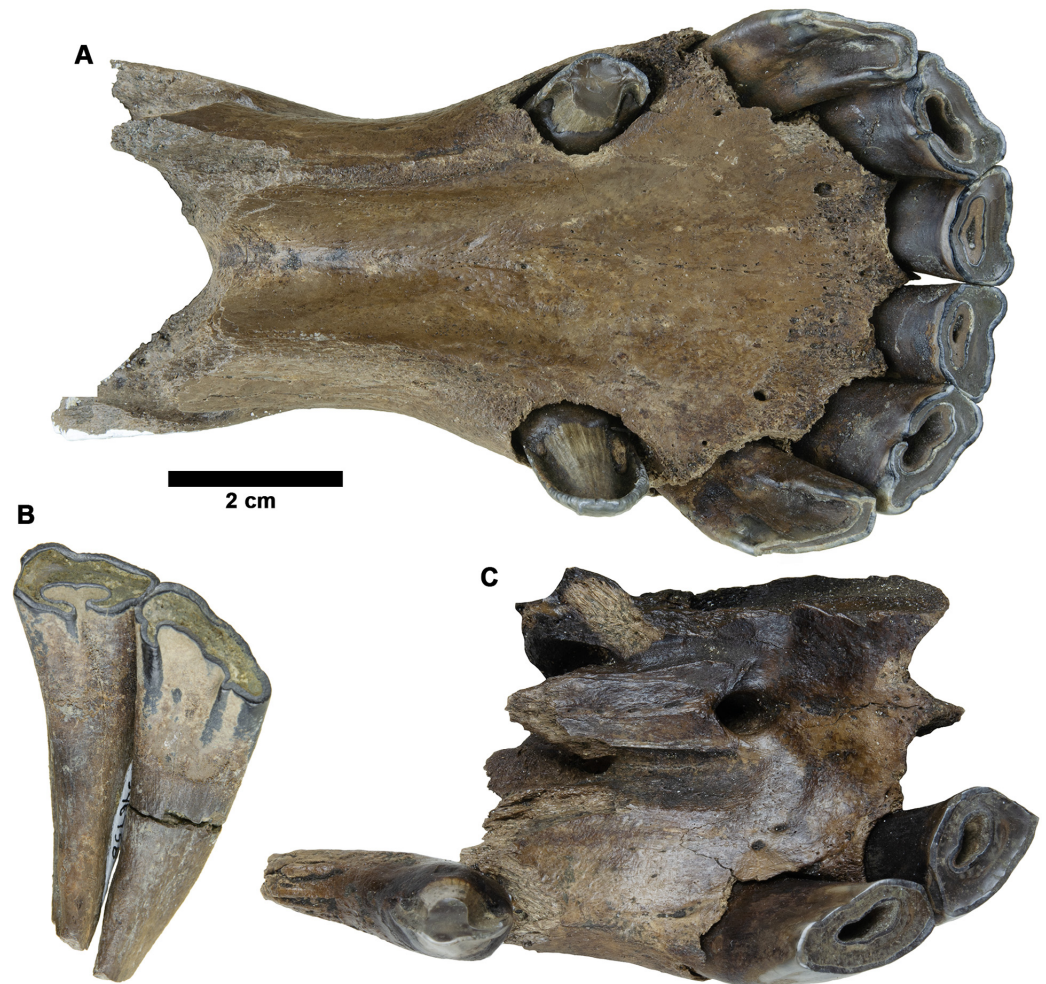
Figure 12. Anterior dentitions of *Equus* sp. A from Steinhatchee River 2A, middle Pleistocene, Florida. (**A**) UF/VP 547407, dorsal view of mandibular symphysis with right and left i1–i3 and c. (**B**) UF/VP 546758, lingual view of associated i2–i3. (**C**) UF/VP 546768, ventral view of premaxillae with left I2–I3 and C.

The P3–M3 have moderately long protocones that connect very soon after wear begins on the occlusal surface (Table 7; Figures 13 and 14); protocones on the P2 are notably shorter than those on the other cheekteeth. The lingual side of the protocone bears a shallow groove that is present for the first 75% of the crown. The pli caballin is large but single in slightly worn premolars, reduced but present on moderately worn specimens, and does not disappear until extremely heavy wear. The pli caballin is smaller in molars and lost sooner with wear than in premolars. A hypoconal groove is visible on the occlusal surface until very late wear, except on the M3 where it is closed off and usually attached to the postfossette. The greatest number of fossette plications are most often found on the posterior side of the prefossette. Fossette plications are reduced in number but still present until crown height decreases below 15 mm. Parastyles and mesostyles are broader and extend farther buccally in P3s and P4s than in molars (Figure 14). Estimates for unworn mesostyle crown height are 70–73 mm for the P2 (based on UF/VP 547412) and 90–93 mm for the P4, M1, and M2 (based on UF/VP 547423 and 547425).

Table 7. Measurements in mm of upper cheekteeth of *Equus* sp. A from the Steinhatchee 2A locality, Dixie County, Florida. Wear classes: 0, unworn or very slightly worn tooth; 1, crown height (CH) 75–95% of unworn CH; 2, CH 50–75% of unworn CH; 3, CH 25–50% of unworn CH; 4, CH < 25% of unworn CH. Measurements: MSCH, mesostyle crown height; APL, anteroposterior length on occlusal surface; BAPL, anteroposterior length at base of crown; TRW, occlusal transverse width (mesostyle to the most lingual point of the protocone; PRL, protocone length; PRW, protocone width; ROC, radius of curvature along mesostyle. An "a" before a value indicates an approximation due to breakage.

UF/VP Cat. No.	Tooth ID	Wear Class	MSCH	APL	BAPL	TRW	PRL	PRW	ROC
546766	DP2	2	21.2	34.5		18.4	5.6	3.6	
547433	DP3	1	31.9	29.5	26.5	20.5	9.4	2.8	
546766	DP3	2	27.0	27.5	23.8	18.3	7.7	3.6	
547431	DP4	0	39.2	30.4	25.2	17.1	10.2	2.2	
546766	DP4	1	32.1	27.0	23.3	18.3	8.8	3.7	
546767	DP4	2	a27	28.5	26.8	18.6	8.7	2.7	
547434	DP3or4	3	20.8			20.8	9.0	3.8	
547435	DP3or4	3	15.0	27.1	25.5	21.4	8.7	5.2	
547432	DP4	2	26.8	29.3	26.1	20.7	8.0	3.8	
547422	P2	2	58.2	37.1	32.6	23.6	7.7	4.0	140
547410	P2	2	56.2	34.8	31.1	24.4	8.3	4.9	150
547407	P2	2	54.0	34.6	31.7	22.8	8.2	4.8	110
547378	P2	3	25.5	35.2	27.1	22.8	8.9	5.0	
546768	P2	3	21.5	33.7	32.1	25.0	8.0	5.8	
547407	P3	2	68.1	26.8	22.3	24.8	11.1	4.9	130
546769	P3	2	a45				10.4		
547424	P3	3	47.5	25.3	22.8	25.3	11.9	4.8	
547411	P3	3	37.1	25.3	22.8	25.0	12.6	4.7	
547414	P3	3	35.8	25.4	23.0	16.1	10.9	5.2	
546768	P3	3	33.1	24.8	21.1	25.9	10.2	5.2	
547378	P3	3	32.9	26.3	21.2	24.4	11.4	4.6	
546771	P4	1	79.7	27.4	23.5	25.3	11.7	4.8	200
546770	P4	3	44.1	25.5	22.4	26.6	10.7	4.6	
547378	P4	3	37.3	24.0	20.4	24.3	10.6	4.5	
546768	P4	3	34.4	22.9	19.6	24.9	10.5	5.0	
547423	P3or4	0	a86						175
547413	P3or4	0							175
547417	M1	1	a89	26.2	18.7	20.3			120
547416	M1	1	85.5	28.9	20.1	21.2	11.6	4.2	120
547418	M1	2	70.4	23.3	19.6	22.4	10.3	4.0	130
547428	M1	3	a33	20.6	17.6	23.0	10.7	4.4	
546775	M1	3	38.4	22.4	19.6	25.3	10.3	5.5	
546768	M1	3	26.2	21.1	19.8	22.6	10.7	4.9	
547378	M1	3	26.2	21.9	19.7	23.1	9.6	4.3	
547425	M2	0	a90						110
547409	M2	1	76.5	26.0	19.7	21.5	12.0	3.5	90
546773	M2	1	76.4	25.5	21.9	23.5	12.1	4.7	140
546772	M2	2	61.3	24.2	20.5	23.0	10.1	4.7	110
47419	M2	3	50.3	23.2	20.4	23.2	10.2	4.5	110
547426	M2	3	46.0	23.9	19.8	23.1	12.1	4.0	105
547427	M2	3	39.8	23.1	21.6	23.3	12.9	4.2	
547378	M2	3	32.8	21.7	19.1	22.5	11.1	4.5	
546768	M2	3	30.3	21.8	19.4	22.8	11.3	4.8	
546774	M1or2	4	14.3	20.8		22.6	9.1	5.0	
547429	M3	1	a80		27.9	15.9	10.4	3.3	120
547421	M3	2	52.2	23.7	23.7	20.0	11.7	4.1	120
546768	M3	3	35.4	23.0		20.6	10.7	4.1	
547378	M3	3	25.2	26.7		21.4	11.1	4.2	

Figure 13. *Equus* sp. A from Steinhatchee River 2A, middle Pleistocene, Florida. UF/VP 547378, lateral (**A**) and ventral (**B**) views of partial left maxilla with P2–M3.

Character state variation in the p2–m3 with respect to tooth position and the amount of wear is shown in Table 8. Pli caballinids are generally more prominent and persist longer in premolars than molars. The depth and shape of the linguaflexid and depth of the ectoflexid vary, even between similarly worn teeth from the same position. For example, the p4s of UF/VP 547379 and 547443 have very similar crown heights (Table 9), yet the p4 of UF/VP 547443 has a much deeper ectoflexid than that of UF/VP 547379. The same differences in ectoflexid depth are observed in the m1s of UF/VP 547408 and 547997 and the m2s of UF546758 and 547446. Nevertheless, some generalities are apparent, with p2s having the shallowest ectoflexids and m3s with deep ectoflexids consistently present by wear stage 2 (Table 8; Figure 15A–C). Linguaflexids on the p3 and p4 are most often either U-shaped or asymmetrical with the anterior half more U-shaped (metaconid lingual margin concave) and the posterior half more V-shaped (metastylid lingual margin straight or nearly so). Most m1s and m2s have U-shaped linguaflexids, while in m3s a V-shaped linguaflexid is the dominant mode. Protostylids are uncommon on p3s–m3s and, if present, are weak and limited to the bottom third of the crown. Of the four associated lower dentitions, only the p3–m3 of UF/VP 547407 have protostylids, and their development is equal on corresponding right and left teeth. The sample size is small, but all three dp3s and dp4s have both protostylids and hypostylids. The latter are taller and better developed on the dp3s than the dp4s.

Table 8. Lower cheektooth characters of *Equus* sp. A from the Steinhatchee 2A locality, Florida. Wear classes defined in Table 7. Abbreviation: poflx., postflexid.

UF/VP Catalog No.	Tooth ID	Wear Class	Pli Caballinid	Ectoflexid Depth	Linguaflexid	Metaconid/Metastylid
547441	p2	1	long	very shallow	very shallow	equal in size
547407	p2	2	short	very shallow	very shallow	equal in size
547408	p2	2	very short	very shallow	small U-shape	equal in size
547455	p2	3	long	very shallow	small U-shape	equal in size
547379	p2	3	short, blunt	shallow	very shallow	equal in size
546758	p2	3	none	shallow	absent	metastylid larger
547407	p3	2	short	moderate	broad, deep asymmetrical	equal in size
547408	p3	2	none	moderate	deep U-shape	equal in size
547379	p3	3	short, blunt	moderate	broad, shallow U-shape	metastylid slightly smaller
546758	p3	3	short, blunt	moderate	broad, deep U-shape	equal in size
546759	p3	3	short, blunt	moderate	broad, shallow U-shape	metastylid slightly smaller
546762	p4	0	long	shallow	broad, shallow V-shape	equal in size
547454	p4	1	long	shallow	shallow, asymmetrical	equal in size
547407	p4	1	short	moderate	broad, deep asymmetrical	metastylid slightly smaller
546776	p4	1	short	moderate	shallow U-shape	metastylid slightly smaller
547408	p4	2	short, blunt	moderate	deep U-shape	metastylid slightly smaller,
547442	p4	2	long	moderate	shallow U-shape	metastylid smaller,
547443	p4	2	none	deep	deep, asymmetrical	metastylid slightly smaller
547379	p4	2	short, blunt	moderate	broad, shallow U-shape	metastylid slightly smaller
546761	p4	3	short, blunt	moderate	deep, asymmetrical	metastylid slightly smaller
547453	m1	0	none	shallow	broad U-shape	equal in size
547445	m1	1	short	moderate	deep, asymmetrical	equal in size
546763	m1	1	none	moderate	deep U-shape	equal in size
547407	m1	2	short	moderate	broad V-shape	metastylid slightly smaller
547451	m1	2	short, blunt	deep	deep U-shape	metastylid slightly smaller
547997	m1	2	short	moderate	deep U-shape	metastylid slightly smaller
547408	m1	2	short, blunt	deep	broad U-shape	metastylid slightly smaller
547379	m1	3	none	deep	deep U-shape	metastylid slightly smaller
546758	m1	3	none	deep	broad U-shape	metastylid slightly smaller
547444	m2	1	long	shallow	shallow, asymmetrical	metastylid slightly smaller
547407	m2	1	short	moderate	broad V-shape	equal in size
547408	m2	2	short	deep	deep U-shape	equal in size
547379	m2	3	none	deep	deep U-shape	equal in size
546758	m2	3	none	deep	deep U-shape	metastylid slightly smaller
547446	m2	3	none	moderate	deep U-shape	metastylid slightly smaller
546764	m2	3	none	deep	deep V-shape	metastylid smaller
547407	m3	1	short	shallow	broad V-shape	metastylid slightly smaller
547447	m3	1	short	moderate	deep U-shape	equal in size
547408	m3	2	short, blunt	deep	deep V-shape	metastylid slightly smaller
547448	m3	2	short, blunt	deep	deep V-shape	metastylid slightly smaller
547379	m3	2	short, blunt	deep	broad V-shape	metastylid slightly smaller
547449	m3	3	none	deep	broad V-shape	metastylid slightly smaller
546758	m3	3	short, blunt	deep	deep V-shape	metastylid slightly smaller

Table 8. *Cont.*

UF/VP Catalog No.	Tooth ID	Wear Class	Pre- vs. Postflexid	Postflexid Base	Isthmus Plications
547441	p2	1	equal	numerous plications	none
547407	p2	2	poflx. more lingual	one plication anteriorly, rest undulating	none
547408	p2	2	poflx. more lingual	just undulations	one into postflexid
547455	p2	3	equal	just undulations	none
547379	p2	3	poflx. more lingual	just undulations	none
546758	p2	3	equal	just undulations	none
547407	p3	2	poflx. more lingual	two plications	none
547408	p3	2	poflx. slightly more lingual	just undulations	none
547379	p3	3	poflx. slightly more lingual	one plication and some crenulations	one into preflexid
546758	p3	3	poflx. slightly more lingual	just undulations	none
546759	p3	3	poflx. slightly more lingual	one plication anteriorly, rest undulating	one into preflexid
546762	p4	0	poflx. more lingual	numerous plications	none
547454	p4	1	poflx. more lingual	numerous plications	none
547407	p4	1	poflx. more lingual	one plication anteriorly, rest undulating	none
546776	p4	1	poflx. more lingual	two plications and some crenulations	none
547408	p4	2	poflx. more lingual	crenulated	none
547442	p4	2	poflx. more lingual	one plication anteriorly	none
547443	p4	2	poflx. more lingual	crenulated	none
547379	p4	2	poflx. more lingual	one plication posteriorly	one into preflexid
546761	p4	3	poflx. more lingual	just undulations	none
547453	m1	0	poflx. slightly more lingual	two plications and some crenulations	none
547445	m1	1	poflx. slightly more lingual	two plications and some crenulations	none
546763	m1	1	equal	three plications	none
547407	m1	2	equal	one plication anteriorly	none
547451	m1	2	poflx. slightly more lingual	just undulations	none
547997	m1	2	poflx. more lingual	one plication anteriorly	none
547408	m1	2	poflx. slightly more lingual	crenulated	none
547379	m1	3	equal	one plication anteriorly	none
546758	m1	3	poflx. slightly more lingual	crenulated	none
547444	m2	1	poflx. slightly more lingual	two plications and some crenulations	none
547407	m2	1	poflx. slightly more lingual	crenulated	none
547408	m2	2	poflx. slightly more lingual	crenulated	none
547379	m2	3	poflx. slightly more lingual	just undulations	none
546758	m2	3	poflx. slightly more lingual	crenulated	none
547446	m2	3	poflx. slightly more lingual	flat	none
546764	m2	3	equal	flat	none
547407	m3	1	poflx. slightly more lingual	just undulations	none
547447	m3	1	poflx. slightly more lingual	one plication anteriorly	none
547408	m3	2	equal	just undulations	none
547448	m3	2	equal	just undulations	none
547379	m3	2	equal	just undulations	none
547449	m3	3	equal	just undulations	none
546758	m3	3	equal	just undulations	none
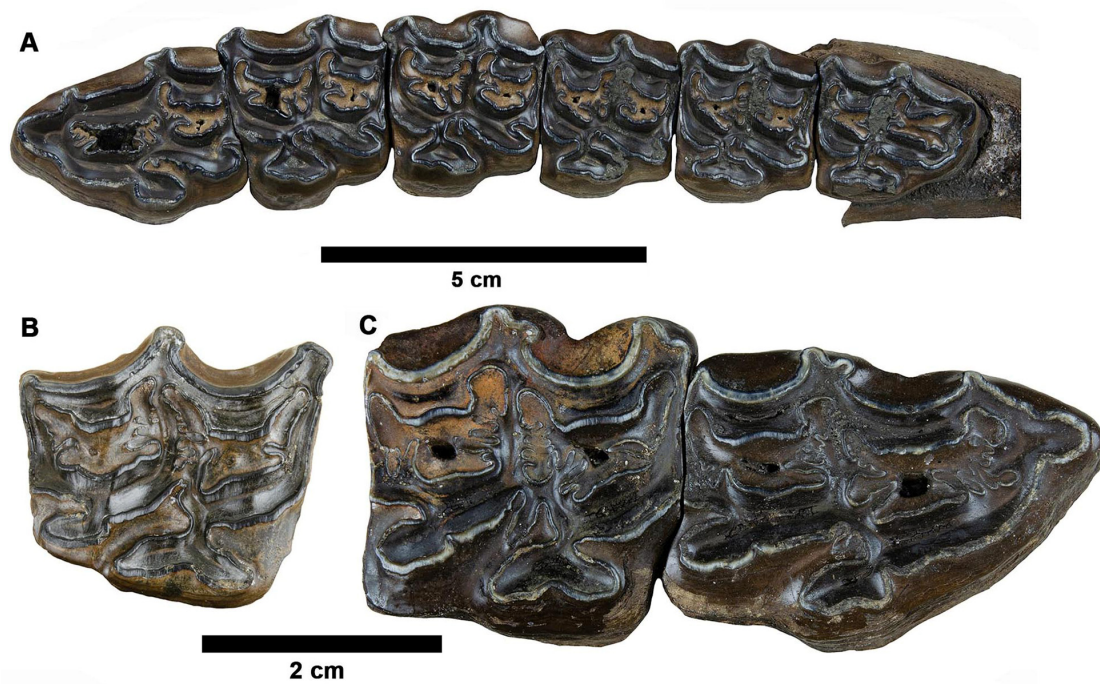
Figure 14. Upper cheekteeth of *Equus* sp. A from Steinhatchee River 2A, middle Pleistocene, Florida. (**A**) UF/VP 546768, ventral (occlusal) view of left P2–M3. (**B**) UF/VP 547409, occlusal view of right M2. (**C**) UF/VP 547407, occlusal view of associated right P2–P3.
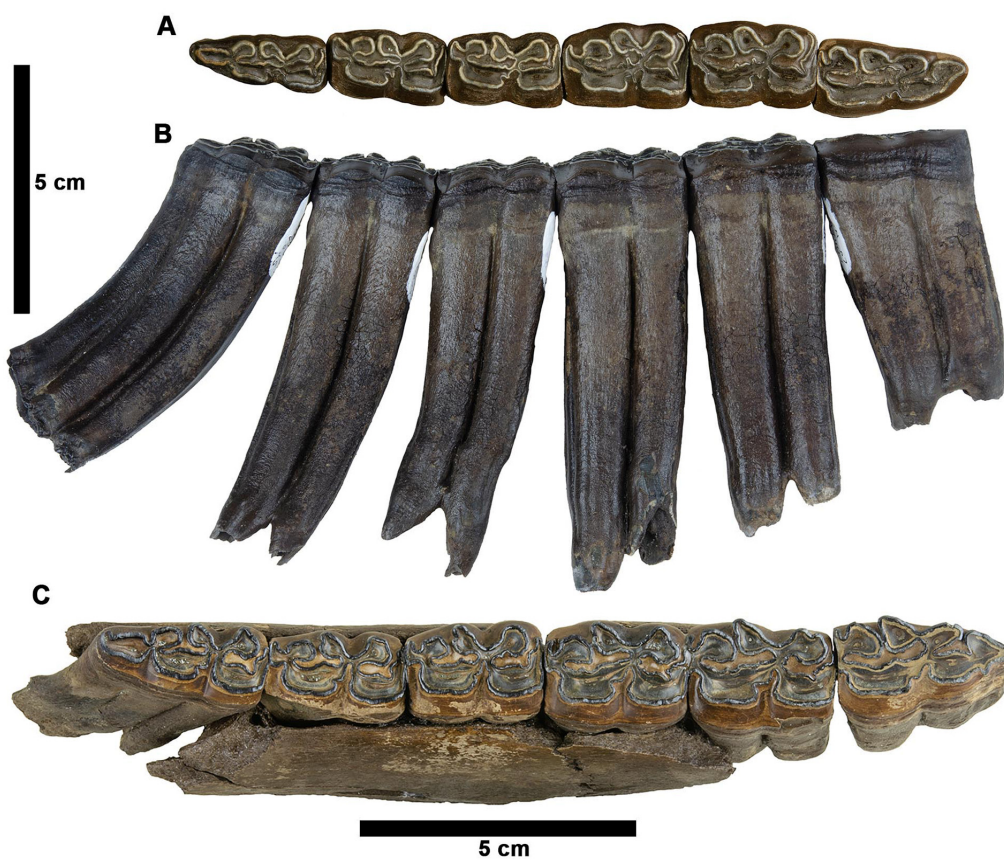
Figure 15. Lower cheekteeth of *Equus* sp. A from Steinhatchee River 2A, middle Pleistocene, Florida. (**A**,**B**) UF/VP 547407, occlusal and buccal views of associated right p2–m3. (**C**) UF/VP 547379, occlusal view of associated right p2–m3.

Table 9. Measurements in mm of lower cheekteeth of *Equus* sp. A from the Steinhatchee 2A locality, Dixie County, Florida. Wear classes as in Table 7. Measurements: mcch, metaconid crown height; apl, occlusal anteroposterior length; bapl, anteroposterior length at base of crown; atrw, anterior transverse width (metaconid to protoconid); ptrw, posterior transverse width (metastylid to hypoconid); mtms l, metaconid-metastylid length; pstflx l, postflexid length.

UF/VP SPECNO	Tooth ID	Wear Class	mcch	apl	bapl	atrw	ptrw	mtms l	pstflx l
547436	dp2	1	24.4	35.2	30.5	9.3	9.7	14.4	17.5
547438	dp3	1	31.8	31.7	25.8	9.5	9.8	14.5	15.2
547439	dp4	1	36.3	32.7	26.0	8.9	8.3	13.6	16.1
547440	dp3or4	4	10.3	27.8	26.1	11.7	12.0	16.5	11.9
547441	p2	1	a60	31.5	26.4	11.0	13.4	13.4	16.9
547407	p2	2	54.5	30.7	25.2	10.1	12.8	14.6	16.2
547408	p2	2	42.3	30.3	25.9	11.5	13.8	14.2	14.7
547379	p2	3	34.2	33.2	29.3	12.2	15.2	16.0	16.1
546758	p2	3	28.8	30.0	24.1	10.9	13.3	12.9	13.7
547455	p2	3		31.4		11.4	13.2	14.2	14.3
547407	p3	2	74.1	26.7	23.0	13.6	14.3	15.1	13.6
547408	p3	2	61.1	26.2	22.5	14.0	13.9	16.5	12.3
547379	p3	3	41.0	28.4	26.1	14.9	16.4	17.4	14.8
546758	p3	3	37.1	25.9	20.5	15.3	15.4	15.9	11.7
547454	p4	1	a85	24.7	21.9	11.0	10.8	12.2	12.6
547407	p4	1	85.1	26.1	21.7	13.3	13.6	14.0	12.8
546776	p4	1	76.1	26.7	23.2	13.0	13.5	15.9	14.8
547408	p4	2	72.7	25.5	22.3	12.9	13.1	14.9	12.5
547442	p4	2	71.2	27.8	23.4	13.7	15.5	16.0	15.9
547443	p4	2	58.9	25.5	22.5	14.1	13.5	15.4	13.2
547379	p4	2	54.4	27.1		14.8	15.3	16.4	13.6
546761	p4	3	48.2	24.5	22.0	13.7	13.4	14.8	11.9
546758	p4	3	39.8	24.7	19.5	14.3	14.3	15.3	11.3
547459	p3or4	3	a36	26.7			14.6	17.5	13.1
547460	p3or4	4	20.5			15.0	15.4	17.0	17.5
547445	m1	1	87.4	27.4	23.4	12.9	12.2	14.9	12.5
546763	m1	1	78.0	24.4	20.9	13.6	12.4	14.0	10.1
547407	m1	2	73.0	23.2	19.4	11.0	11.2	12.4	10.1
547451	m1	2	67.8	23.8	20.6	11.5	11.1	12.7	9.8
547997	m1	2	62.7	25.4	22.8	13.5	13.9	14.4	9.9
547408	m1	2	60.2	23.5	19.7	11.1	11.1	13.3	9.4
546758	m1	3	a35	24.1	19.2	13.0	11.8	12.8	8.3
547379	m1	3		25.4		13.4	13.1	14.3	9.1
547444	m2	1	87.9	25.6	19.1	10.1	9.4	11.5	14.3
547407	m2	1	81.4	24.3	18.7	11.2	10.9	12.4	13.6
547408	m2	2	66.3	24.3	21.0	11.3	11.0	12.6	12.3
547379	m2	3	48.7	24.9		12.9	12.3	13.5	14.8
546758	m2	3	38.7	23.5	19.0	12.6	11.6	13.2	11.7
547446	m2	3	33.0	24.0	20.4	14.0	13.7	14.0	
546764	m1or2	3	30.0	23.7		12.0	11.4	13.1	7.4
546765	m1or2	3	a29	23.5		13.0	12.7	12.1	9.7
547447	m3	1	a68		30.3	11.8	9.9	13.3	10.4
547407	m3	1	80.8	26.9	27.9	9.4	9.0	11.8	10.2
547408	m3	2	62.8	28.4	29.5	10.1	10.0	12.0	8.2
547448	m3	2	48.2	31.6		11.8	10.0	12.2	8.8
547449	m3	2	40.6	31.4	30.0	12.9	11.5	13.5	10.2
547379	m3	3	43.6	30.7	31.8	12.8	10.7	13.3	8.9
546758	m3	3	35.9	29.8	28.4	11.3	10.6	12.4	8.6

All the major limb bones of *Equus* recovered from STR 2A are well preserved, showing no bite marks or other signs of mammalian scavenging, no weathering cracks, nor water wear (Figure 16). But all were broken into two or more pieces. UF/VP 546791, a tibia, is

the only limb bone with a completely unbroken shaft (Figure 16D), however, much of its proximal articular surface is sheared off. In a few cases, such as the metacarpals UF/VP 548008 and 547381 (Figure 16A,B) and the tibia UF/VP 547836, all the pieces were collected so that the entire bone could be put back together. Despite careful collecting, only portions of limb bones were recovered most of the time. The size and morphology of the limbs fall within the observed range of those belonging to *Equus* sp. A from Leisey Shell Pit 1A [72] (Table S7; Figure 17). Of the two complete metacarpals, UF/VP 547381 is from a young adult, with traces of the epiphyseal plate visible near its distal end. That accounts for its notable greater slenderness than UF/VP 548008 (Table S7). Log-ratio diagrams show that the proportions of the STR 2A *Equus* limb bones are more similar to those of Ir3 *Equus* sp. A from the Tri-Britton and LaBelle Highway pit sites than to the Ir1 Leisey Shell Pit sample (Figure 17). Indeed, the proportions of measurements taken on the proximal and distal ends of the metapodials of the STR 2A and Ir3 samples are closer to those of late Rancholabrean *Equus* from Florida than those from Leisey Shell Pit (Figure 17A,B).

Figure 16. Anterior and posterior limb bones of *Equus* sp. A from Steinhatchee River 2A, middle Pleistocene, Florida. (**A,B**) UF/VP 548008, anterior and posterior views of metacarpal 3. (**C**) UF/VP 546840 anterior view of distal metatarsal 3. (**D**) UF/VP 546791, anterior view of right tibia. (**E,F**) UF/VP 548055, anterior and posterior views of proximal phalanx, digit 3. (**G**) UF/VP 547498, medial view of left calcaneum.
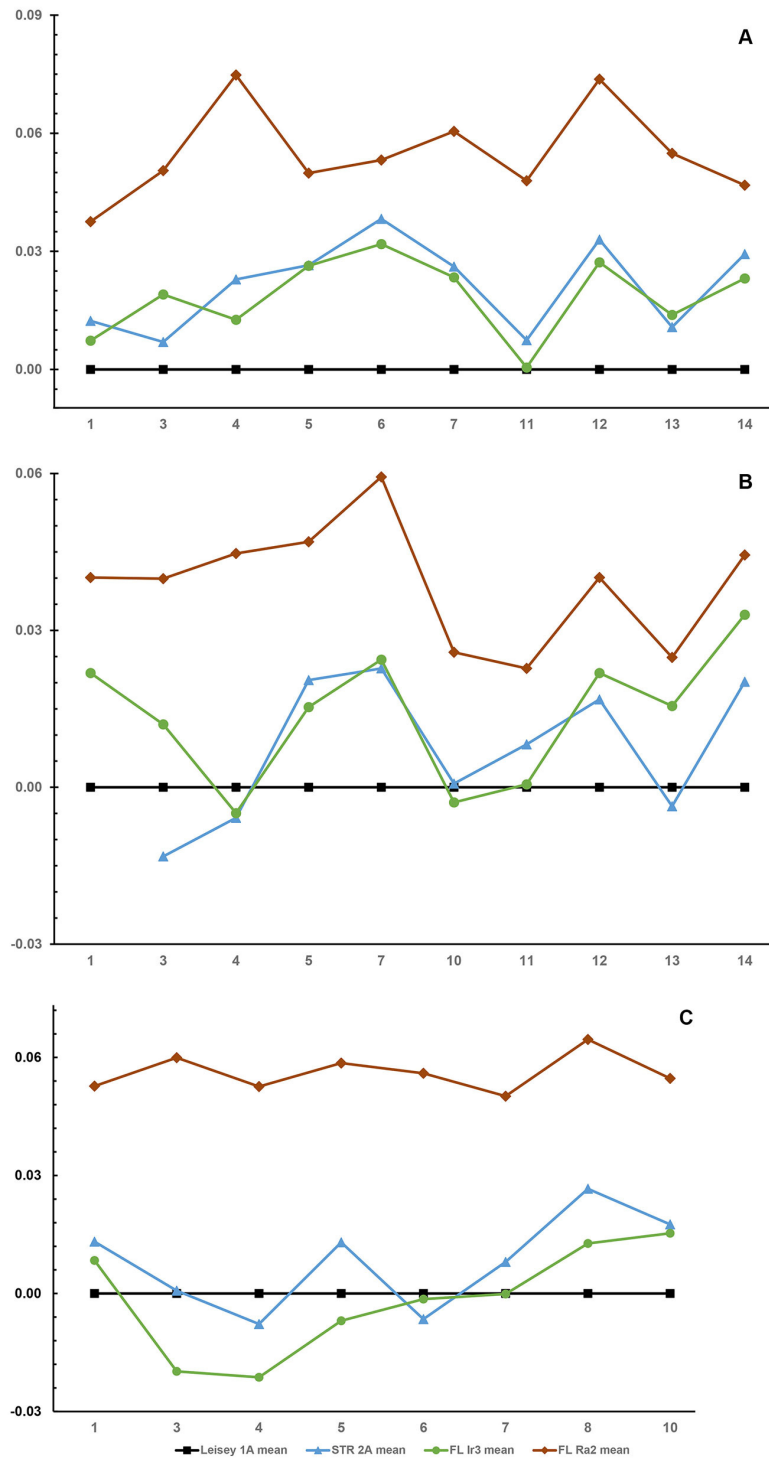
Figure 17. Log-ratio diagrams comparing mean values of limb bone measurements of *Equus* sp. A from Steinhatchee River 2A, middle Pleistocene, Florida; combined sample of Equus from Ir3 sites in Florida; combined sample of Equus from late Rancholabrean (Ra2) sites in Florida. Reference sample is *Equus* sp. A from Leisey Shell Pit 1A [72]. Numerals on x axis refer to standard measurements of equid bones from [73]. Data listed in Table S7. (**A**) metacarpal 3. (**B**) metatarsal 3. (**C**) proximal phalanx, digit 3.

Comments: In a review of Irvingtonian *Equus* from Florida, three species were recognized and given the informal names, *Equus* species A, B, and C [72]. *Equus* sp. A and C both have caballine [73] dental morphology and stout metapodials. They differ in that *E*. sp.

C is 20–25% larger (both teeth and limb bones) and that it has compressed lower incisors that all lacked infundibula. Only the i1 and i2 of *E.* sp. A have complete infundibula. *Equus* sp. B was similar in size to *E.* sp. A, but had a hemionine [72] dentition, complete infundibula on all three lower incisors, and slenderer metapodials. Informal species names were preferred by [72] because all species names for *Equus* in southeastern USA are based on Rancholabrean specimens, and many are based on isolated teeth and potentially not valid. In terms of biochronology, *E.* sp. A was reported from both the Ir1 and Ir3, and possibly the latest Blancan [72]. Its presence during the Ir2 was inferred at the time, but not based on any specimens. Both *Equus* sp. B and C were only known during the Ir1, the former primarily from Leisey Shell Pit 1A and the latter from Haile 16A. There were also a few records of both from other localities, but always based on very limited numbers of specimens.

Given its chronologic range, *Equus* sp. A is of interest to understanding the early evolution of the subgenus *Equus* (*Equus*), the true caballine equids, in North America. The STR 2A sample of *E.* (*E.*) sp. A expands our knowledge of this species both temporally and geographically. It is one of two populations known from northern peninsular Florida, as well as one of the few that are younger than the Ir1. Ideally, future collecting at STR 2A will produce cranial and postcranial fossils of greater completeness than now known, as well as increasing sample sizes for better statistical analyses of measurements on teeth and limb bones.

Order ARTIODACTYLA Owen, 1848
Family CAMELIDAE Gray, 1821
Tribe LAMINI Webb, 1965
Genus *Hemiauchenia* H. Gervais and Ameghino, 1880
Hemiauchenia macrocephala Cope, 1893

Referred Specimens: UF/VP 546755, 548431 two right M1s or M2s; UF/VP 556641, right P3; UF/VP 546859, 548432 two right proximal metacarpals; UF/VP 546864, 548437 two proximal phalanges; UF/VP 546863, distal condyle of metapodial; UF/VP 546865, 546866 two medial phalanges.

Description: UF/VP 546755 and 548431 are both identified as upper molars based on the presence of four well-separated roots, tooth width and length that are about equal, and two fully selenodont lingual cusps, the protocone and hypocone (Figure 18A,B). The distal (posterior) side of both crowns are flat for occlusion with a succeeding molar, unlike the condition in the M3s. Both also differ from lamine M3s in having approximately the same distance between the two buccal roots as between the two lingual roots (buccal roots have greater separation in M3s) and a greater ratio of basal posterior width to basal anterior width (Table 10). The DP4s of lamines are also fully molarized and have four large roots, but they differ from these two specimens in smaller basal crown dimensions and more narrowly separated lingual roots. Remnants of a thin layer of cementum still cover about half of the outer surface of the crowns. A thicker layer of dental calculus is present overlying the cementum of the buccal sides of both UF/VP 546755 and 548431. Where the cementum has been lost on the sides of the crowns, the visible surface of enamel is crenulated.

The crown height taken on the lingual side of the hypocone for UF/VP 548431 is 16.4 mm, while that of UF/VP 546755 is 10.3. Unworn and very slightly worn M2s of *H. macrocephala* have values in the range of 31–34 mm, while in M1s this range is 29–32 mm (Table S8). Thus, UF/VP 548431 has lost about half of its original crown height, and UF/VP 546755 about two-thirds. On the lesser worn molar, the parastyle and mesostyle are prominently visible on the occlusal surface, a faint metastyle is present, and the fossettes are still large (Figure 18A). The parastyle and mesostyle are smaller, the metastyle absent, and fossettes greatly reduced in the more heavily worn molar (Figure 18B).

The upper premolar, UF/VP 556641, is double-rooted and the lingual crest is limited to the posterior portion of the crown (Figure 18C). It is well worn, so like the molars it came from an older adult animal. Also like the molars, much of the enamel is covered by cementum, and the buccal side has moderate amounts of dental calculus.

Figure 18. Upper teeth and limb bones of *Hemiauchenia macrocephala* from Steinhatchee River 2A, middle Pleistocene, Florida. (**A**) UF/VP 548431, occlusal view of right M1 or M2. (**B**) UF/VP 546755, occlusal view of right M1 or M2. (**C**) UF/VP 556641 occlusal view of right P3. (**D,E**) UF/VP 546859, anterior and proximal views of right metacarpal 3–4. (**F,G**) UF/VP 546864, lateral and anterior views of proximal phalanx, digit 3 or 4.

UF/VP 546864 and 548437 (Figure 18F,G) match the referred lamine proximal phalanges in the UF/VP collection and are distinguished from those of other Pleistocene artiodactyls from Florida by having a longer, slenderer diapophysis and a slightly concave proximal articular surface with a shallow, ventrally limited groove for insertion of the metapodial keel. The epiphyseal line is still visible on the larger specimen, UF/VP 546864, but is not visible on UF/VP 548437. The suspensory ligament scar on UF/VP 546864 is less prominent. These indicate UF/VP 546864 is from an ontogenetically younger specimen than UF/VP 548437 despite its larger size. The differences in size between UF/VP 546864 and 548437, especially their lengths, is likely due to UF/VP 546864 being from the forelimb and UF/VP 548437 from the hindlimb. Forelimb proximal phalanges are 12–15% longer than those from the hindlimb in three modern skeletons of *Lama* in the FLMNH mammalogy collection. UF/VP 546865 and 546866 are mirror images of each other, and each has a visible epiphyseal line. They articulate well with UF/VP 546864, as does UF/VP 546863, suggesting that these four specimens are associated. As was the case with the STR 2A sample of *Equus*, the major limbs of the lamine have little or no surface damage, but none are complete (Figure 18D,E).

Table 10. Comparison of the length, width, and proportions of the two lamine upper molars from the STR 2A locality with samples of *Hemiauchenia macrocephala* and *Palaeolama mirifica* from Florida grouped by biochronologic age. Measurements of the teeth used to generate these statistics are presented in Table S8. BL, length at base of crown; BAW, anterior width at base of crown; and BPW, posterior width at base of crown. All measurements are in mm. Provided statistics for BL, BAW, and BPW are mean ± standard deviation and sample size in the first line and observed range in the second line. Provided statistics for BPW/BAW and BPW/BL are median and sample size in the first line and observed range in the second line.

SAMPLE	BL	BAW	BPW	BPW/BAW	BPW/BL
UF/VP 546755 STR 2A	20.9	21.2	21.6	102.0%	103.3%
UF/VP 548431 STR 2A	21.8	22.0	21.7	98.5%	99.5%
H. macrocephala M1					
Blancan	19.42 ± 0.91, 9 17.6–20.9	20.68 ± 1.14, 9 18.3–21.6	20.69 ± 0.93, 9 18.8–21.6	101.56%, 8 96.2–102.9%	105.24%, 7 97.2–111.8%
Irvingtonian 1	19.29 ± 1.15, 30 17.2–22.0	20.02 ± 0.81, 30 19.0–22.0	20.67 ± 0.90, 29 19.3–22.1	102.78%, 29 94.1–111.9%	110.14%, 28 94.6–118.0%
Irvingtonian 3	19.52 ± 0.25, 2 19.3–19.7	21.07 ± 0.43, 3 20.6–21.5	21.89 ± 1.81, 3 20.7–24.0	102.04%, 3 97.8–111.6%	115.26%, 2 108.8–121.7%
Rancholabrean	19.45 ± 1.09, 14 17.0–21.8	21.09 ± 1.26, 15 18.8–23.5	21.33 ± 1.10, 13 19.1–22.8	100.91%, 13 94.8–107.3%	109.64%, 12 103.6–117.8%
H. macrocephala M2					
Blancan	20.50 ± 0.58, 9 19.6–21.1	21.50 ± 0.81, 10 19.7–22.4	20.63 ± 1.16, 10 18.0–21.2	94.53%, 10 89.9–98.6%	100.66%, 9 97.2–111.8%
Irvingtonian 1	20.32 ± 1.41, 24 16.9–22.4	21.32 ± 0.98, 23 19.9–23.9	20.70 ± 1.15, 22 18.5–23.0	97.11%, 22 87.8–104.3%	102.56%, 21 84.3–116.6%
Irvingtonian 3	20.95 ± 0.92, 3 19.9–21.6	21.01 ± 0.59, 3 20.5–21.7	21.96 ± 1.07, 3 21.0–23.1	104.11%, 2 102.3–106.7%	106.81%, 2 106.7–108.0%
Rancholabrean	22.51 ± 1.26, 11 20.6–24.4	22.24 ± 0.94, 13 20.3–23.3	21.60 ± 1.21, 13 19.5–24.0	97.03%, 12 92.9–100.1%	94.38%, 11 88.6–105.9%
H. macrocephala M3					
Blancan	22.69 ± 1.89, 9 20.5–26.7	21.22 ± 2.83, 11 12.9–23.4	18.72 ± 1.64, 10 15.9–21.0	87.49%, 10 79.7–134.3%	80.56%, 9 71.0–92.5%
Irvingtonian 1	24.00 ± 2.32, 21 19.1–28.6	20.69 ± 1.11, 21 19.0–23.5	18.22 ± 1.05, 21 15.9–20.1	87.63%, 20 82.3–96.4%	76.16%, 20 67.2–102.1%
Irvingtonian 3	25.13 ± 0.38, 2 24.9–25.4	22.26 ± 1.05, 2 21.5–23.0	19.89 ± 1.29, 22 19.0–20.8	89.29%, 2 88.2–90.4%	79.18%, 2 74.7–83.7%
Rancholabrean	25.99 ± 1.92, 13 21.6–28.3	22.11 ± 1.07, 13 20.1–23.9	19.43 ± 1.12, 14 17.3–21.6	86.04%, 12 80.7–94.4%	74.05%, 13 67.4–82.9%
P. mirifica M1					
Irvingtonian 1	16.29 ± 1.00, 88 13.9–19.5	19.51 ± 0.88, 91 17.5–21.6	19.13 ± 0.76, 91 17.4–21.0	97.72%, 90 91.2–104.0%	117.02%, 85 101.6–139.1%
Irvingtonian 3	17.06 ± 0.87, 9 15.7–18.3	20.16 ± 0.48, 8 19.3–20.8	19.27 ± 0.57, 9 18.3–19.9	96.86%, 8 92.9–98.8%	115.05%, 9 103.1–124.8%
Rancholabrean	17.61 ± 0.87, 31 15.8–19.1	20.63 ± 1.02, 34 18.4–22.8	20.01 ± 1.12, 32 17.1–22.4	96.20%, 31 90.6–103.3%	113.80%, 29 98.5–126.0%
P. mirifica M2					
Irvingtonian 1	18.06 ± 1.04, 80 14.7–20.3	21.98 ± 0.91, 82 20.1–24.4	19.86 ± 0.91, 80 17.9–22.1	89.95%, 79 83.5–97.6%	109.82%, 79 94.9–140.0%
Irvingtonian 3	18.76 ± 0.65, 15 17.5–20.0	22.46 ± 0.71, 14 21.1–23.7	20.01 ± 0.80, 14 18.8–21.8	89.28%, 13 85.9–92.7%	105.94%, 14 98.2–116.0%
Rancholabrean	19.54 ± 1.16, 37 16.9–21.9	22.61 ± 0.94, 38 20.2–24.4	20.52 ± 0.92, 36 18.1–23.1	90.41%, 35 83.4–99.6%	105.59%, 34 88.7–120.6%
P. mirifica M3					
Irvingtonian 1	19.92 ± 1.66, 64 16.4–23.7	21.36 ± 0.97, 70 19.4–24.0	17.75 ± 0.86, 70 15.8–20.0	83.32%, 67 76.3–91.2%	89.39%, 63 77.2–110.8%
Irvingtonian 3	20.04 ± 1.22, 8 17.8–22.0	21.47 ± 1.19, 8 19.4–23.4	17.95 ± 1.13, 8 16.7–19.8	83.14%, 8 80.4–91.2%	86.01%, 8 81.1–107.0%
Rancholabrean	21.91 ± 1.83, 44 18.3–25.5	21.88 ± 1.03, 50 19.3–24.2	18.23 ± 1.04, 47 15.2–20.4	83.81%, 47 74.4–90.6%	83.81%, 44 70.4–99.5%

Comments: The two recognized genera of lamines in Florida during the Pleistocene are *Hemiauchenia* and *Palaeolama* [74,75]. While there were three recognized species of *Hemiauchenia* in Florida during the Blancan NALMA, *H. macrocephala*, *H. blancoensis*, and *H. gracilis* [74,76], only one, *H. macrocephala*, persisted into the Irvingtonian and survived

until the end of the Rancholabrean. *Palaeolama mirifica* is the sole recognized species of the genus in North America and is common at many Irvingtonian and Rancholabrean sites in Florida [4,74], with a single known specimen reported from the very late Blancan [77].

The basal crown dimensions of UF/VP 546755 and 548431 fall within the observed ranges of the M1 and M2 of *H. macrocephala* and the M2 of *P. mirifica* (the M1 of the latter species is smaller than the two STR 2A molars; Table 10). However, the ratios for posterior width relative to anterior width for both STR 2A molars are outside the known range for the M2 of *P. mirifica* but match those of *H. macrocephala* M1s and M2s (Table 10). As UF/VP 546755 and 548431 are from the same side, their differences in crown height are within the range of first and second molars from the same individual, and associated specimens are common at STR 2A, it would at first seem likely that they would be the first and second molars from one individual. However, such teeth wear into each other, so that they fit tightly together. As that is not the case with UF/VP 546755 and 548431, it is more likely they came from two individuals. The worn P3 could be associated with either one of them.

Morphologic features supporting referral of UF/VP 546755 and 548431 to *Hemiauchenia* instead of *Palaeolama* include the presence of widespread coronal cement and the lack of a pronounced rib on the buccal side of the crown between the parastyle and mesostyle. The P3 UF/VP 556641 belongs to *Hemiauchenia* instead of *Palaeolama* based on having two roots instead of three, a lingual crest limited to the posterior half of crown, and coronal cement. Referral of UF/VP 546864 and 548437 to *Hemiauchenia* instead of *Palaeolama* is based on having lengths greater than 90 mm and ratios of minimum diapophysis width to greatest length of less than 17%. Values for length, proximal width, distal width, and other dimensions of the two phalanges are all within the known range of *H. macrocephala*.

Genus and Species Indeterminate

Referred Specimens: UF/VP 546858 left proximal radioulna*; UF/VP 548466 right distal radioulna; UF/VP 548432 left pisiform; UF/VP 556642, right trapezoid; UF/VP 548436 left proximal metacarpal fragment; UF/VP 548433, distal metacarpal*; UF/VP 546860 left proximal femur*; UF/VP 546861 left distal femur*; UF/VP 546862 right proximal tibia*; UF/VP 548434, 548435 two mid-shaft metapodial sections. *Indicates juvenile or subadult specimen lacking fused epiphysis.

Comments: The listed specimens all derive from a member of the Lamini but are not complete enough to confidently determine if they come from *P. mirifica* or *H. macrocephala*.

Family CERVIDAE Gray, 1821

Tribe ODOCOILEINI Pocock, 1923

Genus *Odocoileus* Rafinesque, 1832

Odocoileus virginianus (Zimmermann, 1780)

Referred Specimens: UF/VP 548439, left dentary fragment with p3–m2; UF/VP 547389, antler, proximal (shed); UF/VP 547390, antler tine; UF/VP 548452, lumbar vertebra; UF/VP 548440, right proximal radius; UF/VP 548441, left proximal metacarpal 3–4; UF/VP 548442, distal metacarpal 3–4; UF/VP 548445, proximal left epiphysis of tibia; UF/VP 548443, left distal tibia; 548444, right distal tibia; UF/VP 548450, left astragalus; UF/VP 548448, 548449, right astragali; UF/VP 548465, right cubonavicular; UF/VP 548446, right proximal metatarsal 3–4; UF/VP 548447, distal metatarsal 3–4; UF/VP 548451, distal phalanx.

Description: UF/VP 547389 preserves a 21 cm long portion of the proximal end of a shed antler with the broken bases of two tines (Figure 19A). The first tine is located about 10.5 cm from the burr, the second about 20 cm. The main beam is helically curved. The lower premolars of UF/VP 548439 display typical cervoid features. The m1 has a small ectostylid, while the m2 lacks one (Figure 19B). A stylid is also present on the lingual side of the p4 hypoconid. All four teeth have well-developed anterior cingulids. All the listed referred postcranial elements are of the same size and morphology as extant *Odocoileus virginianus*. As with the other STR 2A ungulates, all limb bones are broken, usually mid-shaft, while the more compact carpals, tarsals, and phalanges are complete (Figure 19C,D).

Figure 19. *Odocoileus virginianus* (**A**–**D**) and *Mammuthus columbi* (**E**) from Steinhatchee River 2A, middle Pleistocene, Florida. (**A**) UF/VP 547389, proximal end of shed antler. (**B**) UF/VP 548439, lateral view of partial left dentary with p3–m2. (**C**) UF/VP 548447 anterior view of distal end of metatarsal 3–4. (**D**) UF/VP 548450, anterior view of left astragalus. (**E**) UF/VP 548419, anterior or posterior view of unerupted tooth plate.

Comments: The chronologic range of *O. virginianus* in Florida is from the late Blancan to the present [4,28]. Its fossils are found in varying numbers at most fossil locations throughout the state within this time interval. Of all the ungulate lineages that persisted from the early to the very late Pleistocene in Florida, *O. virginianus* shows the least morphologic change.

Superorder AFROTHERIA Stanhope et al., 1998
Order PROBOSCIDEA Illiger, 1811
Family ELEPHANTIDAE Gray, 1821
Genus *Mammuthus* Brookes 1828
Mammuthus columbi (Falconer, 1857)

Referred Specimens: UF/VP 548419–548422, four isolated, unworn dental plates; UF/VP 546756 two unworn dental plates (associated?); UF/VP 548423, ectocuneiform.

Description: The six dental plates derive from possibly one or, more likely, two unerupted cheekteeth (Figure 19E; Table 11). The bases of all the plates are broken. The heights and widths are too large for one of the deciduous premolars and likely too small for a third molar.

Table 11. Measurements in mm of *Mammuthus columbi* tooth plates from Steinhatchee River 2A, Dixie County, Florida.

Catalog Number	Plate Height (As Preserved)	Maximum Plate Width	Plate Thickness
UF/VP 548419	86.7	76.8	8.5–10
UF/VP 548420	105.3	65.3	7.7–8.8
UF/VP 548421	96.5	56.1	7.7–9.3
UF/VP 548422	107.0	56.0	8.1–11.4
UF/VP 546756a	88.6	56.3	7.5–9.1
UF/VP 546756b	77.7	59.2	7.3–9.0

Comments: Three proboscidean taxa are recognized from the Ir of Florida [78]: *Mammut americanum* (Mammutidae), *Cuvieronius hyodon* (Gomphotheriidae), and *Mammuthus columbi* (Elephantidae). Species-level taxonomy for *Cuvieronius* and *Mammuthus* used by [78] is here updated to follow more current studies [79–81]. Tooth plates such as those recovered at STR 2A are only present in the Elephantidae [82], so despite their incompleteness, they can positively be referred to *M. columbi*. The ectocuneiform UF/VP 548423 is narrow in ventral or dorsal view, consistent with an identification of *Mammuthus* [83]. All other proboscidean fossils from STR 2A (listed below) do not contain any diagnostic features that would permit them to be identified to the family level.

Family, Genus, and Species Indeterminate

Referred specimens: UF/VP 548424, fragment of the proximal end of a humerus; UF/VP 548426, small tusk fragment; UF/VP 548470, 10 mid-shaft sections of ribs; UF/VP 548471, petrosal; UF/VP 548475, subadult caudal vertebra lacking epiphysis.

5. Discussion

5.1. Biochronology of STR 2A

Table 12 shows the chronologic ranges of 58 mammalian taxa which are useful for age determination of Irvingtonian sites in Florida. Species whose ranges extend from the late Blancan through the Irvingtonian and into the Rancholabrean (e.g., *Dasypus bellus*, *Hemiauchenia macrocephala*) are not listed in Table 12. Some long-ranging taxa experienced changes in size or morphology over time, such that their "stage of evolution" can assist with age determination.

Table 12. Biochronologic ranges of mammalian species in Florida through the Irvingtonian and adjacent NALMAs. FA, first appearance; LA, last appearance; OA, only appearance; X, present; Ir, Irvingtonian; Ra, Rancholabrean. Based on [12,21], with some revisions to update taxonomy and new records.

Taxon	Latest Blancan	Ir1	Ir2	Ir3	Ra1	Ra2
Didelphis virginiana				FA	X	X
Holmesina floridanus	X	LA				
Holmesina septentrionalis			FA	X	X	LA
Glyptotherium texanum	X	LA				
Glyptotherium floridanum					FA	LA
Pachyarmatherium leiseyi	X	LA				
Megalonyx leptostomus	LA					
Megalonyx wheatleyi		FA	X	LA		
Paramylodon harlani	X	X	X	X	X	X
Eremotherium eomigrans	X	LA				
Eremotherium laurillardi					FA	LA
Aenocyon edwardii	X	LA				
Aenocyon armbrusteri		FA	X	X	LA	
Aenocyon dirus					FA	LA
Arctodus pristinus	X	X	X	LA		
Tremarctos floridanus					FA	LA
Procyon megalokolos	LA					
Procyon lotor		FA		X	X	X
Puma concolor					FA	X
Panthera onca			FA	X	X	X
Xenosmilus hodsonae	X	LA				
Smilodon gracilis	X	X	LA			
Smilodon fatalis				FA	X	LA
Chasmaporthetes ossifragus	LA					
Tapirus lundeliusi	LA					
Tapirus haysii	X	LA				
Tapirus veroensis				FA	X	LA
Equus sp. "A"	FA	X	X	LA		
Equus sp. "B"		OA				
Equus sp. "C"		OA				
Mammuthus columbi		FA	X	X	X	LA
Mylohyus fossilis		FA		X	X	LA
Platygonus bicalcaratus	LA					
Platygonus vetus		OA				
Platygonus cumberlandensis				OA		
Platygonus compressus					FA	LA
Hemiauchenia gracilis	LA					
Capromeryx arizonensis	LA					
Bison latifrons					FA	LA
Glaucomys volans				FA	X	X
Sigmodon minor	LA					
Sigmodon curtisi	OA					
Sigmodon libitinus		OA				
Sigmodon bakeri			FA	X	LA	
Sigmodon hispidus					FA	X
Ondatra idahoensis	LA					
Ondatra annectens		OA				
Neofiber leonardi				OA		
Neofiber alleni				FA	X	X
Synaptomys morgani		OA				
Synaptomys australis					FA	LA
Orthogeomys(?) *propinetis*	X	LA				
Geomys pinetis		FA		X	X	X
Thomomys orientalis				FA	X	LA
Erethizon kleini	LA					
Erethizon dorsatum		FA		X		X
Sylvilagus webbi	X	LA				
Sylvilagus palustris					FA	X

Biochronology of the STR 2A locality and its local fauna is hindered by a relatively depauperate mammalian fauna, especially its lack of small rodents, and that several taxa that are present have little biochronologic value due to long chronologic ranges. The

co-occurrence of *Mammuthus columbi* and *Equus* sp. A constrain the age of STR 2A to the Irvingtonian NALMA. This age determination is consistent with the absence of *Bison* at STR 2A. Absences of taxa have lesser weight in biochronologic analysis than do presences, but Florida Rancholabrean faunas with large numbers of *Equus* very rarely completely lack *Bison*. The absences of *Eremotherium* and *Glyptotherium* also support an Ir2 or Ir3 age, as both these taxa apparently were extirpated in Florida during the Ir1 and did not reappear until the Rancholabrean (but see below). The metapodials of *Equus* sp. A from STR 2A show greater resemblance to those from the Ir3 populations than those from the Ir1. This favors an age of Ir2 or Ir3 as opposed to Ir1. The fossils of *Paramylodon* at STR 2A are larger than the same skeletal elements from Ir1 *Paramylodon*, and more similar in size to individuals from the Rancholabrean. This again favors an age younger than the Ir1 for STR 2A. The *Tapirus* from STR 2A likely represents a new taxon currently not known from any other locality. This would generally mean that its occurrence has no chronologic value. Two or three species of *Tapirus* have co-existed at various times through the late Neogene and early Pleistocene of Florida, but in every known case the co-existing species differed greatly in size [12,61,63]. The STR 2A *Tapirus* is the same general size as *Tapirus lundeliusi* from the late Blancan and *T. veroensis* from the Ir3 and Rancholabrean (Table 5). Thus, the size of the STR 2A *Tapirus* supports an age of either Ir1 or Ir2 for the site, when other medium-sized species are absent.

The strongest evidence for the age of the STR 2A locality and its fauna derives from the astragalus and metatarsals of *Holmesina*. The Ir2 McLeod specimens were regarded as the oldest sample of *Holmesina septentrionalis* as they shared 11 character states in the postcranial skeleton with Rancholabrean populations that were not observed in Ir1 specimens of *Holmesina floridanus* [24]. Also, the teeth of AMNH FM 99233, a partial dentary from McLeod, also fell within the range of variation in Rancholabrean *H. septentrionalis* as opposed to Ir1 *H. floridanus* in both size and morphology. However, in at least one character, size of the entepicondylar fossa on the distal humerus, the McLeod specimen, was intermediate between Ir1 specimens of *H. floridanus* and Rancholabrean *H. septentrionalis* [24]. The astragalus from STR 2A, an element not known from McLeod, is also intermediate in nature, sharing some features with *H. floridanus* and some with *H. septentrionalis*. As described above, metatarsals 1, 2, and 4 also show a mix of features found in *H. floridanus*, in *H. septentrionalis*, and some that are intermediate between the two. This stage of evolution for the STR 2A *Holmesina* supports an age very close to, but slightly older than, that of McLeod. Placing STR 2A in the Ir2 with McLeod is also compatible with the age estimates derived from *Tapirus*, *Equus*, and *Paramylodon* and the absences of *Bison*, *Eremotherium*, and *Glyptotherium*. Future collecting at STR 2A should recover fossils of additional taxa that will test this age estimation.

5.2. Significance of the Steinhatchee River 2A Local Fauna

Florida is the only region in eastern North America with a dense fossil record of terrestrial vertebrates spanning the entire Pleistocene Epoch. In the FLMNH collection alone, over 800 Pleistocene localities in the state have produced over 253,000 fossils of tetrapod vertebrates. Quantitative analysis of evolutionary trends and speciation rates during this critical period is hindered by a very uneven distribution of these localities through geologic time. About 43% of the known Pleistocene tetrapods from Florida date to the early Pleistocene (Gelasian and Calabrian, roughly equivalent to the late Blancan and early Irvingtonian NALMAs) and about 50% date to the late Pleistocene (late Rancholabrean NALMA). The middle Pleistocene (Chibanian), approximately equivalent to the middle and late Irvingtonian (Ir2 and Ir3, respectively), and the early Rancholabrean (Ra1), has far fewer localities that have provided only about 7% of the known tetrapod fossils from the Pleistocene of Florida. The poorer quality of the middle Pleistocene fossil record of tetrapods means that it is very likely that some of the last appearances listed for the Ir1 in Table 12 actually occurred at a younger time. Likewise, some of the first appearances shown in Table 12 for the I3 and Ra1 may have occurred during an older interval.

The STR 2A locality is apparently the first Ir2 site to be discovered in Florida in over 80 years. Only a small portion of the entire site has been searched for fossils. Its remote location will make large-scale excavations challenging, but the quality and importance of the fossils already discovered suggest such efforts would be fruitful. The STR 2A *Holmesina* provides a good example of the site's potential. There are five other xenarthran genera known from the early and late Pleistocene of Florida. Three of these, the sloths *Megaloyx* and *Paramylodon* and the armadillo *Dasypus*, were thought to be single lineages with varying degrees of anagenetic evolution through the epoch [4,54,55,84,85]. This was because there were enough known middle Pleistocene specimens in each case that seemingly evolutionarily connected the early and late Pleistocene populations. No fossils of the two other genera, the sloth *Eremotherium* and the glyptodont *Glyptotherium*, are positively known from the Ir2 or Ir3 in Florida. A fossil of *Eremotherium eomigrans* (AMNH FM 95773) was reported to be from the Ir2 McLeod locality [86], but it was actually collected 17 years prior to the discovery of this site with only very generalized locality information. Also, no specimens of this sloth were collected during the extensive 1941 Galusha excavation of the McLeod site. We do not think there is sufficient evidence that this specimen was collected at McLeod, and thus its geologic age is uncertain without further information. *Eremotherium* and *Glyptotherium* are hypothesized to have become locally extinct towards the end of the Ir1 followed by a dispersal event of a different species sometime in the early Rancholabrean. Their absence at STR 2A helps corroborate this hypothesis. The evolutionary pattern of the fifth genus, *Holmesina*, was less clear. Specimens from the Ir3 and even the few from the Ir2 McLeod site for the most part resembled those of the Rancholabrean species. The lack of intermediate or transitional specimens left open the possibility of extinction of *H. floridanus* in the Ir1 followed by the dispersal of *H. septentrionalis* in the late Ir2. The intermediate nature of the STR 2A *Holmesina* instead implies that its evolutionary history was more like those of *Paramylodon*, *Megalonyx*, and *Dasypus*.

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