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A NEW EARLY PLEISTOCENE TAPIR (MAMMALIA: PERISSODACTYLA) FROM FLORIDA, WITH A REVIEW OF BLANCAN TAPIRS FROM THE STATE

Richard C. Hulbert Jr.

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A NEW EARLY PLEISTOCENE TAPIR (MAMMALIA: PERISSODACTYLA) FROM FLORIDA, WITH A REVIEW OF BLANCAN TAPIRS FROM THE STATE

Richard C. Hulbert Jr.[1]

ABSTRACT

Florida has the best late Blancan (early Pleistocene, 2.6–1.6 Ma) record of *Tapirus* in North America. The genus is currently known from 25 fossil localities of Blancan age, ranging through most of the peninsular region of the state. Three species are recognized from this time interval in Florida: the relatively large-sized *Tapirus haysii* Leidy; the moderate-sized **Tapirus lundeliusi sp. nov.**; and a much smaller, as yet unnamed species. *Tapirus haysii* was previously known from the early Irvingtonian (ca. 1.6 to 1.0 Ma) in Florida; the specimens reported here from seven localities extend its range into the Blancan, which is in accord with Blancan records from North Carolina (type locality) and the central United States. The Blancan finds of *T. haysii* in Florida are all relatively sparse, mostly consisting of one or two isolated teeth per locality. The unnamed small Blancan species of *Tapirus* is slightly better known: three jaw fragments each with a single tooth; four isolated teeth; a phalanx; and a navicular from a total of five different localities. It is significantly smaller than any extant species of *Tapirus* and all of those previously described from the Pleistocene of North America. 'Dwarf' tapirs are known from the Hemphillian of the southeastern United States (e.g., *Tapirus polkensis*) and the late Miocene of Europe (e.g., *Tapirus pannonicus*), but this is the first case of their persistence into the Pleistocene. The small Blancan tapir is on average slightly larger than *Tapirus polkensis*, and is the same size as an undescribed species of *Tapirus* present in the late Hemphillian Palmetto Fauna of central Florida.

Tapirus lundeliusi sp. nov. is described on the basis of multiple skeletons from the Haile 7C and 7G localities of north-central Florida, and more limited samples from nine other Blancan sites. It apparently became extinct near the Blancan-Irvingtonian boundary, with its youngest confirmed record at the Inglis 1A locality. *Tapirus lundeliusi* is of moderate size for the genus, similar to extant *Tapirus terrestris* and *Tapirus pinchaque*, and the middle to late Pleistocene species *Tapirus veroensis*. It is significantly smaller than *Tapirus haysii*. The skull of *T. lundeliusi* differs from those of *T. veroensis* and *T. haysii* in retaining a number of primitive features, such as having a small maxillary flange, longer nasal bone, shorter lacrimal bone, and ontogenetically rapid fusion of interparietal to occipital. Derived features of *T. lundeliusi* include a reduced frontal shield and increased relative mandibular condyle height. Phylogenetic analysis places *T. lundeliusi* as the sister taxon of *T. veroensis* + *T. haysii*, and the clade formed by these three North American fossil species is formally designated as **Tapirus (Helicotapirus) subgen. nov.** Among other species of *Tapirus*, the extant *T. bairdii* and the late Neogene *T. polkensis* are most closely related to *T. (Helicotapirus)*. They all share a large, triangular interparietal; broad, flat posterior lacrimal process; and extensive meatal fossa on the dorsal surface of the frontal and nasal bones.

Key Words: Tapiridae; *Tapirus*; new species; Blancan; Florida; phylogenetic analysis; biochronology

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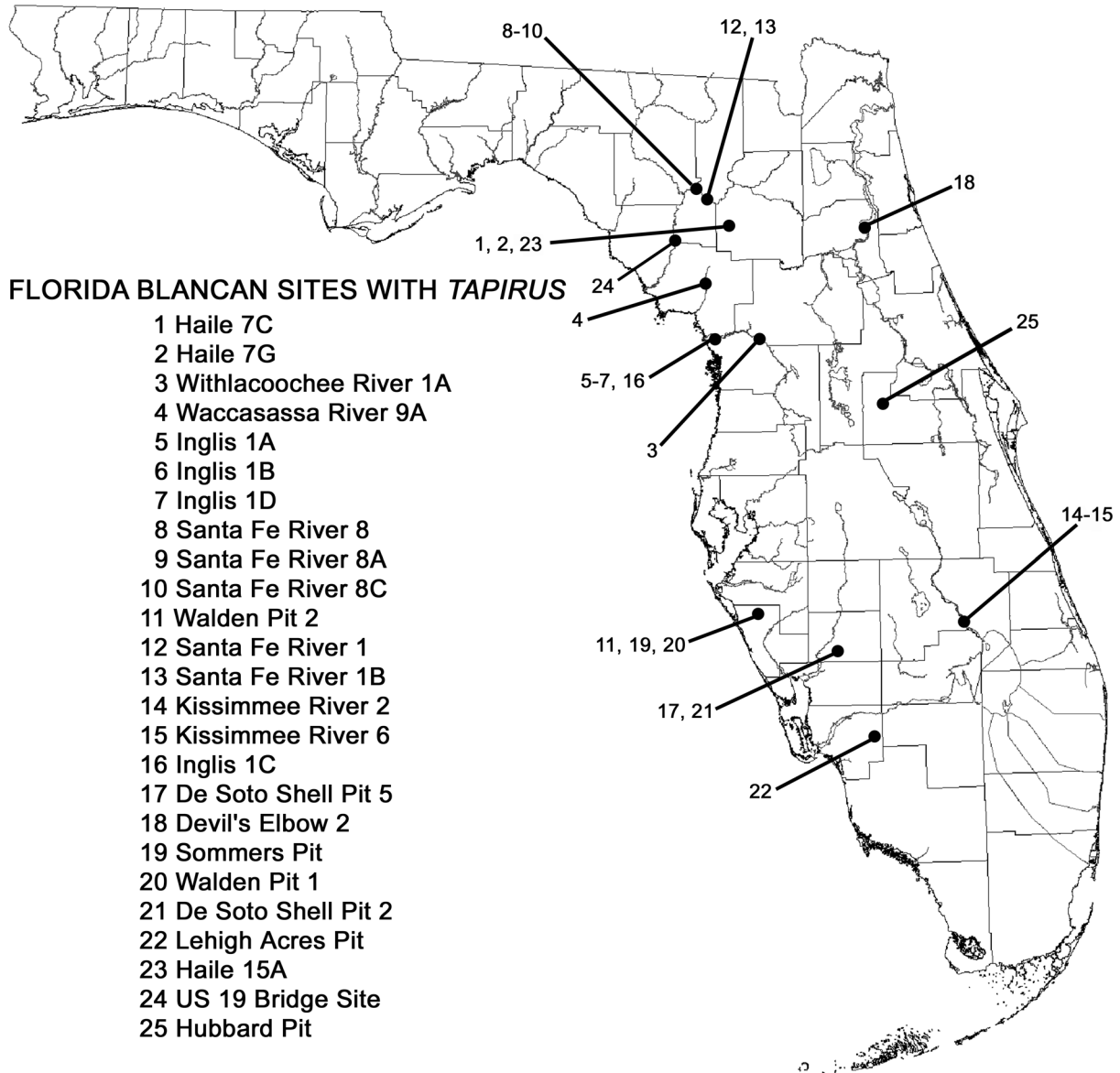
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INTRODUCTION

Fossils referred to the extant genus of tapir, *Tapirus* Brisson 1762, are relatively abundant in Irvingtonian and Rancholabrean faunas in Florida, and have received considerable study (e.g., Sellards 1918; Simpson 1929 1945; Bader 1957; Ray 1964; Lundelius & Slaughter 1976; Ray & Sanders 1984; Hulbert 1995; Graham 2003). Two species are currently recognized from Florida during this interval, *Tapirus haysii* Leidy in the early Irvingtonian and *Tapirus veroensis* Sellards in the late Irvingtonian through Rancholabrean (Hulbert 1995). The situation is quite different for the preceding Blancan land mammal age (4.4–1.6 Ma) in Florida, for which there are no formally described species of *Tapirus*.

Webb (1974) was the first to indicate the presence of *Tapirus* in the Blancan of Florida, listing records in a table from three localities, Santa Fe River 1B, Haile 15A, and Inglis 1A (Fig. 1; Appendix 1), but no descriptions were provided nor identifications to the species level. Ray et al. (1981) and MacFadden and Hulbert (2009) noted that Webb's (1974) list of Santa Fe River 1B mammals is actually a composite listing of Blancan mammals (or those thought at the time to be Blancan) from all Santa Fe River fossil sites, not just the 1B locality. Furthermore, as detailed by MacFadden and Hulbert (2009), the Santa Fe River 1B locality actually produced both Blancan and Rancholabrean vertebrates, contrary to the assertions of Webb (1974), who was followed by Kurtén and Anderson (1980), that site contained only Blancan fossils.

Two size classes of *Tapirus* have been found in the Santa Fe River 1 region (Fig. 1): a rarer, larger form that is within the size range of *Tapirus haysii* and a much more numerous group of smaller teeth and bones that is within the size ranges of both the Rancholabrean *Tapirus veroensis* and the new Blancan species described below. The Santa Fe River 1 and 1B specimens of *T. haysii* are all isolated teeth (Fig. 2A-C). Their primary significance is to

FLORIDA BLANCAN SITES WITH *TAPIRUS*

1 Haile 7C
2 Haile 7G
3 Withlacoochee River 1A
4 Waccasassa River 9A
5 Inglis 1A
6 Inglis 1B
7 Inglis 1D
8 Santa Fe River 8
9 Santa Fe River 8A
10 Santa Fe River 8C
11 Walden Pit 2
12 Santa Fe River 1
13 Santa Fe River 1B
14 Kissimmee River 2
15 Kissimmee River 6
16 Inglis 1C
17 De Soto Shell Pit 5
18 Devil's Elbow 2
19 Sommers Pit
20 Walden Pit 1
21 De Soto Shell Pit 2
22 Lehigh Acres Pit
23 Haile 15A
24 US 19 Bridge Site
25 Hubbard Pit

Figure 1. Map of Florida showing location of fossil localities of Blancan age that have produced fossils of *Tapirus*. See Appendix 1 for detailed geographic information. *Tapirus lundeliusi* sp. nov. was found at localities numbered 1 through 11; *Tapirus haysii* at localities 12 through 18; and *Tapirus* sp. indeterminate at localities 15 and 19 through 25.

show that *T. haysii* was present in the late Blancan of Florida (contrary to Hulbert 1995). The smaller teeth of *Tapirus* from the Santa Fe River 1 region probably represent a mixture of Rancholabrean *T. veroensis* and the new Blancan species, but most isolated teeth of the two species can not be classified with confidence using morphology and standard linear measurements. Linear discriminant analyses between the two taxa for each cheektooth position have misclassification rates ranging from 13 to over 45 percent, with most falling in the range of 25 to 30 percent. Discriminant scores for most Santa Fe River 1 teeth grouped them with *T. veroensis*, with only a few specimens classified as the Blancan species. However, a hypothesis that they are all *T. veroensis* can not be falsified, because of the high misclassification rates. For that reason they are not included in this study.

There are no problems with mixing or reworking of specimens from the two other Blancan localities with *Tapirus* listed by Webb (1974), Haile 15A and Inglis 1A. However, the single Haile 15A specimen, UF 17468, is a fragmentary lower cheektooth. As noted by Robertson (1978), it is adequate to document the presence of the genus in the fauna, but is not specifically diagnostic. The Inglis 1A sample of *Tapirus* consists primarily of isolated postcranial elements, with a few isolated teeth, two dorsal skull elements, and three partial maxillae. This sample was also listed by Webb and Wilkins (1984) and Graham (2003), but has never been described or figured until now, nor referred to a species.

Two skeletons of *Tapirus*, a subadult, UF 121736, and a juvenile, UF 162351, were found during the first major period of excavations at the late Blancan Haile 7C locality in 1989–1991 (Appendix 1). These were the first skeletons of tapirs older than late Pleistocene ever found in Florida, and also preserved the first known skulls of Blancan tapirs from the state. The skull of UF 121736 differs significantly in a number of features from *Tapirus veroensis*. Following its preparation in the early 1990s, it was evident that it represented a new species. However, formal description was delayed for several reasons including, the lack of a complete nasal bone in UF 121736 (which provide
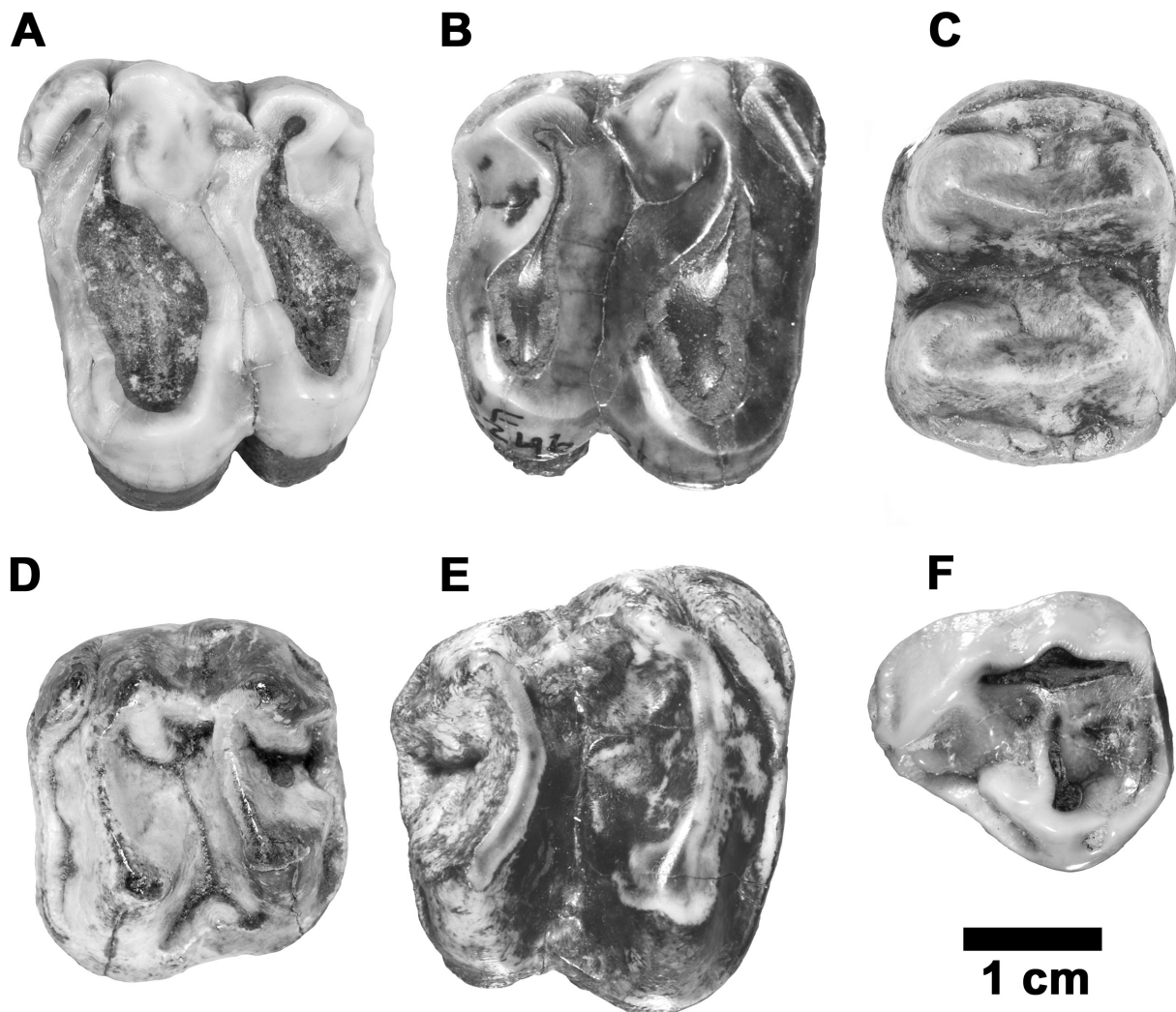
Figure 2. Teeth of *Tapirus haysii* from the late Blancan of Florida, in occlusal view. **A**, UF 213920, left M1 or M2; **B**, UF 224631, right M1 or M2; **C**, UF 177842, left p4; **D**, UF 51250, left P4; **E**, UF 177843, right M3; **F**, UF 177844, left P1. Localities listed in text and Appendix 1.
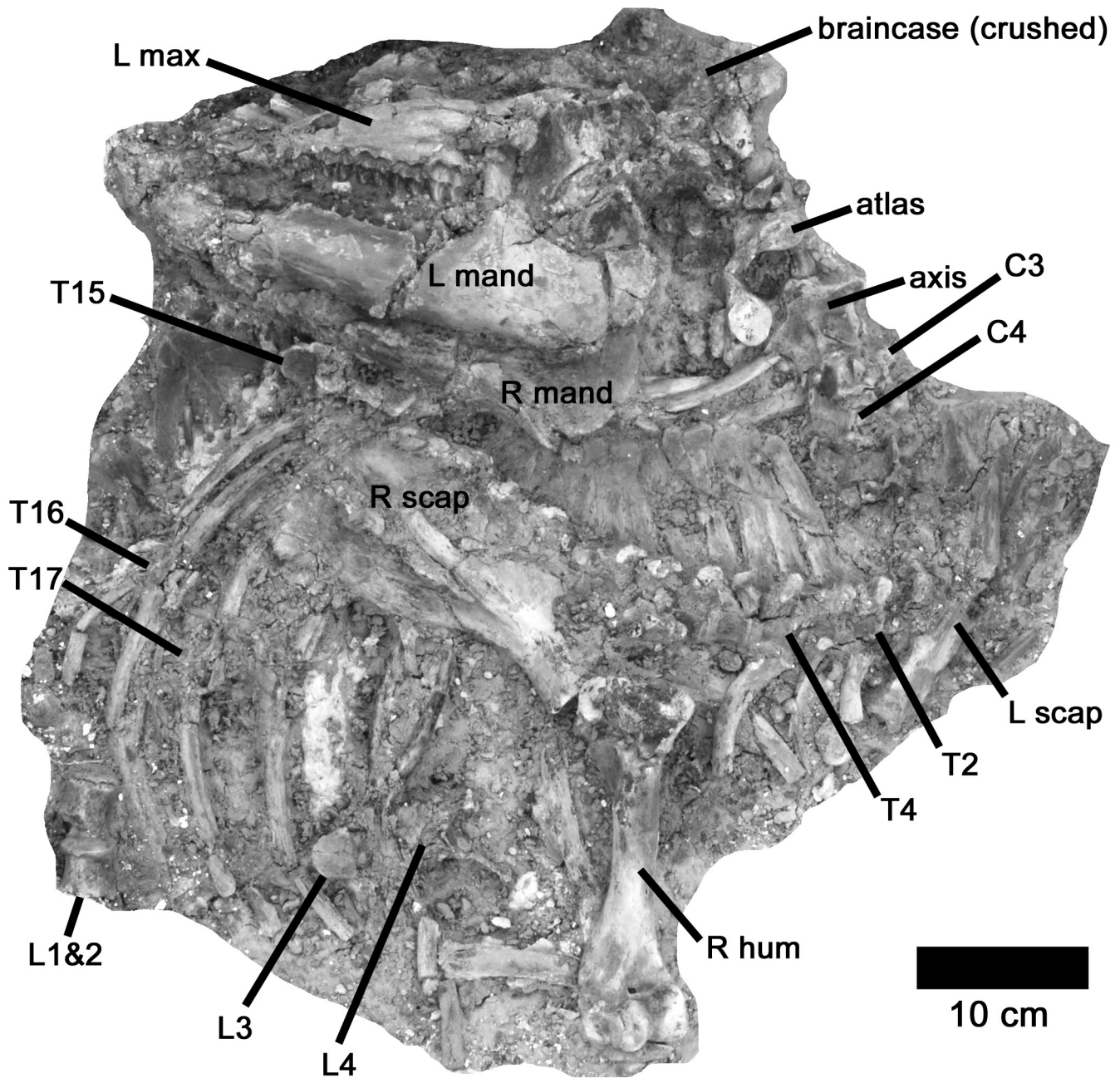
Figure 3. Portions of an articulated juvenile skeleton of *Tapirus lundeliusi* sp. nov., UF 247102, from Haile 7G. Other portions of this skeleton, including remainder of forelimbs and both hind limbs removed prior to photography. Degree of association of the tapir skeletons from Haile 7C and 7G ranged from nearly fully articulated, such as this individual, to those scattered over an area of several square meters with little or no direct articulation. Abbreviations: C, cervical vertebra; hum, humerus; L, left (unless followed by numeral); L (followed by numeral), lumbar vertebra; mand, mandible; max, maxilla; R, right; scap, scapula; T, thoracic vertebra.

key characters in this genus), the relative young ontogenetic ages of the two specimens (which therefore might not display fully adult character states for some features), and the low sample size which greatly limited quantitative comparisons with other species.

S. D. Emslie led a second excavation at Haile 7C in December 1994–January 1995, with the primary purpose of finding additional specimens of fossil birds (see Emslie 1998). The third Haile 7C tapir skeleton (UF 160715), and first adult, was found by volunteer Reed Toomey early in this dig. Although missing many of the bones of the manus and pes, UF 160715 is otherwise extremely complete and well preserved. Its skull preserved the nasal bones, unlike that of UF 121736. Several partial skeletons of tapirs consisting of only postcranial elements were also found during the 1994–1995 excavation. Morgan and Hulbert (1995) noted the presence of a new species of tapir from Haile 7C in a brief description of the site. Three additional tapir skeletons with skulls, two adults and a juvenile, were collected during the last major field season at Haile 7C, in the Fall of 2000.

The quantity of known Blancan tapir specimens in Florida changed dramatically with the discovery of the Haile 7G locality in the Spring of 2005. Located less than 100 m east of Haile 7C (Fig. 1), Haile 7G had very similar sediments (laminated blue-gray clays mixed with limestone boulders and interspersed with lenses and thin layers of sand-size fragments of limestone), also frequently produced associated to fully articulated skeletons (Fig. 3), and shared most of the fauna of its neighbor (Table 1). While proximity of vertebrate fossil localities in the Haile limestone mining region of Florida does not necessarily mean that the sites will be the same age, it is the case for Haile 7C and 7G. But the Haile 7G locality was of greater size and produced vastly more vertebrate skeletons. From May 2005 to April 2008 we collected over 500 tetrapod skeletons at Haile 7G, and *Tapirus* was the most common mammal at the site, represented by over 70 partial to nearly complete skeletons, all representing the same species found at Haile 7C. As of 2010, about half of the Haile 7G skulls and mandibles had been prepared and are available for study, and many of these are juveniles. But the combined sample from Haile 7C and 7G, augmented by those from Inglis 1A, Santa Fe 8, and elsewhere, is exceeded among fossil tapirs in terms of overall numbers of skeletons and large samples of all ontogenetic stages of skeletal and dental development only by that of *Tapirus polkensis* (Hulbert et al. 2009).

The purposes of this study are to formally name and describe this new species of *Tapirus*, concentrating on characters of the skull and dentition, and to place it in a phylogenetic context relative to *Tapirus veroensis*, *Tapirus haysii*, and other species in the genus. A comprehensive quantitative study of the Haile 7G sample (including postcranial skeletal elements) will be done upon its complete preparation and curation. Ecological analyses using stable oxygen and carbon isotopes of the Haile 7G sample of *Tapirus* are on-going (e.g., De Santis & MacFadden 2008). Other late Blancan species of *Tapirus* in Florida are also briefly reviewed.

MATERIALS AND METHODS

All measurements are reported in millimeters. Measurements and general methods are the same as described in Hulbert (2005) and Hulbert et al. (2009). To the comparative samples of *Tapirus veroensis* used in Hulbert (2005), I have added specimens accessioned into the UF collection since 2005, most notably a partial mandible (UF 225215) and isolated teeth (UF 225221–225276) from Steinhatchee River 2, and partial mandibles from Jacksonville Beach (UF 223228), Bedman Creek (UF 223709), Peace River (UF 227141), and Dickerson Coquina Pit (UF 244022). The Hulbert (2005) sample of *Tapirus haysii* has been augmented by recently donated specimens from Leisey Shell Pit 3 (UF 241860, 241870, 241874–241875, 241948–241949, 242001, 243500–243513). The opinion of Ray and Sanders (1984) that *T. haysii* is a valid name and the senior synonym of *Tapirus copei* Simpson is followed here (see also Hulbert 1995, 2005; Sanders 2002; Graham 2003). Dalquest and Schultz (1992) and Smith and Cifelli (2000) promoted the continued

use of *T. copei* instead of *T. haysii*, but without citing any evidence, morphologic or otherwise, to disprove the convincing argument made by Ray and Sanders (1984).

The recent decision by the International Commission on Stratigraphy to move the Gelasian Age to the Pleistocene Epoch (Gibbard et al. 2010), and thus changing the beginning of the Quaternary (and Pleistocene) from about 1.81 to 2.58 Ma, is followed here. Boundaries and subdivisions of North American land mammal ages generally follow Bell et al. (2004), with the Blancan/Irvingtonian boundary at about 1.6 Ma and the Irvingtonian/Rancholabrean boundary at about 0.3 Ma. Thus the later portion of the Blancan land mammal age now falls within the early Pleistocene, not the late Pliocene. All of the Florida fossil localities under study here fall in the later portion of the Blancan, within the interval of about 2.6 to 1.6 Ma. As in Hulbert (2005) and Hulbert et al. (2009), the genus *Tapirus* is defined as all species of Tapiridae sharing a closer common ancestry with the type species of the genus, *Tapirus terrestris* (Linnaeus), than with the type species of all other valid genera in the Tapiridae as defined and used by Colbert (2005).

Phylogenetic analyses were done using a set of 22 cranial, four mandibular, and 13 dental characters (Appendix 2) for nine species of New World *Tapirus* (Appendix 3). The late Miocene Chinese species *Tapirus hezhengensis* was included in one analysis to determine its effect on the relationships between New World *Tapirus*. Character states for *T. hezhengensis* were taken from Deng et al. (2008). To overcome problems with incompleteness, a composite outgroup was made using states from the four best known early Miocene tapirids, *Miotapirus harrisonensis* Schlaikjer, *Nexuotapirus marslandensis* (Schoch & Prins), *Plesiotapirus yagii* (Matsumoto), and *Paratapirus helveticus* (von Meyer). The character state matrix is shown in Appendix 3. Most parsimonious trees were computed by PAST, version 1.91, using the branch-and-bound algorithm and separate analyses with ordered and unordered multi-state characters.

INSTITUTIONAL ABBREVIATIONS

UF, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; **UF/TRO**, Timberlane Research Organization collection, now housed at the Florida Museum of Natural History; **USNM**, U.S. National Museum, Smithsonian Institution, Washington, D.C., USA.

MORPHOLOGICAL ABBREVIATIONS

L, greatest length; **DL**, postcanine diastema length; **HT**, height; **AW**, greatest anterior width measured across the protoloph or protolophid near the base of the crown; **PW**, greatest posterior width measured across the metaloph or hypolophid; **W**, width; **i**, lower incisor; **I**, upper incisor; **c**, lower canine; **C**, upper canine; **m**, lower molar; **M**, upper molar; **p**, lower premolar; **P**, upper premolar (a numeral following a tooth abbreviation indicates a specific tooth locus; e.g., m2 is a second lower molar). A **d** or **D** in front of a tooth abbreviation indicates a deciduous tooth (e.g., DP1).

STATISTICAL ABBREVIATIONS

x, sample mean; s, sample standard deviation; **MIN**, minimum value observed in a sample; **MAX**, maximum value observed in a sample; **OR**, observed range of a sample; **N**, sample size; *CV*, sample coefficient of variation; **p**, probability.

ONTOGENETIC DESCRIPTORS

Hulbert et al. (2009) designated seven general ontogenetic life history stages in *Tapirus* based on tooth eruption and wear. Their temporal durations are not equal, but their use allows comparisons between ontogenetically equivalent individuals.

- **Very young juvenile**: DP1–DP3 and dp2–dp3 with little or no wear are the only fully erupted cheekteeth; DP4 and dp4 may be erupting.
- **Young juvenile**: DP1–DP4 and dp2–dp4 are all fully erupted; M1 and m1 may be erupting; teeth slightly worn.
- **Juvenile**: DP1–M1 and dp2–m1 are all fully erupted and in wear. Crowns of adult premolars and second molars fully formed in crypts.
- **Subadult**: P1–P3, DP4, M1 and p2–p3, dp4, m1 are fully erupted and in wear; M2 and m2 may be erupting; little or no wear on P1–P3 and p2–p3, heavy wear on DP4 and dp4.
- **Young Adult**: P4, M2, p4 and m2 have erupted and are in wear; M3 and m3 either erupting or

Table 1. Mammals present at Florida late Blancan (early Pleistocene) vertebrate fossil localities with *Tapirus lundeliusi* sp. nov. (excluding Chiroptera and Cetacea). With = Withlacoochee River; Wacc = Waccasassa River; SFR = Santa Fe River. An 'X' indicates a well confirmed occurrence at a site while a '?' indicates a possibly occurrence but one whose species-level identification is uncertain either due to incompleteness of available specimens or absence of needed comparisons with related species. After Morgan and Hulbert (1995), Morgan and White (1995), Ruez (2001), Hulbert et al. (2006), Hulbert and Morgan (2009), and Tedford et al. (2009).

	Walden Pit 2	Haile 7C	Haile 7G	With 1A	Wacc 9A	SFR 8	SFR 8A	SFR 8C	Inglis 1A	Inglis 1B	Inglis 1D
Dasypus bellus		X	X	X	X				X		X
Pachyarmatherium leiseyi											X
Holmesina floridanus	X	X	X	X					X		X
Glyptotherium arizonae		X	X		X	X	X	X	X		
Megalonyx leptostomus		X	X	X	X				X		
Paramylodon harlani			X	X	X	X	X	X	X	?	
Eremotherium eomigrans			X						X		
Canis edwardii		X	X	X					X		
Canis lepophagus				?	?						
Urocyon citrinus									X		
Procyon rexroadensis			X	X	X					?	
Procyon lotor	X			?	?				?		
Arctodus pristinus						X	X	X	X	X	
Trigonictis macrodon			X		X	X	X	X	X		
Satherium piscinarium			?		X						
Lontra canadensis			X								
Mustela frenata				?							
Spilogale putorius									X		X
Lynx rufus				X					X		
Lynx rexroadensis				X	?		X		X		
Miracinonyx inexpectata				X					X		X
Smilodon gracilis			X	X					X		
Xenosmilus hodsonae			X	X	?				X		
Chasmaporthetes ossifragus									X		
Scalopus aquaticus		?	X	X					X		X
Blarina carolinensis									X		
Cryptotis parva			?	?					X		
Sylvilagus webbi		?	X	X	X				X		?
Sylvilagus floridanus			X		?				X		
Lepus sp.									X		

Table 1. Continued.

	Walden Pit 2	Haile 7C	Haile 7G	With 1A	Wacc 9A	SFR 8	SFR 8A	SFR 8C	Inglis 1A	Inglis 1B	Inglis 1D
Atzlanolagus n. sp.			X	X							
Sciurus carolinensis				?					X		?
Glaucomys n. sp.									X		
Castor californicus			X		X						
Orthogeomys propinetis			X	X	X				X		X
Unidentified Peromyscini				X					X		
Baiomys sp.			X								
Peromyscus hagermanensis			?								
Peromyscus sarmocophinus									X		X
Reithrodontomys wetmorei			?						X		X
Neotoma sp.		X		X					X		
Sigmodon medius		X	X	X					X		
Sigmodon curtisi									X		X
Ondatra idahoensis		X	X	X					X		
Erethizon poyeri		X	X		X				X		
Erethizon kleini			X	X					X		
Neochoerus dichroplax	X	X	X	X	X				X		
Tapirus lundeliusi	X	X	X	X	X	X	X	X	X	X	X
Nannippus peninsulatus	X			X							
Cormohipparion emsliei	X										
Equus sp.	X	X	X	X	X		X		X	X	
Platygonus bicalcaratus				X	X				X		
Mylohyus floridanus		?								?	
Hemiauchenia macrocephala	?			X	X	X	X	X	X	X	X
Hemiauchenia gracilis				X	X			X	X	X	
Palaeolama mirifica											X
Odocoileus virginianus		X	X	X	X	X	X		X		
Capromeryx arizonensis				X	X			X	X	X	
Mammut americanum									X		
Cuvieronius tropicus	?	X									

fully erupted, but with little or no wear.

- **Full Adult**: Lophs of M3 and m3 moderately worn, but no exposed dentine.
- **Old Adult**: Lophs of M3 and m3 have exposed dentine because of heavy wear.

FOSSIL LOCALITIES AND FLORIDA BLANCAN BIOCHRONOLOGY

The specimens of the new tapir species were collected from ten different localities in central Florida and one in southwestern Florida (Fig. 1; Table 1; Appendix 1). Haile 7C and Haile 7G produced the majority of specimens. Both are relatively large (> 25 m width; > 5 m depth) karst solution features filled with layers of clay, carbonate sand, and boulders that are interpreted to be remnants of a once much larger and deeper sinkhole lake (Morgan & Hulbert 1995; Emslie 1998; Hulbert et al. 2006; Morgan & Emslie 2010). In addition to sedimentology (Shunk et al. 2006), this hypothesized depositional environment is supported by the frequent preservation of complete or nearly complete vertebrate skeletons (a very rare occurrence for Florida karst fossil sites; Fig. 3) and very abundant freshwater taxa including fish, frogs, turtles, alligator, and waterfowl. Tapirs were the most common large mammal at both Haile 7C and 7G. Even though Pleistocene sites in Florida are renown for their relative abundance of tapirs (e.g., Ray & Sanders 1984), they are typically far outnumbered by other medium-sized ungulates such as *Equus*, *Palaeolama*, *Hemiauchenia*, *Odocoileus*, and/or *Platygonus*. The extraordinary abundance of tapirs at Haile 7C and 7G is likely a combination of a vast area of their preferred forested habitat (DeSantis & MacFadden 2007) to generate a large standing population plus an as yet undetermined taphonomic condition to produce the concentrations of skeletons (Hulbert et al. 2006).

The fossils of the new species of *Tapirus* from the remaining nine localities (Appendix 1) are less complete and numerous than at Haile 7C and 7G, and thus serve primarily to supplement the Haile samples and provide information on the chronologic range of the new species. Withlacoochee River 1A is a previously unreported submerged locality (Fig.

1). Fossils were recovered over a 30 m stretch of the river channel, both lying loose on the surface and excavated directly from shallow pockets of gray sandy clay in the Eocene limestone bedrock. The mammalian fauna has a high diversity of xenarthrans, carnivorans, and ungulates (Table 1). The single tapir tooth recovered from this locality, a partial M3, is slightly larger than any found at Haile 7C or 7G. But it is much smaller than M3s of *T. haysii*, and within the size range of *T. veroensis*. Because the latter contains a much larger sample size than currently known for the new Blancan species, this suggests that the potential size range of the new species should include specimens as large as the Withlacoochee River 1A tooth. Waccasassa River 9A (Fig. 1; Table 1) is another previously unpublished Blancan local fauna. Vertebrate fossils were collected from a river bank in association with a molluscan fauna equivalent to that of the Caloosahatchee Formation in southwest Florida.

Fossils of tapirs were collected both from the riverbed in the general Santa Fe River 8 area and from two of the five known in situ deposits in the area, the ones designated Santa Fe River 8A and 8C (Fig. 1; Table 1). In contrast with the fossiliferous deposits from the much more widely studied Santa Fe River 1 region (Morgan & Hulbert 1995; MacFadden & Hulbert 2009), those from Santa Fe River 8 are apparently in situ early Pleistocene sites, and not late Pleistocene or Holocene sites containing reworked Blancan fossils. The only prior published description of a Santa Fe 8 specimen was in Ray et al. (1981).

Fifteen separate fossiliferous karst deposits about 2 km southwest of the town of Inglis (Fig. 1; Appendix 1) were exposed during excavations for the Cross Florida Barge Canal. Of these, only four produced fossils of *Tapirus*, *T. haysii* at Inglis 1C (Ruez 2001), and the new species at Inglis 1A, 1B, and 1D. Inglis 1A has the largest and most diverse fauna of the Inglis sites (Table 1), and has the best sample of the new tapir excluding the two Haile sites. Members of its fauna have been the subjects of numerous publications (e.g., Meylan 1982; Morgan & Hulbert 1995; Emslie 1998; Tedford et al. 2009; Morgan & Emslie 2010). Inglis 1B and 1D

are two of the lesser know Inglis sites. Their faunas are generally a subset to that of Inglis 1A, with a few exceptions, such as the presence of *Mylohyus* at Inglis 1B and *Palaeolama* at Inglis 1D.

Macasphalt Shell Pit was an extensive commercial sand and shell quarry in Sarasota County that produced well studied invertebrate and vertebrate fossil faunas (e.g., Petuch 1982; Hulbert 1988; Jones et al. 1991; Emslie 1992). The late Blancan land vertebrate assemblage associated with the Pinecrest mollusks from this mine is most similar to the Haile 15A and Santa Fe River 1 local faunas from northern Florida (Morgan & Hulbert 1995). No fossils of tapirs were recovered at Macasphalt Shell Pit. However, Pinecrest mollusks were also mined during the 1970s from two nearby, much smaller quarries, Sommers Pit and Walden Pit (Fig. 1; Appendix 1). Vertebrate taxa from Sommers Pit diagnostic of the late Blancan include *Trachemys platymarginata* (Weaver & Robertson), the very small morph of *Holmesina floridanus* (Robertson), *Neochoerus dichroplax* Ahearn and Lance, *Nannippus peninsulatus* (Cope), and *Cormohipparion emsliei* Hulbert. Two separate quarries were mined at Walden Pit, here designated as the more western Pit 1 and more eastern Pit 2, separated by less than 100 m. They are about 1 km north of Sommers Pit. Fossils of terrestrial mammals were uncommon at both quarries, but Walden Pit 1 produced specimens of *N. dichroplax* and *N. peninsulatus*, while the very small morph of *H. floridanus*, *C. emsliei*, and *N. peninsulatus* were recovered from Pit 2. Specimens of *T. platymarginata* were common at both pits. Walden Pits 1 and 2 and Sommers Pit each produced only a single specimen of *Tapirus*, comprising an isolated lower premolar and two mandibular fragments with one tooth each. Despite the very limited nature of these samples, they are important for two reasons. One of the jaw fragments is the only referred specimen of the new species from the southern half of Florida. The other two specimens are significantly smaller than most other known Blancan *Tapirus*, most likely a holdover of a Hemphillian species, and thus bring the total number of late Blancan species of *Tapirus* in Florida to three. This small

taxon is also present at Kissimmee River 6, where it co-occurs with *Tapirus haysii*, Hubbard Pit, and the US 19 Bridge Site (Appendix 1). The latter two are also previously unpublished late Blancan localities.

Morgan and Hulbert (1995) proposed that late Blancan, Irvingtonian, and Rancholabrean vertebrate faunas in Florida could be grouped into eight biochronologic assemblages. These are still valid, although new discoveries have changed the first or last occurrences of some species. Because of a revised definition for the base of the Irvingtonian by Bell et al. (2004), the "earliest Irvingtonian" assemblage of Morgan and Hulbert (1995:85) is now the latest interval of the Blancan. Morgan and Hulbert's (1995) second assemblage was based solely on the Haile 7C local fauna and was admittedly poor defined at that time. The subsequent recovery of the richer Haile 7G and Withlacoochee River 1A local faunas (Table 1) allows for a much better biochronologic separation of Florida late Blancan vertebrate faunas into three distinct assemblages, with approximate numeric ages of 2.2–2.6 Ma for the early late Blancan, 1.9–2.2 Ma for the middle late Blancan, and 1.6–1.9 Ma for the latest Blancan (Hulbert & Morgan 2009).

The early late Blancan interval is characterized by the presence of *Paramylodon garbanii* (Montellano & Carranza-Castañeda) (proper name for Florida specimens formerly referred to the South American species *Glossotherium chapadmalense* Kraglievich; see Morgan 2008 for taxonomy), frequent occurrence of the hipparionine equids *Nannippus* and *Cormohipparion*, and the very small form of *Holmesina floridanus* (as discussed by Hulbert & Morgan 1993). *Tapirus* is typically rare or absent at early late Blancan sites in Florida. Records of *Tapirus haysii* are limited to small samples of isolated teeth at Santa Fe River 1 sites, Kissimmee River 2, and Devil's Elbow, and a metacarpal 5 from Kissimmee River 6 (Fig. 2; Appendix 1). Fossils from Sommers Pit, Walden Pits 1 and 2, and the US 19 Bridge Site also fall within this time interval. All records of the small, unnamed species of *Tapirus* belong to this subinterval of the late Blancan; no younger records

are currently known. Haile 15A and Lehigh Acres Pit each produced a single partial tooth diagnostic only to the family level, but they presumably represent *Tapirus* as it is the only known genus in North America from the late Miocene to the Pleistocene.

The middle late Blancan interval in Florida is defined by the first appearance of *Paramylodon harlani* (Owen), which replaced the much smaller *P. garbanii* of the preceding interval. Other species that make their first appearances in Florida during the middle late Blancan are *Canis edwardii* Gazin, *Sciurus carolinensis* Gmelin, *Reithrodontomys wetmorei* Hibbard, *Ondatra idahoensis* Wilson, *Erethizon kleini* Frasier, and *Erethizon poyeri* Hulbert. The last occurrence of *Sigmodon medius* Gidley occurs during or at the end of this interval. Specimens of *Holmesina floridanus* are significantly larger than those of the preceding assemblage (Hulbert & Morgan 1993). Haile 7C, Haile 7G, and Withlacoochee River 1A are the primary examples of middle late Blancan faunas. The Waccasassa River 9A and Santa Fe River 8 localities also likely belong in this interval, but they lack the necessary taxa to differentiate between this and the succeeding latest Blancan assemblage. For tapirs, only *Tapirus lundeliusi* is known from the middle late Blancan. No records of *Tapirus haysii* are known from Florida during this interval, but geographic coverage of known faunas is limited, so it may have been living elsewhere in the state, or it could have been temporarily extirpated.

The latest Blancan Florida vertebrate interval is defined by the first appearance of *Sigmodon curtisi* Gidley and *Sigmodon minor* Gidley (replacing *S. medius* of the preceding interval). Other species that make their first appearances in Florida during the latest Blancan are *Equus leidyi* Hay, *Spilogale putorius* (Linnaeus), *Peromyscus sarmocophinus* Ruez, and *Atopomys texensis* Patton. Inglis 1A, Inglis 1C, and De Soto Shell Pit are the primary examples of latest Blancan faunas. Both *Tapirus lundeliusi* and *Tapirus haysii* are known from this interval. While *T. haysii* continued into the early Irvingtonian in Florida (Hulbert 1995), there are no younger records of *T. lundeliusi*.

SYSTEMATIC PALEONTOLOGY
Order PERISSODACTYLA Owen 1848
Family TAPIRIDAE Gray 1821
Genus *TAPIRUS* Brisson 1762
Subgenus *HELICOTAPIRUS* subgen. nov.

Type Species.—*Tapirus veroensis* Sellards 1918.

Included Species.—*Tapirus haysii* Leidy 1859; *Tapirus lundeliusi* sp. nov.

Etymology.—From the Greek *helix* (spiral, coil, or curl) plus *Tapirus*. In reference to the spiral shape of the prominent meatal fossa on the frontal and nasal bones of members of this subgenus.

Definition.—All species of *Tapirus* that share a closer common ancestor with *Tapirus veroensis* than they do with *Tapirus* (*Tapirus*) *terrestris* (Linnaeus 1758), *Tapirus* (*Pinchacus*) *pinchaque* (Roulin 1829), *Tapirus* (*Tapirella*) *bairdii* (Gill 1865), or *Tapirus* (*Acrocodia*) *indicus* Desmarest 1819.

Diagnosis.—Species of *Tapirus* that differ from *Tapirus* (*Tapirus*) and *Tapirus* (*Pinchacus*) by having anterior process of maxilla visible in lateral view dorsal to premaxilla; large, triangular interparietal; extensive meatal fossa on frontal and nasal whose medial margin lies very close to midline of skull; lacrimal with weak or absent anterior process and broad, flattened posterior process; relatively shorter postcanine diastema; relatively greater depth of mandibular ramus below molars; anterior margin of ascending ramus projects anteriorly in lateral view; and increased relative length of p2. Additionally they differ from *Tapirus* (*Tapirus*) by having a much shorter sagittal crest. Additionally they differ from *Tapirus* (*Pinchacus*) by having shorter nasal and broader P1, and by lacking posterolabial cingula on upper molars. Species of *Tapirus* that differ from *Tapirus* (*Tapirella*) by having longer posterior process of premaxilla; dorsal maxillary flange small or absent, not extensive to embrace ossified mesethmoid cartilage; dorsal surface of nasal and frontal on same plane; long descending nasal process; narrow sagittal crest in adults; posterodorsal process of maxilla widely exposed dorsal to orbit, forming base of trough for meatal diverticulum; relatively

shorter postcanine diastema; relatively greater depth of mandibular ramus below molars; anterior margin of ascending ramus projects anteriorly in lateral view; and increased relative length of p2. Species of *Tapirus* that differ from *Tapirus* (*Acrocodia*) and *Tapirus* (*Megatapirus*) by having narrow sagittal crest in adults; dorsal surface of nasal and frontal on same plane; greater exposure of lacrimal in lateral view with at most one visible, large foramen; and premaxillary-maxillary suture extends anterior to alveolar margin of C in lateral view; and by lacking posterolabial cingula on upper molars. Additionally they differ from *T.* (*Acrocodia*) by having shallower meatal fossa on frontal and nasal with lateral supraorbital wall; no diastemata between incisors; broader P1 with strong lingual cusp; stronger protoloph on P2; and no or only minimal contact between first and fourth metatarsals. Additionally they differ from *T.* (*Megatapirus*) by having well defined meatal fossa on frontal and nasal; relatively shorter braincase; and external auditory meatus not closed ventrally by converging postglenoid and paroccipital processes.

Occurrence.—Early to latest Pleistocene of the central and eastern United States.

Remarks.—Each of the four extant species of *Tapirus* is the type species of a named subgenus: *T.* (*Tapirus*) *terrestris*; *T.* (*Pinchacus*) *pinchaque*; *T.* (*Tapirella*) *bairdii*; and *T.* (*Acrocodia*) *indicus* (Hershkovitz 1954). Matthew and Granger (1923) named a new subgenus and species of *Tapirus*, *T.* (*Megatapirus*) *augustus*, based on late Pleistocene fossils from China. Starting with Colbert and Hooijer (1953), *Megatapirus* has generally been used at full generic rank, e.g., McKenna and Bell (1997); Tong et al. (2002), Wu et al. (2006), Louys et al (2007). However, Tong et al. (2002) and Tong (2005) hypothesized that "*Megatapirus augustus*" evolved in China from within *Tapirus* (Colbert & Hooijer 1953:90 also implied this is the case), such that its use at the generic level makes *Tapirus* paraphyletic. For that reason I treat it here at its original rank, a subgenus of *Tapirus*.

Simpson (1945) and Ray and Sanders (1984) admonished against formally naming subgenera for North American fossil species of *Tapirus*. But with the greatly increased number of known fossil species and a better understanding of their cranial morphology and phylogenetic relationships, the clade containing *Tapirus veroensis* and two other species is clearly distinct from those represented by the four modern subgenera (Hulbert & Wallace 2005; also see phylogeny section below) and deserving of a formal name. Other than those three species, *Tapirus polkensis* (Olsen) is the most likely to also be included in *T.* (*Helicotapirus*), but its phylogenetic relationships with *T.* (*Tapirella*) and *T.* (*Helicotapirus*) *veroensis* are equivocal at present (see below), so it is not assigned to the new subgenus. *Tapirus webbi* Hulbert and *Tapirus johnsoni* Schultz, Martin, and Corner are clearly not members of *T.* (*Helicotapirus*), and the same is likely also true of *Tapirus simpsoni* Schultz, Martin, and Corner, *Tapirus merriami* Frick, and *Tapirus californicus* Merriam, but they are currently too poorly known to resolve their relationships. All of the relatively well known fossil species of *Tapirus* from South America (e.g., *Tapirus mesopotamicus*), China (e.g., *Tapirus hezhengensis*, *Tapirus sanyuanensis*), and Europe (e.g., *Tapirus arvernensis*, *Tapirus jeanpiveteaui*) differ from *T.* (*Helicotapirus*) in various combinations of cranial and dental characters (based on descriptions in Boeuf 1991; Rustioni 1992; Tong et al. 2002; Tong 2005; Ferrero & Noriega 2007; Deng et al. 2008), and none appear to be referable to the new subgenus. However, an inclusive phylogenetic analysis will be needed to determine this more securely. Given that the southeastern U.S. was always the primary stronghold of *T.* (*Helicotapirus*), it is logical to look for its origins in Neogene tapirs from this region. In addition to the already mentioned *T. polkensis*, other possibilities are the specimens from the late Miocene Withlacoochee River 4A site in Florida described by Hulbert (2005) or the larger, unnamed species of tapir from the early Pliocene Palmetto Fauna (Webb et al. 2008:fig. 6B). Unfortunately neither is known from relatively complete skulls, such that their phylogenetic relationships can be determined for the most part only on the basis of small samples of teeth. For tapirids, that rarely produces satisfactory or conclusive results.

TAPIRUS (*HELICOTAPIRUS*) *LUNDELIUSI*
SP. NOV.
Figures 3–18

Tapirus sp. Webb 1974, table 2.1 (in part); Webb and Wilkins 1984, table 1.

Tapirus n. sp. Morgan and Hulbert 1995, p. 68 and table 2; Hulbert 1999, p. 53A.

"new late Blancan species" of *Tapirus*. Hulbert 2005, pp. 467, 474, 482 & 489, figs. 5D, 12B.

Holotype.—UF 160715, partial young adult skeleton that includes cranium, mandible, vertebrae, ribs, sternebrae, and fore- and hind limb elements. Collected 12–19 December 1994 by A. E. Pratt, R. Toomey, and R. C. Hulbert. Found in near full articulation.

Paratype.—UF 121736, partial subadult skeleton that includes cranium, mandible, vertebrae, ribs, and fore- and hind limb elements. Collected in 1989 and 1990 by R. C. Hulbert and G. S. Morgan.

Etymology.—The species name honors Ernest L. Lundelius of the University of Texas at Austin for his numerous contributions to the study of Pleistocene mammals, including *Tapirus* (Lundelius 1972; Lundelius & Slaughter 1976).

Type Locality.—Haile 7C (see Appendix 1).

Occurrence.—Very early Pleistocene (late Blancan, ca. 1.6–2.6 Ma) of peninsular Florida. Possibly also late Blancan of North Carolina.

Referred Specimens.—Haile 7C: in addition to the holotype and paratype, this locality produced four other skeletons with skulls and mandibles, two young juveniles (UF 162351 and 206877), and two young adults (UF 206876 and 206878), and portions of postcranial skeletons from four other individuals (UF 149299, 160713, 162352, and 177735). Also the following isolated elements: UF 212272, M1; 212273, P3; 212274, I1; 212275, i1; 177736, tibia; 177737, scapula; 177738, patella; 177739, metatarsal 2.

Haile 7G: Very young juveniles: UF 224663, 224664, 224668, 224676, 243306, 244089, 244513, 247104. Young juveniles: UF 224666, 224673, 224681, 242904, 244090, 244512, 244514, 244515, 244516, 247101, 247103. Juveniles: UF 223827, 224662, 224665, 244519, 247102. Subadults: UF 224671, 224682, 224684. Young adults: UF 221720, 224672, 224679, 224685, 224686, 244503, 244511. Full adults: UF 224670, 224674, 224680, 224683, 244502, 244504. Old adult: UF 244600.

Santa Fe River 8: UF 177509, squamosal; 15095, M2 and M3; 177512, I2; 177513, i3; 177510, axis; 177511, radius; 177514–177516, unciforms; 240325, trapezoid; 177520, scaphoid; 177521, pisiform; 177517–177519, magnums; 177522–177523, cuneiforms; 15096, 177524 metacarpal 3s; 177525, metacarpal 4; 17527–177528, metacarpal 5s; 15098, 177531–177532 tibiae; 177533, fibula; 177534–177535, cuboids; 240382, navicular; 177536–177538, ectocuneiforms; 177526, metatarsal 2; 177529, metatarsal 3; 177530, metatarsal 4; 15097, 18476, 177539–177544, phalanges.

Santa Fe River 8A: UF 177546, frontal; 177547, fused supraoccipital, interparietal, and parietal; 16763, associated(?) P1 and p2; 14261, M3; 177548–177550, thoracic vertebrae; 177717–177718, lunars; 45727, pisiform; 177716, unciform; 177719, metacarpal 2; 177720–177721, metacarpal 4s; 14259, 177715 astragali; 14524, calcaneum; 177712–177713, cuboids; 177714, ectocuneiform; 45728, navicular; 177724, 240225, metatarsal 2s; 14257, metatarsal 3; 177722–177723, metatarsal 4s; 14260, 177725–177731, phalanges.

Santa Fe River 8C: UF 177501, scapula; 177502, ulna; 177503, metacarpal 3; 177504, metacarpal 4; 177505, fibula; 177506, astragalus; 177507, calcaneum; 177508, metatarsal 4.

Withlacoochee River 1A: UF 242909, M3; 241366, metatarsal 4.

Waccasassa River 9A: UF 240682, lower molar.

Inglis 1A: UF/TRO 2625 maxilla with M1–M3; UF 66134, nasal; 66125, supraoccipital; 18175, maxilla with M1–M2; 115970, maxilla with P1–P4; 18176, I1; 18177, DP4; 115969, p3; 176712, dp3 or dp4; 176713–176714, two lower cheek tooth fragments; 45305, mandibular symphysis; 22689, 177701, axis vertebrae; 177702–177703, cervical vertebrae; 177704–177709, thoracic vertebrae; 18178, humerus; 45309–45310, 45447, 177835, distal humeri; 177710, lunar; 244473–244474, scaphoids; 244475–244477, magnums; 244478,

unciform; 244479, pisiform; 176715, metacarpal 3; 45549, metacarpal 4; 115971–115975, metacarpal 5s; 45278, distal femur; 45306–45308, tibiae; 45440, astragalus; 18179, 115978, calcanea; 177711, cuboid; 244480–244481, ectocuneiforms; 22690, fused mesocuneiform, ectocuneiform, and metatarsal 1; 45450, 115977, 176701, metatarsal 2s; 18180, 115976 metatarsal 3s; 45448, metatarsal 4; 18181–18183, 45441–45445, 176709–176711, phalanges.

Inglis 1B: UF 97116, P2; 97117, mandible fragment with m3; 97118, p3; 97119, i2; 97120, metacarpal 3; 97121, cuneiform.

Inglis 1D: UF 224247, humerus; 224248, metacarpal 2; 224249, femur; 224250, thoracic vertebra.

Walden Pit 2: UF/TRO 1476, mandible fragment with m3.

Diagnosis.—Species of *T.* (*Helicotapirus*) significantly smaller than *Tapirus haysii*; smaller on average than *Tapirus veroensis*, but with extensive overlap in most measured characters. Sagittal crest slightly more pronounced than in *T. veroensis* and *T. haysii*. Interparietal fused to occipital prior to eruption of M2 (fusion in *T. veroensis* and *T. haysii* occurs after eruption of M2, sometimes not until after eruption of M3). Only a single large lacrimal foramen present medial to the posterior process of lacrimal; not visible in lateral view (*T. veroensis* has two large lacrimal foramina and usually at least one is visible in lateral view). Posterolateral margin of nasal not sharply downturned (present in *T. haysii*). Dorsal table of frontal relatively smaller than in *T. veroensis* and *T. haysii*, with an irregular surface (not smoothly inflated as in *T. veroensis* and *T. haysii*). Small dorsal flange on maxilla medial to posterior process of premaxilla (absent in *T. veroensis* and *T. haysii*). P1 lacks a strong transverse loph, but its width is relatively large.

TAPIRUS (HELICOTAPIRUS) HAYSII LEIDY 1859
Figure 2

Referred Blancan Specimens.—Santa Fe River 1: UF 177841, partial M2 or M3; 177842, associated right and left p4s. Santa Fe River 1B:

UF 213920, 224631 M1s (?). Kissimmee River 2: UF 51250, P3. Kissimmee River 6: UF 52601, metacarpal 5. Inglis 1C: UF 177844, P1. De Soto Shell Pit 5: UF 223920, associated right maxilla with DP2-DP4 and left maxilla with DP1-DP4; 232075, cuboid. Devil's Elbow 2: UF 177843, M3. See Appendix 1 for locality information.

Identification.—These specimens (Fig. 2; Table 2) are much larger than any found in the Haile 7C and 7G samples of *Tapirus lundeliusi*, and instead fall within or near the OR of *Tapirus haysii* (= *Tapirus copei*) from the Irvingtonian of Florida (Ray 1964; Hulbert 1995) and Pennsylvania (Simpson 1945). They are also similar in size to the holotype and referred specimens of *Tapirus haysii* from North Carolina (Ray and Sanders 1984). The matching p4s (UF 177842) have the greatest known L and AW for that tooth among all specimens assigned to *T. haysii* (if western specimens of a large tapir represent a different species, *Tapirus merriami*, as proposed by Jefferson 1989, in contrast to Ray and Sanders 1984). The reference of the Florida Blancan sample to *T. haysii* is also supported by a transverse loph on the P1, UF 177844 (Fig. 2F), a characteristic feature of this species, and one rarely present in *T. lundeliusi* or *T. veroensis*. UF 213920 and 224631 are isolated upper molars that are either relatively large M1s or small M2s. As the other Santa Fe River specimens are of relatively large size, notably UF 188742, an assignment as M1s is considered more likely. The dimensions of the metacarpal 5 all fall within the OR of the early Irvingtonian sample of *T. haysii* from Florida provided by Hulbert (1995), and are significantly larger than those observed in *T. lundeliusi*.

Chronologic Distribution.—The range of *Tapirus haysii* in Florida is emended from that in Hulbert (1995) to be early late Blancan through early Irvingtonian. The lone middle Irvingtonian record of *T. haysii* in Florida listed by Hulbert (1995) was McLeod Rock Pit, based on two juvenile specimens. Increased numbers of juveniles of *Tapirus veroensis* no longer support placing the McLeod fossils in *T. haysii*; they are instead more likely to be early representatives of *T. veroensis*.
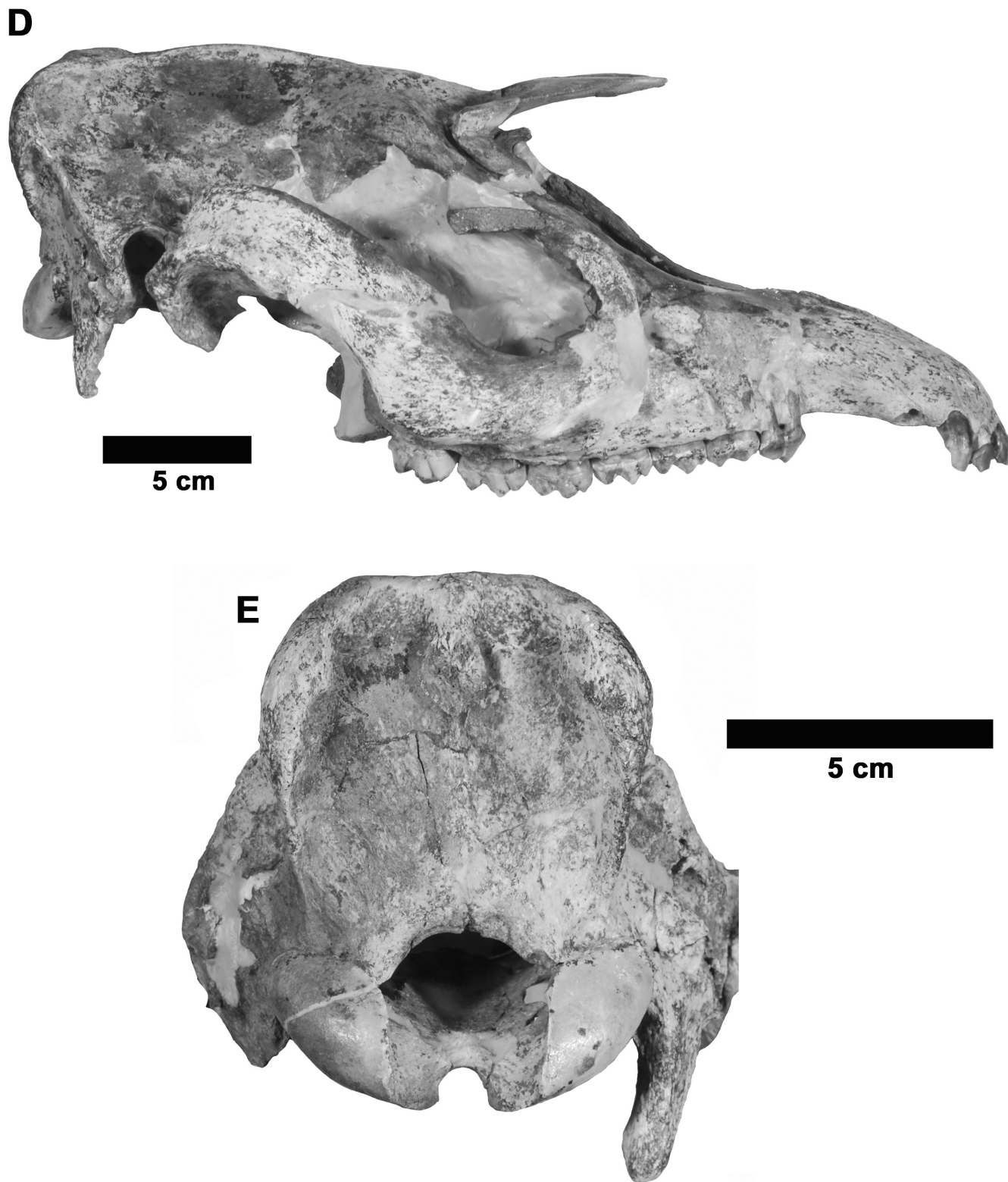
Figure 4. Skull of holotype of *Tapirus lundeliusi* sp. nov., UF 160715, from Haile 7C. **A**, dorsal view; **B**, ventral view; **C**, occlusal view of right P1–M3; **D**, right lateral view; and **E**, posterior view (zygomatic arches removed). This skull was restored so that a cast could be made for public display at the Florida Museum of Natural History.
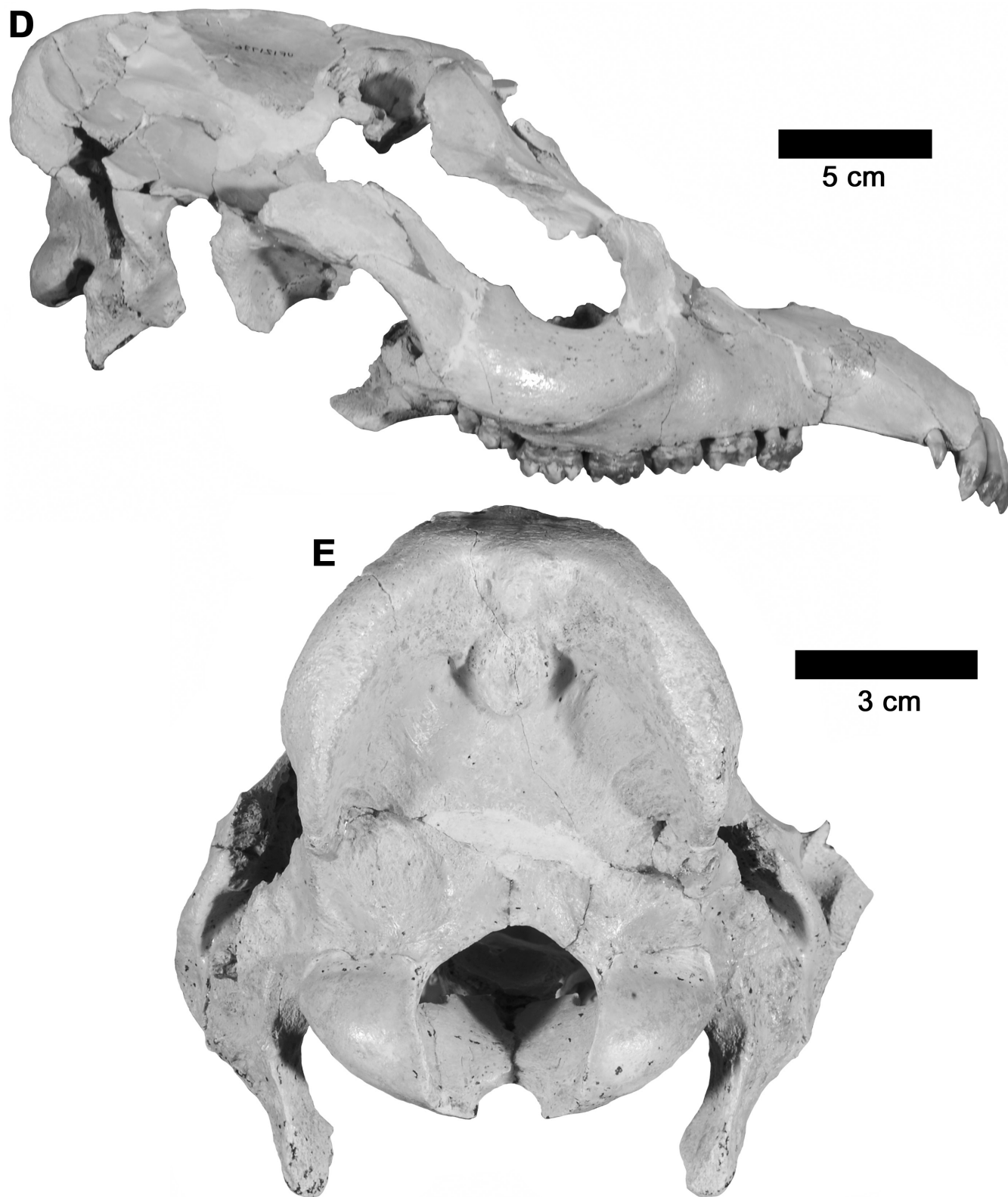
Figure 5. Skull of paratype of *Tapirus lundeliusi* sp. nov., UF 121736, from Haile 7C. **A**, dorsal view; **B**, ventral view; **C**, occlusal view of muzzle with right and left I1–I3, C. **D**, left lateral view (reversed); and **E**, posterior view (zygomatic arches removed). The M2 is not yet fully erupted in this individual.

TAPIRUS SUBGENUS AND SPECIES
INDETERMINATE
Figure 19

Referred Specimens.—US 19 Bridge Site: UF 255357, partial juvenile maxilla with DP3 (missing metacone); UF 255358, mandibular fragment with dp3 (missing most enamel on labial side of crown); UF 248788, talonid of p2; UF 247180, navicular; UF 248789, proximal phalanx of digit 2 or 4; Hubbard Pit: UF 249089, dp3; Kissimmee River 6: UF 51249, p2; Sommers Pit: UF/TRO 1469, unworn p4 (crown only, missing roots); Walden Pit 1: UF/TRO 1489, mandibular fragment with posterior root of p2 and moderately worn p3. See Appendix 1 for more information on localities.

Measurements.—UF 255357: AW, ca. 18.3 mm. UF 255358: L, 19.8 mm. UF 249089: L, 19.5 mm; AW, ca. 12.8 mm; PW, 13.0 mm. UF 51249: L, 20.0 mm; PW, 12.4 mm. UF 248788: PW, 12.4 mm. UF/TRO 1469: L, 20.2 mm; AW, 15.1 mm; PW, 16.7 mm. UF/TRO 1489: L, 17.9 mm; AW, 13.0 mm; PW, 14.2 mm. UF 247180: greatest W of astragalar facet, 29.8 mm; greatest depth of astragalar facet, approximately 21 mm. UF 248789: greatest L, 24.7 mm; proximal W, 16.4 mm; distal W, 13.5 mm.

Tooth Identification.—The sole tooth in UF 255387 is definitely deciduous, as the unerupted permanent premolar is visible in the crypt medial

Table 2. Comparison of dental measurements of late Blancan specimens of *Tapirus haysii* from Florida with samples from the early Irvingtonian of Florida and the middle Irvingtonian Port Kennedy Cave Site in Pennsylvania (MIN–MAX (N)). Values for the latter after Simpson (1945).

Catalogue Number	Tooth Locus	Measure-ment	Value (mm)	Irvingtonian of Florida	Port Kennedy Cave, PA
UF 223920	DP4	L	23.6	22.3–26.1 (5)	——
UF 223920	DP4	AW	26.7	24.9–30.3 (5)	——
UF 223920	DP4	PW	23.2	22.8–27.0 (5)	——
UF 177844	P1	L	20.7	19.7–23.3 (7)	22.4–24.9 (3)
UF 177844	P1	PW	19.6	17.3–22.0 (7)	19.6–21.5 (3)
UF 51250	P3	L	24.0	21.6–24.5 (10)	22.7–24.5 (5)
UF 51250	P3	AW	27.5	25.7–29.0 (10)	27.0–29.5 (4)
UF 51250	P3	PW	26.6	25.4–29.3 (11)	26.1–29.0 (4)
UF 213920	M1	L	25.5	23.9–25.9 (12)	25.8–26.4 (5)
UF 213920	M1	AW	31.7	26.9–30.7 (11)	28.9–31.1 (5)
UF 213920	M1	PW	28.2	24.5–28.5 (12)	25.8–27.9 (4)
UF 224631	M1	L	26.3	23.9–25.9 (12)	25.8–26.4 (5)
UF 224631	M1	AW	30.8	26.9–30.7 (11)	28.9–31.1 (5)
UF 224631	M1	PW	28.0	24.5–28.5 (12)	25.8–27.9 (4)
UF 177841	M2/M3	AW	32.4	30.8–34.5 (19)	31.0–34.9 (9)
UF 177843	M3	L	29.9	27.1–29.1 (6)	26.8–29.2 (5)
UF 177843	M3	AW	32.5	31.5–33.6 (6)	31.0–34.1 (5)
UF 177843	M3	PW	26.8	25.1–28.9 (6)	26.5–29.0 (5)
UF 177842	p4	L	28.8	22.5–25.7 (6)	24.1–24.9 (6)
UF 177842	p4	AW	22.8	19.9–22.0 (7)	18.3–21.7 (8)
UF 177842	p4	PW	22.7	20.2–24.0 (6)	19.5–22.8 (8)

to the labial root. An identification as a DP3 is based on its relative position to the IOF in similar age individuals, the orientation and height of the protoloph, and strength of the parastyle. UF/TRO 1469 is identified as a p4 on the basis of an AW/PW ratio of about 90 percent (which eliminates molars) and absence of a metalophid (which eliminates p2 and p3). In contrast, the complete tooth in UF/TRO 1489 has a metalophid and a small portion of the mental foramen is present ventral to the set of alveoli anterior to the tooth. This combination of features is only present in the p3 of *Tapirus*. UF 249089 and 255358 are identified as dp3s on the basis of the presence of metastylids (not found on permanent teeth), relatively narrower but otherwise molariform morphology, and low crown height. They compare very favorably to the dp3 of UF 223991. An identification of either as a dp4 is regarded as possible but less likely because of their relatively low hypsodonty.

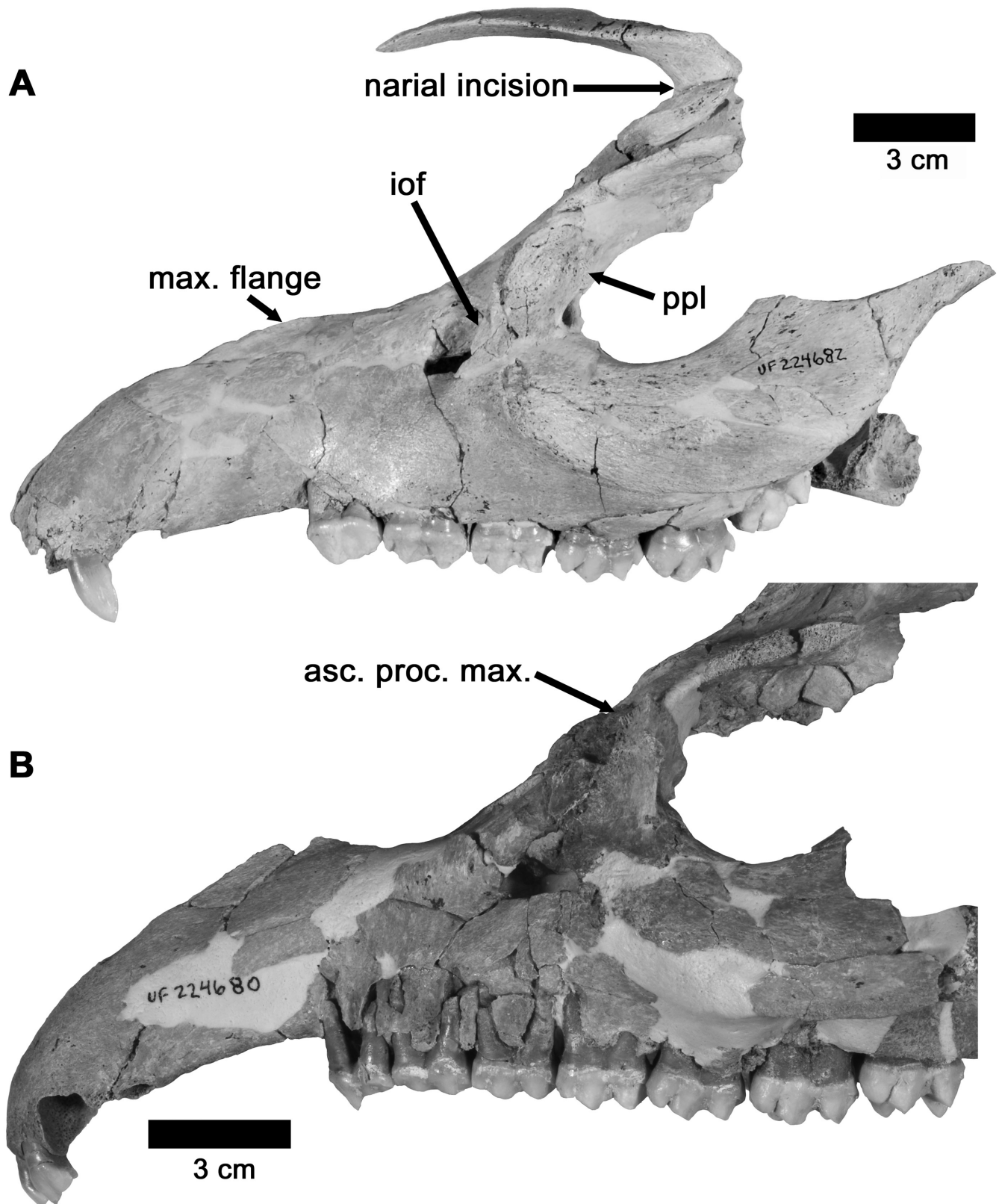## DESCRIPTION OF *TAPIRUS LUNDELIUSI*

CRANIUM

Cranial measurements are listed in Table 3. The rostrum is narrow with a relatively short postcanine diastema (Figs. 4-6). In lateral view, the posterior process of the premaxilla terminates in an acute point approximately dorsal to the anterior margin of the P1; the maxilla is exposed medial to the posterior process of the premaxilla and there forms a slight (UF 160715, 224680, 224682) to modest (UF 121736, 206878, 244502), ca. 30 mm long, vertical flange for embrasure of the nasal septum (Figs. 4D, 5D, 6-7); and the dorsomedial border of the maxilla thins posterior to the maxillary flange and projects medially (but is not rolled ventrally). The narial incision terminates dorsal to the middle or posterior half of the orbit (Figs. 4D, 6A). The posterodorsal ascending process of the maxilla forms the margin of the narial aperture back to the middle of the orbit where it articulates with the descending process of the nasal; this portion of the maxilla is widely exposed dorsally, not twisted laterally (Figs. 4A, 5A). The anterior supraorbital process of the frontal overlaps the lacrimal dorsally and articulates medially with

the maxilla and descending process of the nasal. Dorsal to the orbit, the frontal forms a broad, concave shelf that carried the meatal diverticulum; posterior to the orbit, this groove on the frontal narrows, curves dorsomedially, and becomes shallower, with a poorly demarcated posterior margin. As the groove approaches the midline of the skull it curves anterolaterally, and becomes deeper and broader as it reaches the nasal. The anterior border of the "spiral" groove on the nasal is well defined on all subadult and adult individuals (N = 9) and even on the juvenile UF 162351 (Figs. 8–9). The groove finally ends at the lateral side of the nasal near its widest point. The shape and size of the preserved nasals vary, but in all subadults and adults the lateral edge is posteriorly convex and anteriorly slightly concave (N = 8) or straight (N = 1), they are slightly arched anteroposteriorly, and thin dorsoventrally (Fig. 6A). Nasal length is equal to or greater than twice maximum nasal width in 8 of 9 subadult and adults. In the one very young juvenile with well preserved nasals (UF 247104, Fig. 9), the meatal fossa is faint and the anterior portions of the nasal are not ossified, such that there is no osteological contact along the midline of the right and left nasals (there may have been cartilaginous contact). A second very young juvenile, UF 224668, appears to have the same nasal morphology as UF 247104, although both nasals are incomplete such that their lack of contact can not be ascertained unambiguously. Slightly older juveniles, such as UF 162351, have nasals with an overall morphology resembling those of adults, including a long region of contact along the midline.

The dorsal table of the frontals (the region bounded anteriorly by the nasals and posterolaterally by the temporal crests) is relatively small because the parasagittal ridges are strongly concave and meet anterior to the frontoparietal suture (Fig. 8). The dorsal surface of the frontals is not flat; there is a pronounced medial ridge on the midline, and a smaller and slightly lower but notably raised region on the parasagittal ridge directly posterior to the descending process of the nasal. Internally, the frontals contain sinuses

Table 3. Measurements (in mm) on skulls of *Tapirus lundeliusi* n. sp. from the early Pleistocene of Florida. For comparison, values for other species of *Tapirus* are listed at base of table (when N>1, first line is $x\pm s$, second line is OR(N), and third line is percentage difference of x with mean value of *T. lundeliusi*). Occipital HT measured from ventral surface of basioccipital to dorsal surface of supraoccipital.

| Specimen Number	Basal L	P1-P4 L	M1-M3 L	P1-M3 L	C-P1 DL	Muzzle W	Occipital HT	Occipital Condyle W
UF 160715	330	75.5	69.9	144.3	32.3	43.3	94.5	74.1
UF 121736	334	78.4	—	—	43.6	43.4	93.3	71.3
UF 115970	—	75.45	—	—	—	—	—	—
UF 206876	325	75.2	67.7	142.5	30.0	—	101.6	78.0
UF 206878	—	77.6	71.3	147.8	35.2	—	—	—
UF 224672	—	—	—	—	42.2	—	—	—
UF 224674	—	78.4	70.3	147.65	36.2	—	107.5	81.5
UF 224679	—	—	—	—	40.3	—	—	79.6
UF 224680	—	73.1	66.05	138.6	39.9	45.2	—	—
UF 244502	—	—	73.6	—	—	—	—	—
UF 244503	—	80.1	72.2	152.3	—	—	98.0	86.8
mean ± s	329.7±4.51	76.7±2.27	70.2±2.59	145.5±4.79	37.5±4.82	44.0±1.07	99.0±5.76	78.5±5.49
CV	1.37	2.97	3.70	3.29	12.88	2.43	5.82	6.98
T. johnsoni	353(1)	72.7±4.22	66.2±2.28	137.2±9.44	44.4±4.34	43.2(1)	103.0(1)	77.6(1)
		67.2-77.1(4)	63.6-68.6(4)	130.5-143.9(2)	40.4-49.0(3)			
	108%	95%	94%	94%	118%	98%	104%	99%
T. simpsoni	—	84.9(1)	73.8(1)	159.5(1)	43.9(1)	—	—	—
		111%	105%	110%	117%			
T. polkensis	282.7±8.74	60.3±3.52	55.6±2.43	115.6±6.17	33.5±4.32	39.2±1.76	82.9±2.17	65.1±1.69
	273-290(3)	52.8-66.6(19)	52.8-62.4(15)	108.2-127.8(9)	26.6-41.9(18)	36.0-41.4(7)	80.6-86.1(6)	63.7-67.4(4)
	86%	79%	79%	79%	89%	89%	84%	83%
T. haysii	—	87.2±0.70	80.0±1.47	166.3±0.41	48.5±2.55	52.3±3.32	114.4±2.92	83.0±1.29
		86.7-87.7(2)	77.5-81.3(5)	166.0-166.6(2)	45.6-50.4(3)	48.7-55.9(4)	111.7-117.5(3)	81.5-84.5(4)
		114%	114%	114%	129%	119%	115%	106%
T. veroensis	353.5±12.02	77.9±3.92	70.0±4.33	143.7±8.92	40.7±6.52	48.0±3.42	108.3±3.43	81.7±6.69
	345-362(2)	71.8-84.2(12)	63.6-77.9(11)	133.4-159.0(6)	30.0-50.1(11)	45.2-52.5(6)	105.7-112.2(3)	76.1-89.1(3)
	107%	102%	100%	99%	108%	109%	109%	104%
T. terrestris	350.6±15.83	71.8±3.42	65.4±2.48	134.8±4.93	47.9±4.35	43.0±3.37	122.8±5.99	71.4±3.88
	328-384(16)	66.0-80.8(18)	61.0-71.4(18)	125.3-147.4(18)	40.7-57.4(17)	37.0-50.0(16)	115.5-132.2(16)	64.7-79.3(16)
	106%	94%	93%	93%	128%	98%	124%	91%
T. bairdii	379.5±11.15	74.9±3.23	65.5±2.53	138.1±5.14	54.0±4.41	50.6±2.94	120.3±5.12	83.4±4.10
	361-409(19)	67.2-80.9(21)	61.1-70.8(20)	126.0-148.4(19)	43.5-60.7(22)	44.6-55.1(22)	110.0-132.7(21)	77.1-91.9(19)
	115%	98%	93%	95%	144%	115%	122%	106%
T. indicus	403.3±4.37	89.0±4.22	78.1±6.52	164.0±11.06	53.0±9.31	50.8±1.14	115.7±6.59	88.7±3.47
	399-407(3)	84.5-94.7(4)	70.6-82.4(3)	151.8-173.3(3)	40.1-62.4(4)	49.5-52.3(4)	106.5-122.0(4)	86.9-93.9(4)
	122%	116%	111%	113%	141%	116%	117%	113%

Figure 6. Left lateral views of anterior portions of skulls of *Tapirus lundeliusi* sp. nov. from Haile 7G. **A**, UF 224682, subadult with C, P1–P3, DP4, M1, and erupting M2; **B**, UF 224680, full adult with I2, P1–M3. Abbreviations: asc. proc., ascending process; iof, infraorbital foramen; max., maxilla; ppl, posterior process of lacrimal.
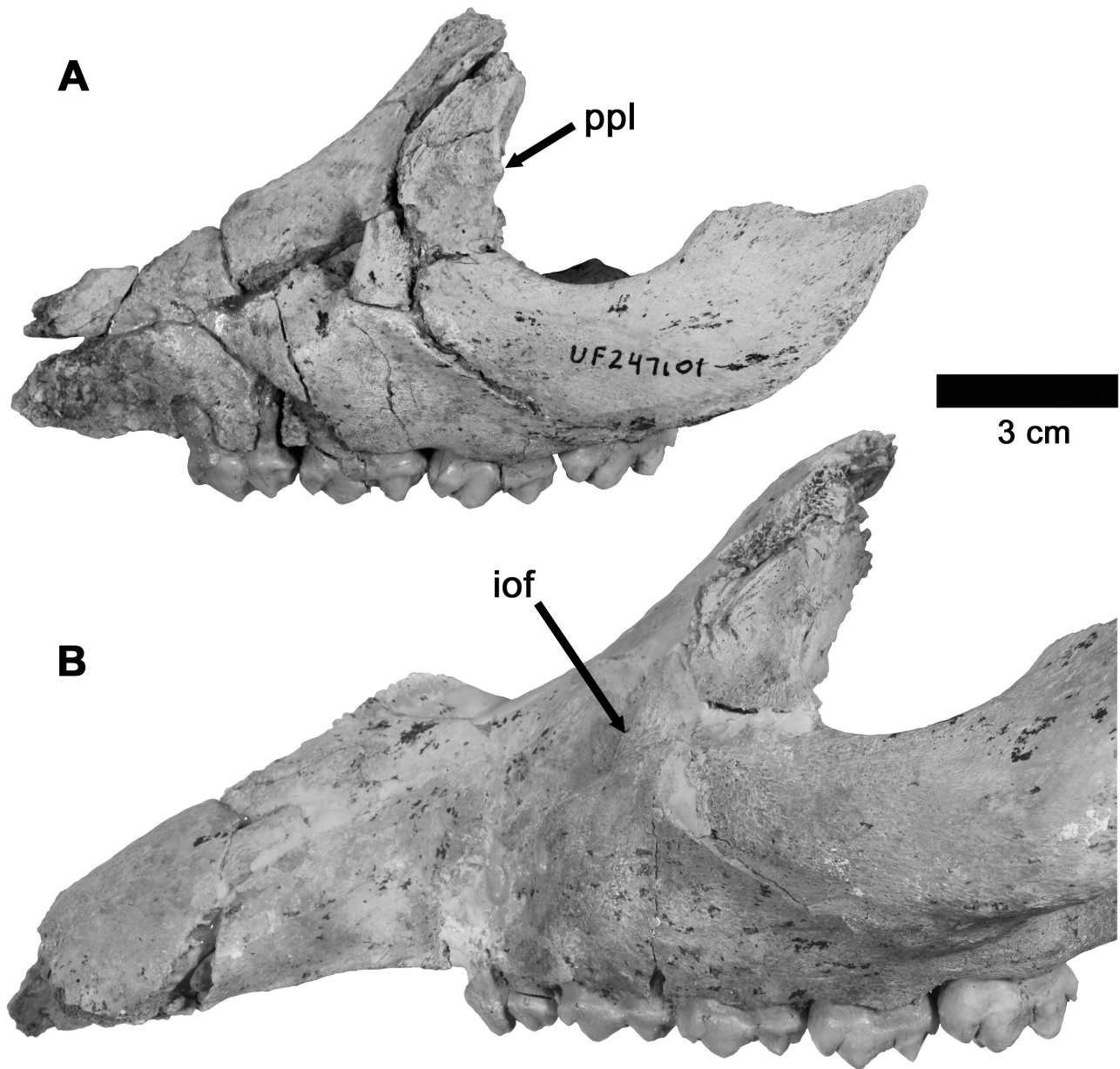
Figure 7. Left lateral views of anterior portions of skulls of *Tapirus lundeliusi* sp. nov. from Haile 7G. **A**, UF 247101, very young juvenile with DP1–DP4; **B**, UF 224662, juvenile with DP1–M1. Abbreviations as in Figure 6.
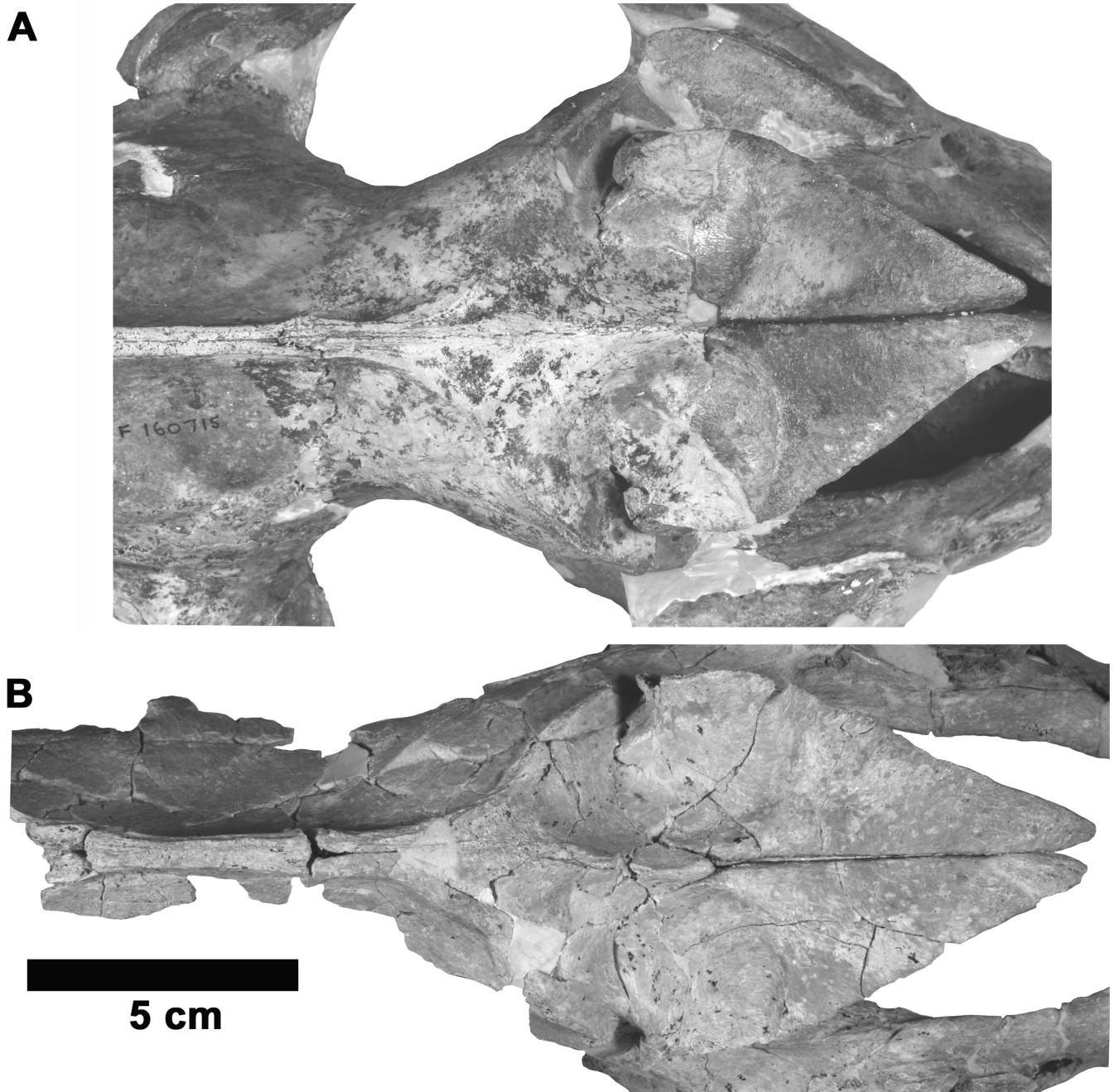
Figure 8. Dorsal views of nasals, frontals, and sagittal crests in adults of *Tapirus lundeliusi* sp. nov. **A**, UF 160715 from Haile 7C; **B**, UF 224680 from Haile 7G. Note variation in length of nasals.

which begin forming in young juveniles. The posteriorly converging parasagittal ridges meet to form the sagittal crest in the posterior portion of the frontal and it continues onto the parietals (Fig. 8). The ontogenetic sequence of skulls from Haile 7C and 7G reveals the developmental pattern of the sagittal crest (Figs. 8-10). Very young juveniles have smoothly rounded parietals without any indication of parasagittal ridges (UF 224664) or very weak ridges far from the midline (UF 224668, 247104). This condition persists into the first part of the young juvenile stage (UF 162351), but the ridges thicken and move towards the midline later in this stage, about the same time as the M1 begins to erupt (UF 206877, 244514, 247103). The parasagittal ridges become narrower and taller

to form a sagittal crest consisting of two distinct ridges separated by a narrow groove in juveniles and subadults (UF 121736, 224682). In young and full adults (UF 160715, 206876, 206878, 224680), this groove is filled to form a single sagittal crest, and the crest is slightly taller than in the subadults. In lateral view, the dorsal profile of the sagittal crest is slightly arched, reaching an acme only several millimeters higher than the dorsal tables of the frontals or occipital (Figs. 4D, 5D). The parasagittal ridges begin to diverge posterolaterally about 40 to 50 mm from the posterior edge of the skull, forming the anterolateral edges of a flat, triangular-shaped region that is continuous with the dorsal surface of the sagittal crest. Much of this flattened region originally ossified as a distinct,
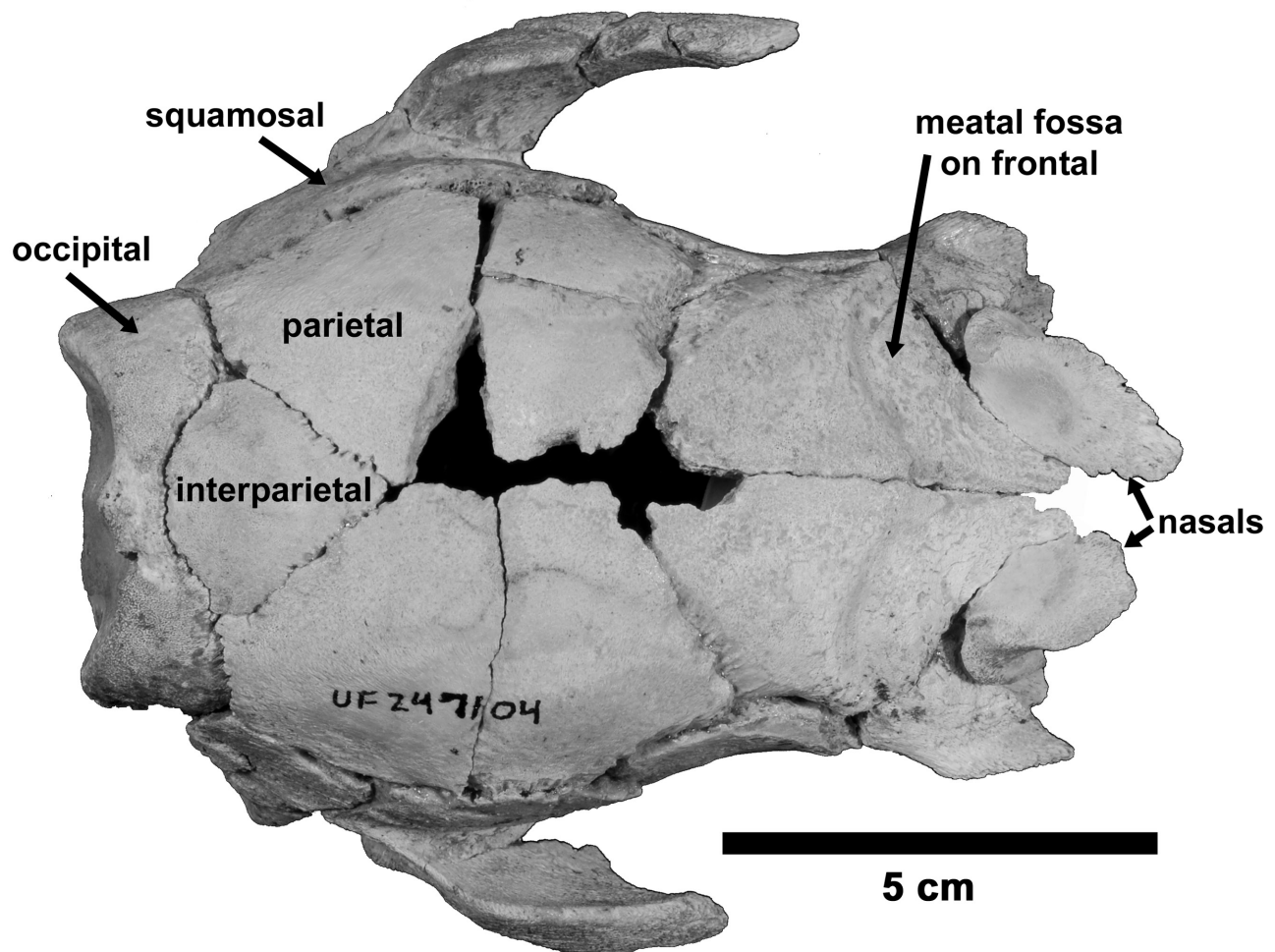
Figure 9. Dorsal view of the braincase in a very young juvenile of *Tapirus lundeliusi* sp. nov., UF 247104 from Haile 7G.
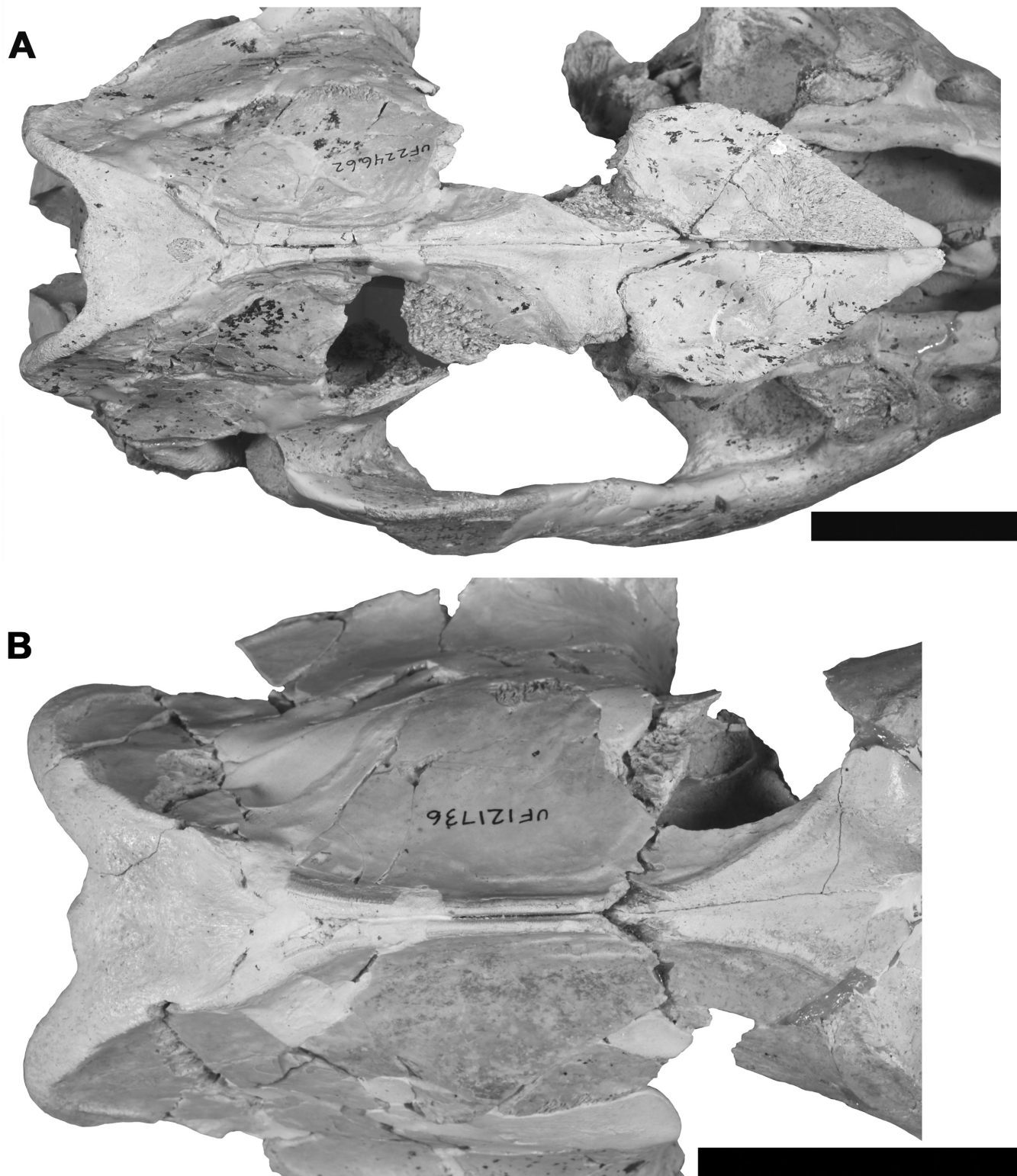
Figure 10. Dorsal views of the skulls of *Tapirus lundeliusi* sp. nov. **A**, juvenile UF 224662 from Haile 7G; **B**, subadult UF 121736 from Haile 7C. Contrast the development of the sagittal crest and the fusion of interparietal and occipital bones in these individuals to the conditions in the very young juvenile in Figure 9. Scale bars are 5 cm in length.

large, triangular interparietal bone (observable in UF 162351, 206877, 224664, 224668, 244514, and 247104). The interparietal fuses with the occipital as early as the young juvenile stage (UF 224666) but more often in the juvenile stage (UF 224662). Fusion of the interparietal with the parietals starts in the subadult stage (UF 224682) and is completed by the young adult stage (UF 160715, 206876). The lambdoidal crests are strongly developed and project primarily posteriorly in young juveniles (Fig. 9), but posterolaterally in subadults and adults (Figs 4A, 10B).

In lateral view, the infraorbital foramen is located dorsal to the DP2 in juveniles (Fig. 7; N = 8) and the P3 in subadults and adults (Fig. 6; N = 11); its posterior margin is formed by a very thin (ca. 5–mm–wide) strut of the maxilla. The lacrimal bone articulates anteriorly with this maxillary strut, dorsally with the ascending process of the maxilla, and ventrally with the jugal (Fig. 7A). Posteriorly, the lacrimal forms the anterior margin of the orbit. The dorsoventral height of the lacrimal greatly exceeds its anteroposterior length, and it has a generally smooth, moderately concave lateral surface (Figs. 5D, 6-7). A distinct anterior lacrimal process is usually absent (N = 8) or merely a small rugosity (N = 2). All specimens in which the bone is preserved have a short, broad, flat posterior lacrimal process. Directly medial to the posterior lacrimal process (and not visible in lateral view; Figs. 6, 11) is a single, large lacrimal foramen (N = 12). On UF 121736, it is 7.5 mm tall and 4 mm wide. There are no other large lacrimal foramina, but there are three to five much smaller ones located dorsal and lateral to the larger opening (Fig. 11A).
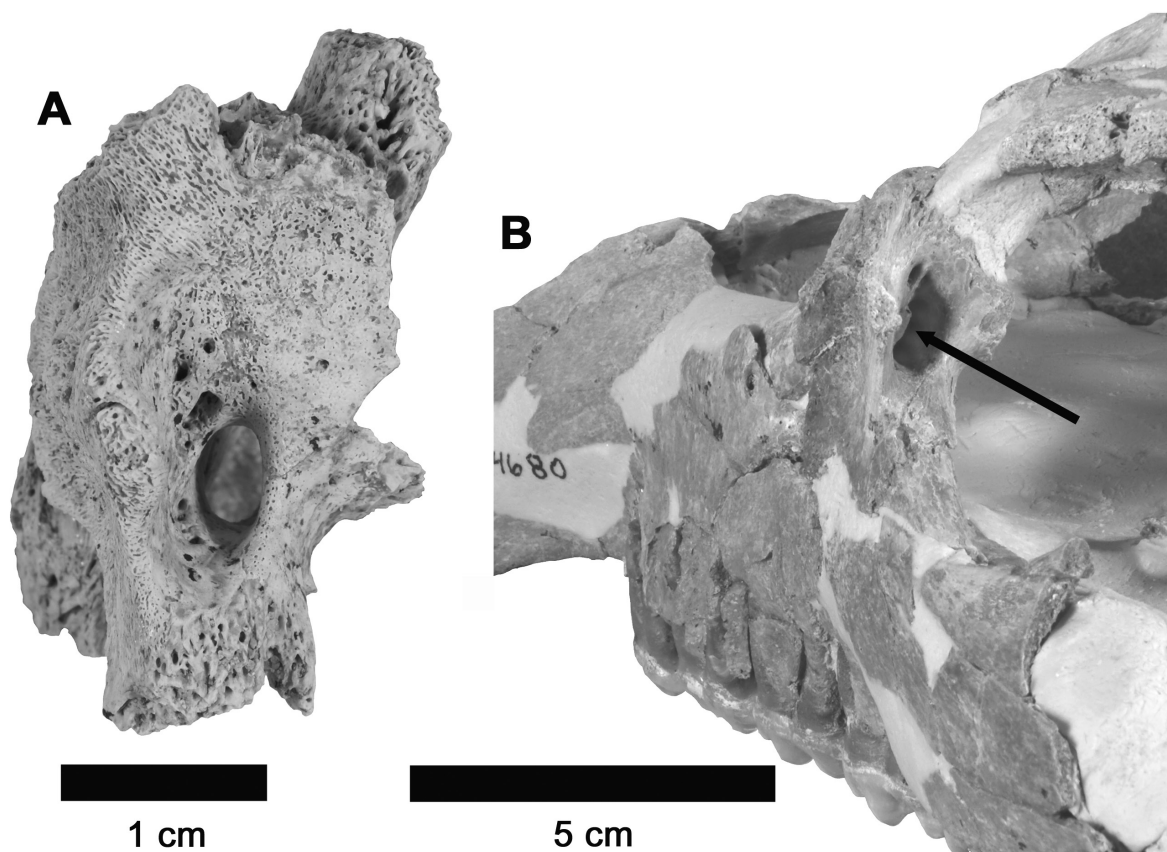
Figure 11. Condition of the lacrimal foramen in *Tapirus lundeliusi* sp. nov. **A**, UF 224673, isolated left lacrimal of young juvenile in posterior view; **B**, UF 224680, left rostrum of adult in posterolateral view, arrow points to lacrimal foramen. Every individual of this species in which the lacrimal is preserved, regardless of ontogenetic age, has a single large lacrimal foramen that is not visible in lateral view.

The lateral opening for the external auditory meatus is circular, ca. 15 to 17 mm in diameter; the meatus is partially closed ventrally by a posterior projection of the postglenoid process and an anterior projection of the mastoid process, but the two do not connect (Fig. 4D). An anteroventrally directed ridge branches off the descending lambdoidal crest about halfway through its length and continues down to the end of the mastoid process of the squamosal. This ridge is more pronounced in adults than subadults. The mastoid process of the petrosal is visible wedged between this ridge and the lambdoidal crest. On UF 160715, the mastoid process is oval, about 16 mm wide and 28 mm tall, and faces more posteriorly than it does laterally. On UF 121736, it is slightly narrower and faces posteriorly and laterally in about equal measure. The stylomastoid foramen opens at the ventral suture between the mastoid and squamosal into a shallow groove that runs ventrally down the squamosal just anterior to its suture with the paroccipital process. The long paroccipital process projects much more ventrally than either the postglenoid process or the occipital condyles (Figs. 4D-E, 5D-E). The back of the skull dorsal to the foramen magnum is oriented nearly perfectly vertically.

The incisive foramen is long, extending from just posterior to the I3 to the level of P1 (Fig. 4B). In most subadults and young adults the incisive foramen ends lateral to the anterior half of the P1, while in full adults it ends lateral to the posterior half of the P1 or even level with the P1/P2 contact. The hard palate formed by the maxillae and palatines is moderately arched transversely and bears several foramina, the largest of which opens anteriorly into a shallow sulcus at about the same level as the anterior border of the M1. The palate ends along the midline at a point on line with the middle of the M2 with a moderate rugosity in adults (UF 160715, 206876, 206878). The choane (internal nares) are relatively narrow. The medial wall of the orbit is not well preserved in any available specimen. The basicranial region is dominated by a very large lacerate foramen lateral to the basioccipital and posterior to the alisphenoid and postglenoid region of the squamosal (Figs. 4B, 5B). The smaller

hypoglossal foramen is located near the posterior margin of the lacerate foramen and is approximately circular with a diameter of 6–9 mm in adults. The width of the foramen magnum is slightly greater than its height. Minimum ventral width between the occipital condyles in adults is about 12 percent of occipital condyle width (N = 3).

Mandible

The ventral border of the ramus is gently curved posterior to the uplifted symphysis (Fig. 12). There are no diastemata between any of the incisors or canine, and the postcanine diastema is relatively short (Table 4). The symphysis has a deeply concave dorsal surface. Posteriorly, the angle is strongly inflected medially and its margin is thick and well developed (Fig. 13). The posteromedial region of the mandible is concave and in subadults and adults bears pronounced ridges that start at the thickened posterior margin. The large mandibular foramen opens posterodorsally and is located at the same height as the cheekteeth (Fig. 14). The mediolateral axis of the mandibular condyle is oblique, with the medial side lower than the lateral side. Dorsoventral height from the angle to the mandibular condyle is relatively greater than in other species of *Tapirus* (Table 4). The anterior margin of the ascending ramus projects anteriorly in lateral view (Figs. 12D, 14B) so that at the level of the condyle it partially overlies the m3. The coronoid process is tall, extending 40–50 mm beyond the height of the condyle. The masseteric fossa is large and deep, with its ventral border poorly defined but located at about the level of the crowns of the cheekteeth. The mental foramen is located ventral to the dp2 or p2 (N = 27). One rare variant is UF 244502 with two mental foramina, one ventral to the p2 and another ventral to the p3. This unusual feature is found on both the right and left dentaries of this individual.
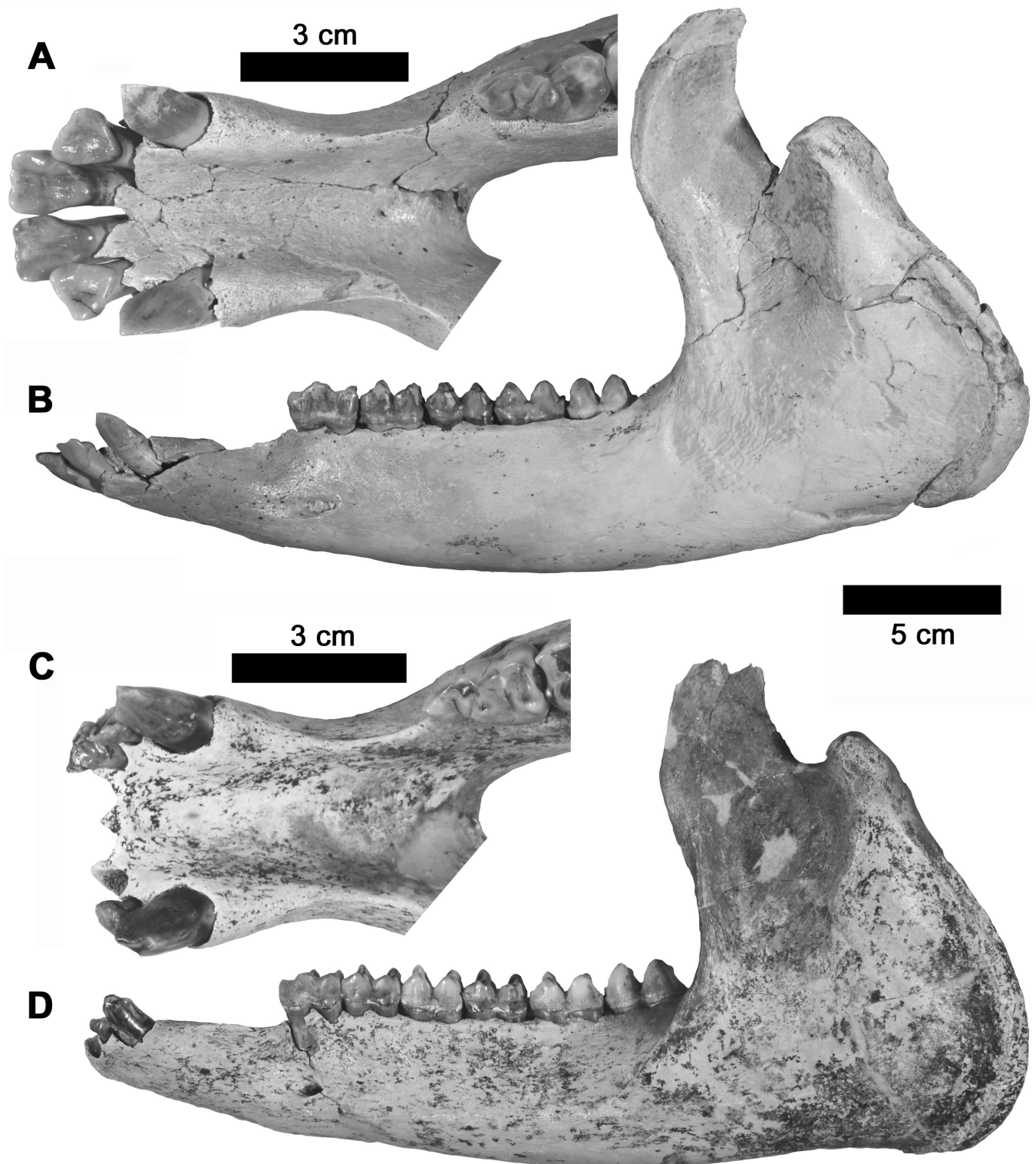
Dentition

The incisors and canines are morphologically like those of other New World *Tapirus*, in particular there is a reduced upper canine, a caniniform I3, an enlarged, spatulate i1, and a greatly reduced i3 (Figs. 5C, 12A, C, 14A). The P1 is slightly

Table 4. Statistics of measurements (in mm) on mandibles of *Tapirus lundeliusi* sp. nov. from the early Pleistocene of Florida and those of other species of *Tapirus*. When N>1, first line is *x±s*, second line is OR(N). For *T. lundeliusi*, third line is *CV*; for other species of *Tapirus*, third line is percentage difference of its mean value with that of *T. lundeliusi*.

	Condylar L	p2-p4 L	m1-m3 L	p2-m3 L	c-p2 DL	Muzzle W	H at p2	H at m3	condyle H
T. lundeliusi	283.9±8.70 278-290(2) 3.06	63.6±2.06 59.9-66.1(8) 3.24	72.6±2.98 69.1-77.6(8) 4.03	135.5±4.82 129.9-143.3(6) 3.56	45.5±3.53 38.5-49.1(11) 7.75	46.2±2.79 43.5-50.6(6) 6.03	42.0±2.18 39.2-44.6(9) 5.20	61.1±3.19 56.2-66.7(8) 5.22	151.3±10.34 139.7-162.9(5) 6.84
T. polkensis	243.2±7.76 237-255(5) 86%	50.0±2.33 46.8-53.8(16) 79%	57.5±23.83 52.4-61.6(16) 79%	107.2±4.14 101.2-114.4(11) 79%	39.2±4.37 32.5-47.0(18) 86%	36.9±2.24 32.5-39.2(10) 80%	33.1±2.63 27.4-37.7(13) 79%	44.8±3.10 38.3-49.8(14) 73%	112.4±3.08 109.0-116.5(6) 74%
T. johnsoni	298.0±9.54 288-307(3) 105%	59.7±2.44 55.8-63.0(13) 94%	69.4±2.48 66.0-73.6(12) 96%	128.6±4.41 122.0-136.0(11) 95%	58.1±5.20 52.5-564.2(4) 128%	42.7±2.14 40.4-44.6(3) 92%	46.1±3.00 42.4-49.7(4) 110%	56.8±1.98 53.9-60.8(9) 93%	136.9±2.34 134.7-140.0(4) 90%
T. webbi	329.3±3.89 326.5-332(2) 116%	65.6±1.87 62.1-68.3(8) 103%	76.6±2.42 72.2-79.4(6) 105%	143.1±4.14 137.5-147.5(4) 106%	58.1±1.96 55.2-61.2(6) 128%	50.0±4.21 46.6-55.7(4) 108%	44.8±1.92 41.1-46.6(6) 107%	56.3±3.52 50.0-61.7(11) 92%	128(1) 85%
T. haysii	343.6±13.54 326-359(4) 121%	72.9±3.50 67.7-78.5(6) 115%	82.8±4.83 76.7-89.6(6) 116%	158.1±6.13 153.4-166.1(5) 117%	59.4±6.11 52.4-68.4(5) 131%	52.9±1.60 51.1-54.2(3) 114%	52.6±5.15 45.5-58.2(7) 125%	71.6±4.15 67.3-78.2(5) 118%	173.0±2.65 171-176(3) 114%
T. veroensis	308(1) 109%	63.9±3.06 59.1-67.1(6) 100%	72.0±3.02 65.9-76.8(22) 99%	134.2±0.39 133.9-134.7(3) 99%	47.4±4.08 41.9-53.4(7) 104%	44.7±2.28 41.1-48.0(6) 97%	44.3±2.91 42.1-49.8(6) 105%	59.6±3.44 53.7-65.9(23) 97%	131.1±4.20 128.2-136.2(4) 87%
T. terrestris	286.7±15.31 267-315(16) 101%	60.4±3.16 55.9-67.1(16) 95%	67.6±2.78 63.0-74.8(16) 93%	127.2±5.76 118.5-141.1(15) 94%	55.5±5.35 48.2-67.6(17) 122%	44.2±4.04 36.6-53.8(15) 96%	45.5±5.29 37.6-55.2(17) 108%	51.9±3.64 46.9-57.4(16) 85%	123.3±6.76 111.2-133(12) 82%
T. bairdii	304.0±9.60 289-323(21) 107%	62.0±2.56 58.3-67.9(19) 97%	66.8±2.33 61.7-70.9(20) 92%	128.2±4.74 119.7-138.5(18) 95%	65.3±4.61 53.9-73.1(22) 144%	51.1±3.46 47.6-61.4(22) 111%	47.6±2.15 41.7-51.3(22) 113%	55.2±3.09 51.3-64.6(21) 90%	133.5±5.73 123.5-144(15) 88%
T. indicus	336.8±3.88 332.5-340(3) 119%	74.4±3.70 69.5-77.6(4) 117%	81.1±7.43 70.4-87.3(4) 112%	155.2±12.31 137.9-165.3(4) 115%	58.3±4.99 53.3-64.3(4) 128%	55.8±5.97 50.8-64.2(4) 121%	54.1±2.46 51.6-56.5(3) 129%	60.4±2.15 58.1-62.3(3) 99%	155.5(1) 103%

Figure 12. Mandibles of *Tapirus lundeliusi* sp. nov. from Haile 7C. **A & C**, occlusal views of symphysis; **B & D**, lateral views of left mandible. **A–B**, UF 121736, subadult paratype with i1–12, c, p2–p3, dp4, m1–m2; **C–D**, UF 160715, young adult holotype with i3, c, p2–m3. Scale bar of 5 cm on right applies to both B and D.

longer than wide (Figs. 4C, 15A-C, 16C; Table 5); its morphology is best shown on the slightly worn UF 16763, 121736, 224671, and 224682. The labial portion of the P1 crown is united in a sharp ectoloph; the paracone and metacone are situated close to each other; and the paracone is the tallest cusp on the P1 although neither it nor the metacone extend much beyond the level of the remainder of the ectoloph (Fig. 6A). A narrow, low, posterior cingulum wraps around the back of the P1, connecting the ectoloph with the bulbous, main lingual cusp. A slight crest extends labially from

the lingual cusp towards the metacone in four of seven unworn or slightly worn P1s, while the other three lack any trace of a transverse loph. About half of the P1s have a much smaller and lower cuspule located anterior to the main lingual cusp, while the other half lack such a structure. With wear, the P1 ectoloph remains a sharp ridge (UF 160715, 115920, 206876, 224686, 224674), while the lingual cusp wears flat and merges with the smaller cuspule (if present).

The AW of the P2 is on average 91 percent of PW (N = 18). The P2 metacone and paracone

5 cm

Figure 13. Posterior view of right and left mandibles of UF 160715, holotype of *Tapirus lundeliusi* sp. nov.
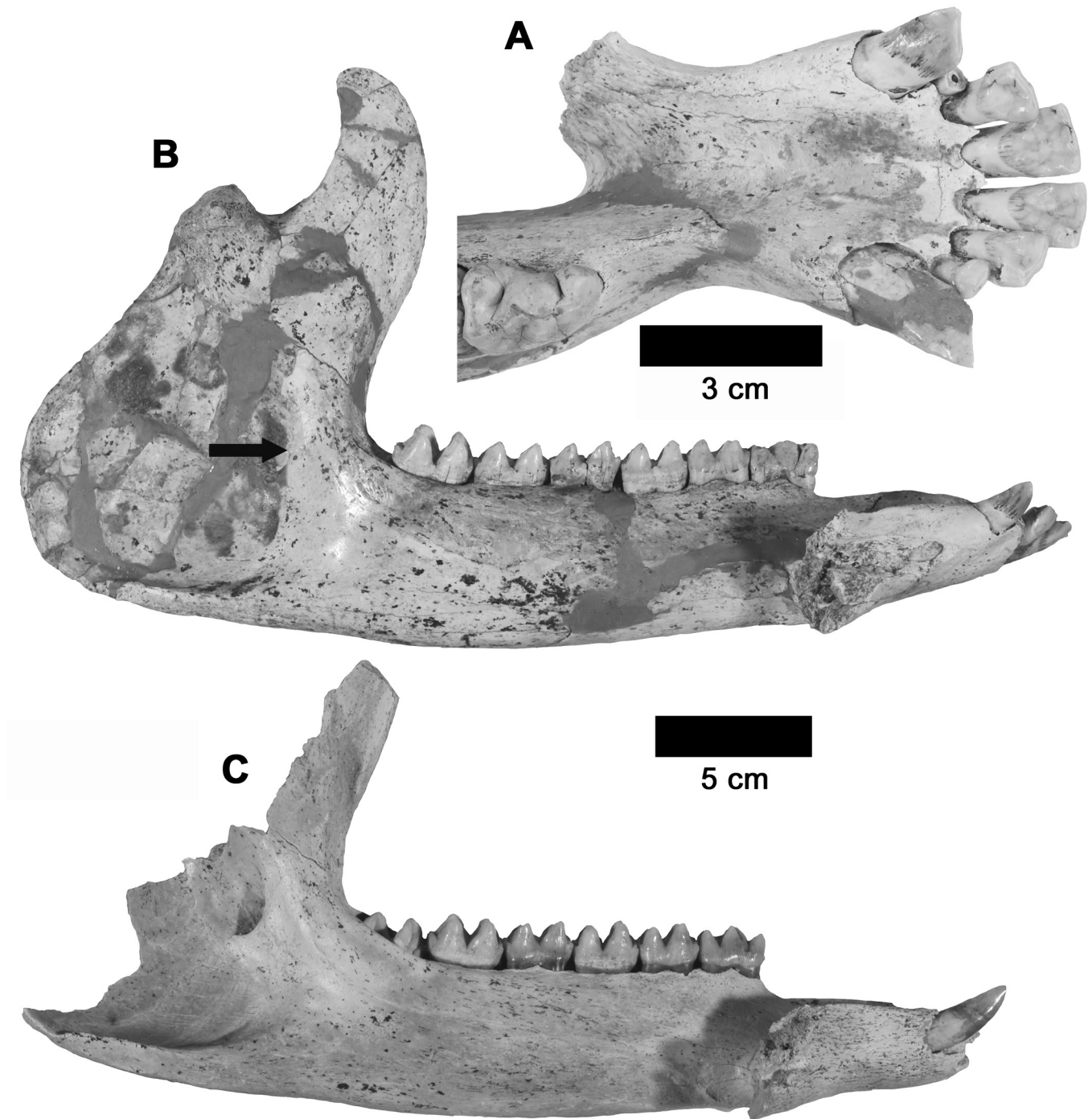
Figure 14. Mandibles of *Tapirus lundeliusi* sp. nov. **A**, occlusal view of symphysis, and **B**, medial view of right mandible (reversed) of UF 206878, adult mandible with i1–i3, c, p2–m3 from Haile 7C; **C**, medial view of UF 221720, young adult mandible with right c and left p2–m3 from Haile 7G. Arrow in B points to location of mandibular foramen. 5 cm scale bar applies to B and C.

are well separated, unlike those of the P1, but in the unworn state also barely project beyond the level of the rest of the ectoloph (Figs . 6A, 15E, 16C). The P2 has a small parastyle and anterior and posterior cingula. The transverse lophs are oriented obliquely, especially the weak protoloph that extends from the protocone towards the parastyle where it connects near the base of the ectoloph. The metaloph is oriented more transversely than the protoloph, and is taller, uniting about halfway along the height of the ectoloph. As in the succeeding teeth, the metaloph curves posteriorly just prior to uniting with the metaloph, so that it connects with the metacone.

The P3 (Figs. 4C, 15A-C, 16C; Table 5) is more molariform than the P2 in that AW exceeds PW in most individuals (14 of 16) and the transverse lophs are not as oblique. Compared to the P2, the protoloph is stronger and unites with the paracone instead of the parastyle, and the parastyle is larger. When unworn, the P3 ectoloph is sharply depressed between the paracone and metacone. The P4 continues these trends, basically being a larger version of the P3 with a stronger parastyle and taller cusps and lophs (Figs. 4C, 15A-C). The M1 through M3 also have large parastyles that are separated from the paracones by deep creases; AW greatly exceeds PW, especially on the M3. A small cusp is variably present on the anterior side of the protoloph close to the anterior cingulum. Small lingual and labial cuspules are also variably present between the protocone and hypocone, or paracone and metacone, respectively, of the P3–M3. None of the teeth have a cingulum around the labial base of the metacone.

The DP1 is approximately the same size as the P1 (Table 7), slightly lower crowned, and has a well formed but narrow transverse loph the extends from the lingual cusp to the ectoloph (Fig. 16A). The DP2 is about the same length as the P2, but much narrower, and has a stronger protoloph, a much lower crown, and an equally weak parastyle. The DP3 and especially the DP4 are morphologically more like lower crowned molars than their permanent successors, with strong styles and PW shorter than AW (Fig. 16). As in the

permanent premolars, no posterolabial cingula are present on the deciduous premolars.

Lower cheekteeth (Figs. 12B, D, 14C, 17; Table 6) have the classic bilophodont morphology of *Tapirus*. Hypolophids on premolars are complete and in unworn teeth are only slightly lower than the protolophids (Figs. 12B, 17A). Protolophids and hypolophids on unworn molars are of equal height. The p2 has a well developed metalophid (cristid obliqua) and paralophid; the former blocks the transverse valley between the protolophid and hypolophid. Average p2 L/p3 L is 112 percent (N = 12; OR = 104–119). The p3 also has a pronounced metalophid, but it is not as tall as that of the p2. L of the p3 is similar to that of the p4 (Table 6), but the p3 is on average narrower, such that mean PW/L is 80 percent in p3 and 87 percent in p4 (N = 14). AW is always less than PW in the p3, with a mean AW/PW of 91 percent. AW is slightly greater relative to PW in the p4, with a mean AW/PW of 94 percent, and AW slightly exceeds PW in 2 of 13 individuals (UF 244502 and 224672). The p4–m3 lack a metalophid. Prominent anterior and posterior cingulids are present on unworn and slightly worn p3–m3, but lateral and lingual cingulids are absent. The anterior and posterior cingulids are soon obliterated by interdental wear (Fig. 17). The posterior cingulid of the m3 lacks a prominent hypoconulid, and instead has only a slightly thickened central stylid. With rare exceptions (e.g., UF 206876, 206878), AW on m1 and m2 exceeds PW, with very similar mean AW/PW ratios, 104 percent in m1 (N = 16) and 103 percent in m2 (N = 12). The PW of the m3 is relatively narrower than that of the m1 and m2, with a mean AW/PW of 111 percent (N = 12).

The lower deciduous premolars are on average longer, narrower, and less high crowned than their permanent replacements (Fig. 18; Table 7). The dp2 has a strong metalophid like the p2, but the dp3 does not. The hypolophids are complete and as tall as the protolophids on the dp2–dp4. Small metastylids are present in unworn and slightly worn dp2–dp4 on the posterolingual side of the metaconids; these are rapidly lost to wear. The dp3 and dp4 are molariform in their overall
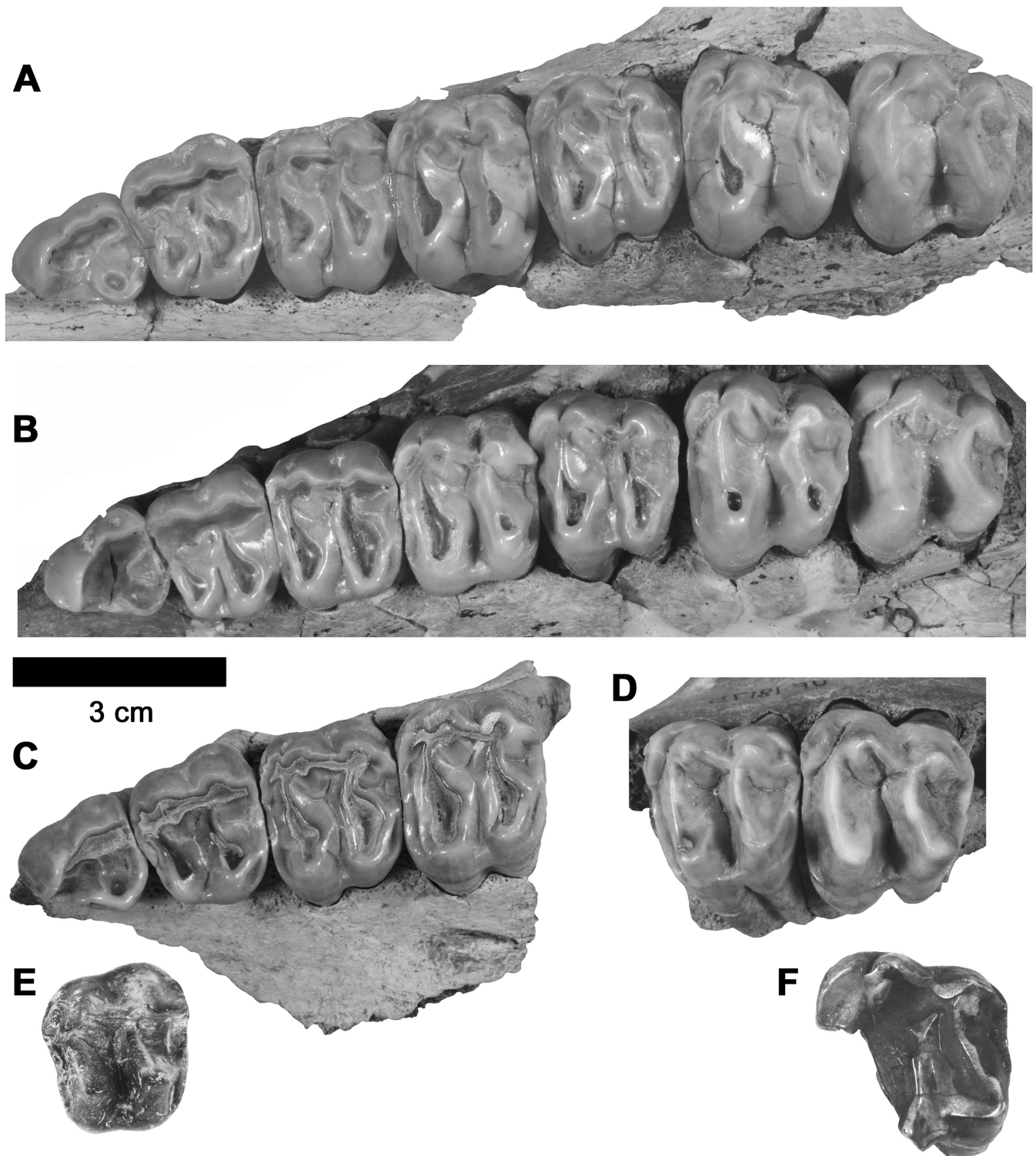
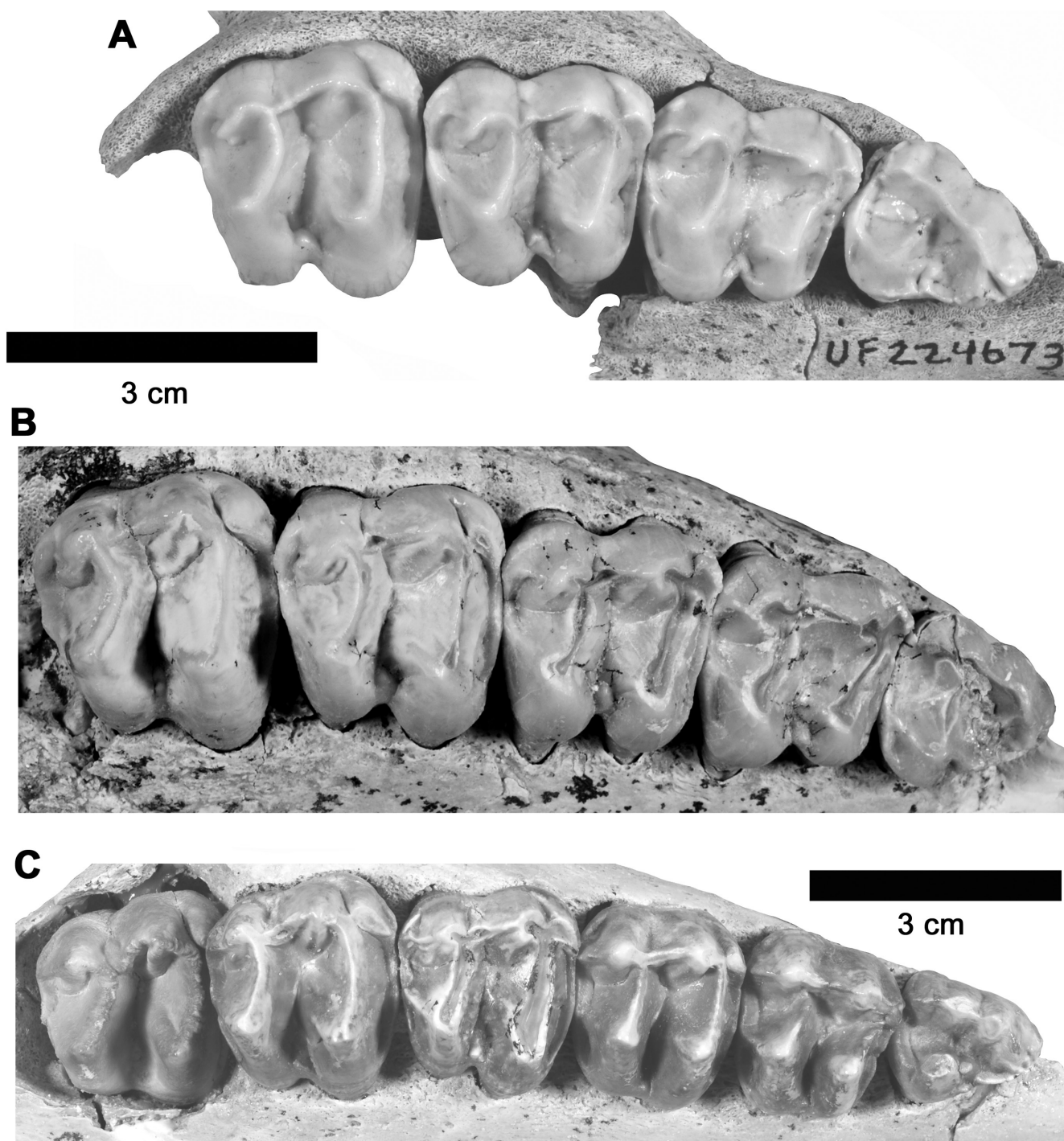**Figure 15.** Adult upper cheek teeth of *Tapirus lundeliusi* sp. nov. in occlusal view. **A**, UF 224674, left P1–M3, from Haile 7G; **B**, UF 224680, left P1–M3, from Haile 7G; **C**, UF 115970, left P1–P4, from Inglis 1A; **D**, UF 18175, right M1–M2 (reversed), from Inglis 1A; **E**, UF 97116, right P2 (reversed), from Inglis 1B; **F**, UF 242909, partial right M3 (reversed) from Withlacoochee River 1A.

Table 5. Measurements of individual cheek teeth of the holotype, paratype, and referred specimens of *Tapirus lundeliusi* sp. nov. from the Haile 7C locality, Alachua County, Florida.

	Locus	L	AW	PW	Locus	L	AW	PW
UF 160715	P1	18.5	—	17.4	—	—	—	—
UF 160715	P2	19.1	21.3	22.4	p2	21.9	—	14.9
UF 160715	P3	19.4	23.7	23.0	p3	19.1	14.4	16.0
UF 160715	P4	20.8	25.6	24.5	p4	21.0	16.8	18.5
UF 160715	M1	21.9	26.3	22.5	m1	21.9	17.0	16.8
UF 160715	M2	24.4	28.0	23.3	m2	24.1	18.1	17.3
UF 160715	M3	25.3	28.2	22.6	m3	24.6	18.3	17.2
UF 121736	P1	18.1	—	16.2	—	—	—	—
UF 121736	P2	19.4	20.6	22.2	p2	23.8	—	14.4
UF 121736	P3	19.9	24.1	22.7	p3	21.0	14.3	16.0
UF 121736	DP4	20.9	24.8	21.5	dp4	22.2	15.5	15.6
UF 121736	M1	22.1	26.0	22.9	m1	22.9	17.5	16.8
UF 121736	M2	23.7	25.8	22.2	m2	23.7	—	—
UF 121736	M3	25.6	26.5	22.1	m3	25.8	18.1	17.5
UF 206876	P1	17.2	—	15.2	—	—	—	—
UF 206876	P2	19.8	21.2	22.9	p2	23.4	—	14.6
UF 206876	P3	20.2	23.8	23.4	p3	20.8	15.4	17.0
UF 206876	P4	21.3	24.3	23.8	p4	21.4	17.1	18.8
UF 206876	M1	22.0	25.8	23.1	m1	22.5	17.4	17.8
UF 206876	M2	23.7	27.0	23.5	m2	24.0	18.0	18.2
UF 206876	M3	24.7	26.8	22.1	m3	26.0	18.3	16.4
UF 206878	P1	19.3	—	15.8	—	—	—	—
UF 206878	P2	19.3	21.8	24.1	p2	22.7	—	15.4
UF 206878	P3	20.1	25.3	24.5	p3	21.5	15.2	17.2
UF 206878	P4	21.2	26.6	25.5	p4	21.7	17.4	19.7
UF 206878	M1	21.6	26.1	22.5	m1	23.3	17.5	18.1
UF 206878	M2	24.5	27.6	24.0	m2	25.4	18.8	19.2
UF 206878	M3	25.3	27.8	22.3	m3	26.2	18.6	18.0
UF 212272	M1	22.4	26.7	23.8	—	—	—	—

Figure 16. Juvenile and subadult upper cheek teeth of *Tapirus lundeliusi* sp. nov. from Haile 7C and 7G in occlusal view. **A**, UF 224673, right DP1–DP4; **B**, UF 224662, right DP1–M1; **C**, UF 121736, right P1–P3, DP4, M1–M2. Upper scale bar applies to A and B; lower scale bar to C.

Table 6. Univariate statistics for permanent cheekteeth of *Tapirus lundeliusi* sp. nov. from the early Pleistocene of Florida and *Tapirus veroensis* from the middle and late Pleistocene of Florida, Georgia, and South Carolina. Rightmost two columns show the results of two-tailed *t*-tests for significant differences of the means for each tooth measurement. NS = not significant (i.e., $p > 0.05$).

	Tapirus lundeliusi sp. nov.						*Tapirus veroensis*							
	N	x	s	MIN	MAX	CV	N	x	s	MIN	MAX	CV	t	significance
P1 L	16	18.56	0.86	17.0	19.8	4.65	38	18.77	1.06	15.7	20.6	5.67	-0.699	NS
P1 PW	16	17.00	1.00	15.2	18.4	5.88	38	16.44	1.53	13.7	19.4	9.31	1.334	NS
P2 L	18	19.44	0.84	18.0	21.6	4.34	39	19.84	0.97	18.0	21.9	4.90	-1.513	NS
P2 AW	18	21.45	0.90	19.7	22.9	4.21	39	21.31	1.04	18.9	23.3	4.89	0.479	NS
P2 PW	18	23.51	0.87	22.2	25.1	3.71	35	23.56	1.23	21.4	25.8	5.21	-0.134	NS
P3 L	18	19.97	0.55	18.6	20.7	2.74	36	20.49	0.94	18.9	22.6	4.60	-2.166	$p<0.05$
P3 AW	15	24.64	0.77	23.7	26.1	3.14	35	24.74	1.08	22.4	26.6	4.35	-0.322	NS
P3 PW	16	24.08	0.89	22.7	25.7	3.68	33	24.69	1.16	22.3	26.7	4.70	-1.839	NS
P4 L	17	21.35	0.60	19.9	22.2	2.81	48	21.65	1.25	18.7	23.6	5.76	-0.963	NS
P4 AW	15	26.60	0.87	24.3	27.5	3.26	46	26.93	1.37	24.0	29.3	5.10	-0.872	NS
P4 PW	16	25.33	0.81	23.8	26.9	3.20	47	26.27	1.40	23.0	28.9	5.33	-2.553	$p<0.05$
M1 L	18	22.35	0.76	20.7	23.9	3.41	51	22.78	1.16	20.2	25.5	5.09	-1.456	NS
M1 AW	18	26.56	0.56	25.8	27.7	2.12	47	26.48	1.16	24.1	28.8	4.39	0.287	NS
M1 PW	17	23.41	0.62	22.5	24.9	2.67	48	24.07	1.02	22.2	26.3	4.24	-2.520	$p<0.05$
M2 L	18	24.57	0.96	22.7	26.2	3.89	55	24.93	1.16	22.8	27.6	4.67	-1.185	NS
M2 AW	18	28.29	1.02	25.8	29.6	3.60	52	28.75	1.42	25.0	31.9	4.94	-1.256	NS
M2 PW	16	24.33	1.01	22.2	26.0	4.17	50	25.80	1.17	23.1	28.3	4.53	-4.516	$p<0.001$
M3 L	16	25.23	0.85	23.4	27.0	3.38	56	24.80	1.24	22.0	27.9	5.02	1.283	NS
M3 AW	15	27.84	0.96	26.2	29.2	3.45	50	28.48	1.65	24.7	31.7	5.79	-1.422	NS
M3 PW	15	22.86	1.17	21.1	25.8	5.11	50	24.07	1.44	20.3	27.0	5.98	-2.971	$p<0.05$

Table 6. Continued.

	Tapirus lundeliusi sp. nov.						*Tapirus veroensis*							
	N	x	s	MIN	MAX	CV	N	x	s	MIN	MAX	CV	t	significance
p2 L	15	23.55	0.89	21.9	24.7	3.79	40	23.62	1.12	20.9	25.5	4.75	-0.232	NS
p2 PW	14	14.71	0.94	12.8	15.9	6.40	38	14.88	1.18	11.8	17.3	7.91	-0.474	NS
p3 L	15	21.00	1.10	19.1	23.2	5.23	47	21.39	1.21	18.0	24.6	5.65	-1.127	NS
p3 AW	14	15.33	0.66	14.3	16.4	4.31	48	15.97	1.18	14.1	19.0	7.40	-1.953	NS
p3 PW	14	16.80	0.57	16.0	17.7	3.38	48	18.02	1.37	15.5	20.9	7.57	-3.259	$p<0.01$
p4 L	14	21.67	1.04	19.8	23.6	4.82	48	22.24	1.29	19.6	24.5	5.78	-1.519	NS
p4 AW	13	17.65	0.70	16.4	19.3	3.96	47	18.94	1.27	15.2	21.2	6.73	-3.496	$p<0.01$
p4 PW	14	18.78	0.68	17.5	19.9	3.64	46	20.27	1.46	17.4	23.4	7.22	-3.678	$p<0.01$
m1 L	17	23.13	0.99	21.5	25.2	4.26	50	22.55	1.07	20.3	25.8	4.77	1.956	$p<0.05$
m1 AW	17	18.16	0.82	17.0	20.0	4.54	48	18.71	1.01	16.6	20.8	5.40	-2.011	$p<0.05$
m1 PW	16	17.35	0.67	16.1	18.5	3.84	49	17.56	0.95	15.8	20.6	5.40	-0.801	NS
m2 L	13	25.15	1.23	23.4	26.8	4.89	66	25.45	1.23	21.8	27.6	4.83	-0.811	NS
m2 AW	13	19.27	0.91	18.0	21.7	4.70	65	20.18	0.97	17.8	22.3	4.80	-3.113	$p<0.01$
m2 PW	12	18.61	0.91	17.3	20.5	4.88	65	19.21	1.03	16.0	21.8	5.35	-1.914	NS
m3 L	13	26.32	1.20	24.6	29.3	4.56	63	26.63	1.38	23.9	29.8	5.19	-0.737	NS
m3 AW	12	19.23	1.10	18.1	21.9	5.72	62	19.95	1.00	18.0	22.8	5.01	-2.247	$p<0.05$
m3 AW	13	17.32	0.70	16.4	18.8	4.02	63	17.90	0.95	16.2	20.3	5.33	-2.070	$p<0.05$
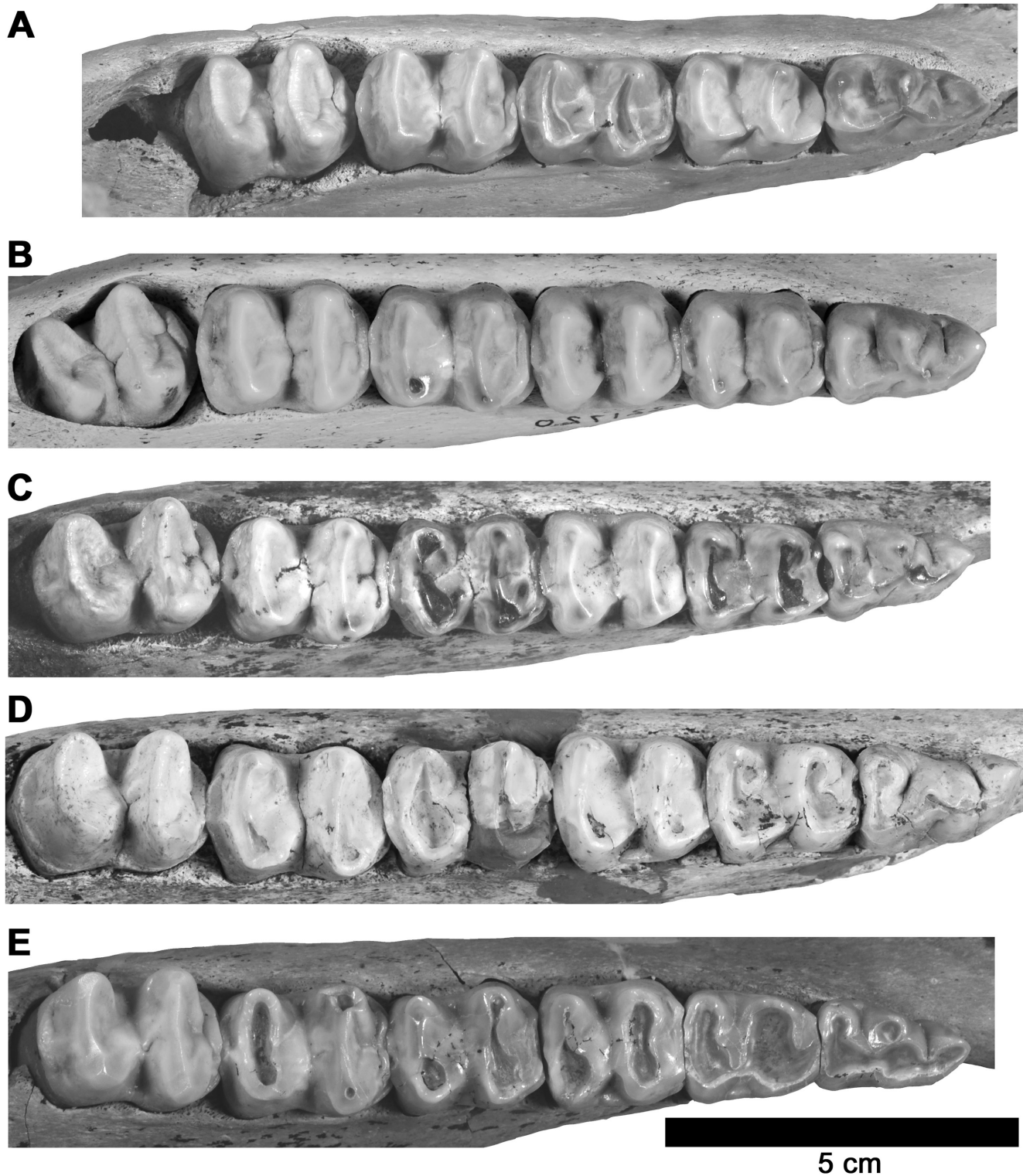
Figure 17. Lower cheek teeth of *Tapirus lundeliusi* sp. nov. from Haile 7C and 7G in occlusal view. **A**, UF 121736 with right p2–p3, dp4, m1, and erupting m2; **B**, UF 221720 with left p2–m2 and erupting m3 (reversed); **C**, UF 160715 with right p2–m3; **D**, UF 207868 with right p2–m3; **E**, UF 224680 with right p2–m3.
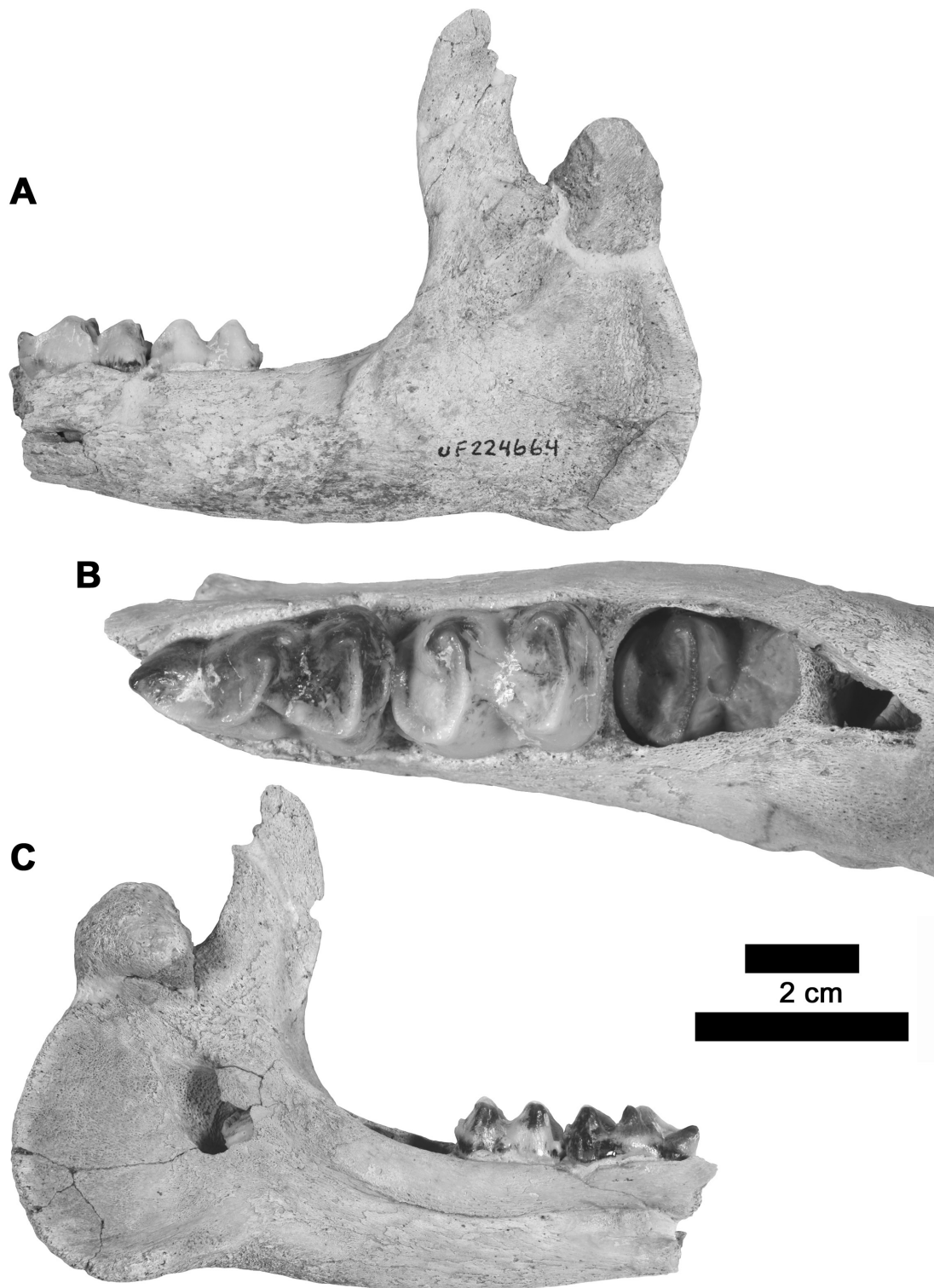
Figure 18. Left mandible of very young juvenile of *Tapirus lundeliusi* sp. nov., UF 224664, from Haile 7G in **A**, lateral; **B**, occlusal; and **C**, medial views. Teeth present are fully erupted but essentially unworn dp2–dp3, fully formed but unerupted dp4 in crypt, and forming m1 in crypt (partially visible through broken area just anterior to mandibular foramen in C). Upper scale bar applies to A and C, lower scale bar to B.

Table 7. Univariate statistics for deciduous cheekteeth of *Tapirus lundeliusi* sp. nov. from the early Pleistocene of Florida and *Tapirus veroensis* from the middle and late Pleistocene of Florida, Georgia, and South Carolina. Rightmost two columns show the results of two-tailed t-tests for significant differences of the means for each tooth measurement. NS = not significant (i.e., $p > 0.05$).

	Tapirus lundeliusi n. sp.						*Tapirus veroensis*							
	N	x	s	MIN	MAX	CV	N	x	s	MIN	MAX	CV	t	significance
DP1 L	14	18.17	0.82	16.6	19.4	4.54	5	17.71	0.85	16.4	18.5	4.82	1.065	NS
DP1 PW	14	16.91	0.60	16.0	18.0	3.55	5	16.48	1.01	15.4	17.6	6.13	1.136	NS
DP2 L	14	19.86	0.60	18.4	20.9	3.04	14	20.00	1.03	18.0	21.3	5.15	-0.447	NS
DP2 AW	9	18.95	0.60	18.0	19.9	3.17	13	18.59	0.98	16.5	20.2	5.28	0.985	NS
DP2 PW	12	20.11	1.07	18.2	21.4	5.33	13	19.96	0.94	18.6	21.2	4.69	0.393	NS
DP3 L	12	20.73	0.71	19.4	22.0	3.42	12	20.84	0.95	19.5	22.4	4.56	-0.334	NS
DP3 AW	11	21.31	0.77	20.3	22.8	3.61	12	21.32	0.74	19.7	22.3	3.48	-0.030	NS
DP3 PW	10	20.97	1.10	19.2	22.2	5.23	10	20.82	0.67	19.3	21.7	3.20	0.370	NS
DP4 L	10	21.56	0.71	20.8	22.8	3.28	11	22.43	1.03	20.6	23.5	4.58	-2.256	*p<0.05*
DP4 AW	10	24.26	0.44	23.3	24.8	1.81	11	25.22	0.88	23.8	26.9	3.51	-3.097	*p<0.01*
DP4 PW	8	21.76	0.86	20.6	23.1	3.96	11	22.53	1.29	20.2	24.0	5.73	-1.477	NS
dp2 L	12	25.67	0.72	24.5	27.0	2.79	9	25.92	1.19	24.2	27.7	4.59	-0.599	NS
dp2 PW	10	14.59	0.64	13.6	15.6	4.36	10	15.06	0.80	13.8	16.0	5.28	-1.441	NS
dp3 L	16	21.62	0.66	20.6	22.7	3.04	8	22.26	1.15	20.8	24.1	5.16	-1.758	NS
dp3 AW	13	14.78	0.74	13.8	16.1	5.02	7	15.66	0.92	14.3	16.7	5.87	-2.336	*p<0.05*
dp3 PW	16	14.93	0.79	13.6	16.3	5.28	8	15.68	1.11	14.1	17.0	7.07	-1.918	NS
dp4 L	13	23.11	0.61	22.2	24.3	2.65	19	23.32	1.03	21.8	24.7	4.42	-0.665	NS
dp4 AW	11	16.07	0.34	15.5	16.5	2.14	19	17.36	0.86	16.1	19.2	4.94	-4.743	*p<0.001*
dp4 PW	12	16.19	0.62	15.3	17.3	3.82	20	16.64	0.69	15.6	18.0	4.13	-1.852	NS

proportions and morphology, although differ from true molars in that mean AW and PW are about the same (Figs. 17A, 18B). Isolated dp4s and m1s can be distinguished on the basis of AW/L ratios; those with ratios less than 73 percent are dp4s, greater than 73 percent, m1s. Lower crown height and thinner enamel also characterize the dp4 relative to the m1.

DESCRIPTION AND COMPARISONS OF *TAPIRUS* SP. FROM SOMMERS PIT, WALDEN PIT 1, KISSIMMEE RIVER 6, HUBBRD PIT, AND US 19 BRIDGE SITE

A species of *Tapirus* smaller in average size than any extant species is found at five Blancan localities in Florida. The isolated p4 from Sommers Pit (UF/TRO 1469) is unworn and probably had not fully erupted prior to death (Fig. 19D). The hypolophid is very slightly lower in height than the protolophid. The tooth is smaller than any p4 referred to *Tapirus lundeliusi*. Its L does fall within the OR of *T. lundeliusi*, but that is misleading as the anterior and posterior cingulids have not been removed by interdental wear with the adjacent teeth. Its L is only matched by those of *T. lundeliusi* with well worn teeth, such as UF 224680. The AW of UF/TRO 1469 (15.1 mm) is about 3.5 standard deviations less than the mean of *T. lundeliusi*, while its PW (16.7 mm) is smaller by about 3 standard deviations. Both widths are below the minimum values recorded for *T. lundeliusi* and *Tapirus veroensis* (Table 6).

The p3 of UF/TRO 1489 (Fig. 19C) from Walden Pit 1 is from a smaller, older individual than UF/TRO 1469. Its L, AW, and PW are all smaller than the minimum values of p3s of *T. lundeliusi* and *T. veroensis* (Table 6), often by a large margin. UF 51249 is a moderately worn p2, with the characteristic paralophid and metalophid of tapirid p2s (Fig. 19B). Its L and PW are smaller than the minimum values of p2s of *T. lundeliusi* and the minimum p2 L for *T. veroensis* (Table 6). The narrowest p2s of *T. veroensis* have widths similar to UF 51249, but such specimens are rare. The PW of UF 248788 is identical to that of UF 51249; L can not be measured due to breakage.

UF 249089 (Fig. 19E-F) from Hubbard Pit is a slightly worn dp3 (or, less likely, a dp4) that is missing the roots; minor damage to the anterolingual base of the crown prevents accurate determination of its AW. Both the L and PW of UF 249089 fall below the OR of either the dp3 or the dp4 of *T. lundeliusi* and *T. veroensis* (Table 7). The ratio of PW/L in UF 249089 is 0.67. The dp3s of *T. lundeliusi* have similar ratios (x = 0.685, N = 15, OR = 0.64–0.74), while the dp4s are slightly broader (x = 0.701, N = 12, OR = 0.68–0.73). Most (22 of 27) dp3s and dp4s of *T. veroensis* are also slightly broader, with PW/L $\geq$ 0.70.

The navicular (UF 247180) has the characteristic shape of this element in *Tapirus*, but is of small size. Greatest transverse width of its astragalar facet, 29.8 mm, is 4.0 standard deviations below the mean for a sample of naviculars of *T. lundeliusi* and well below its observed range (x = 35.7; s = 1.49; OR = 31.9–38.1; N = 22). Slight breakage on UF 247180 prevents accurate measurement of the depth of the astragalar facet, but the value would have been very close to 21 mm. Again, this value lies outside the range for *T. lundeliusi* (x = 25.5; s = 1.25; OR = 23.5–28.7; N = 22). In contrast, the dimensions of UF 247180 are very similar to those of the Gray Fossil Site sample of *Tapirus polkensis* (astragalar facet width: x = 29.2; s = 1.96; OR = 26.1–33.3; N = 17; astragalar facet depth: x = 21.3; s = 1.14; OR = 20.0–23.9; N = 17).

Small tapirs, those significantly smaller in body size than any extant species, are known from the Hemphillian (late Miocene–early Pliocene) of Florida and Tennessee (Fig. 19A; Hulbert 2005; Hulbert et al. 2009), but have not previously been reported from the Pleistocene of North America. The p3 of UF/TRO 1489 is larger than average members of the Tennessee sample of *Tapirus polkensis*, but falls within that population's OR (Hulbert et al. 2009). When compared to the two species of *Tapirus* in the late Hemphillian Palmetto Fauna of Florida (Webb et al. 2008), the L and AW of UF/TRO 1489 more closely resemble those of the larger, unnamed species, while its PW is more similar to that of *T. polkensis*. In contrast, UF/TRO

1469 is larger than p4s referred to *T. polkensis* from both Florida and Tennessee (Hulbert et al. 2009), and its L, AW, and PW are all within the ORs of the larger, unnamed Palmetto Fauna tapir. The L of the p2, UF 51249, is greater than any referred specimen of *T. polkensis* from Florida or Tennessee (n = 31), and instead is very similar to the two known p2s of

the larger, unnamed species in the Palmetto Fauna (19.3 for UF 23948 and 20.1 for UF 124191). Its PW (along with that of UF 248788), however, is slightly less than those of these two specimens, and within the range of *T. polkensis*. The L and PW of UF 249089 and L of UF 255358 exceed those of dp3s of *T. polkensis* from both Florida
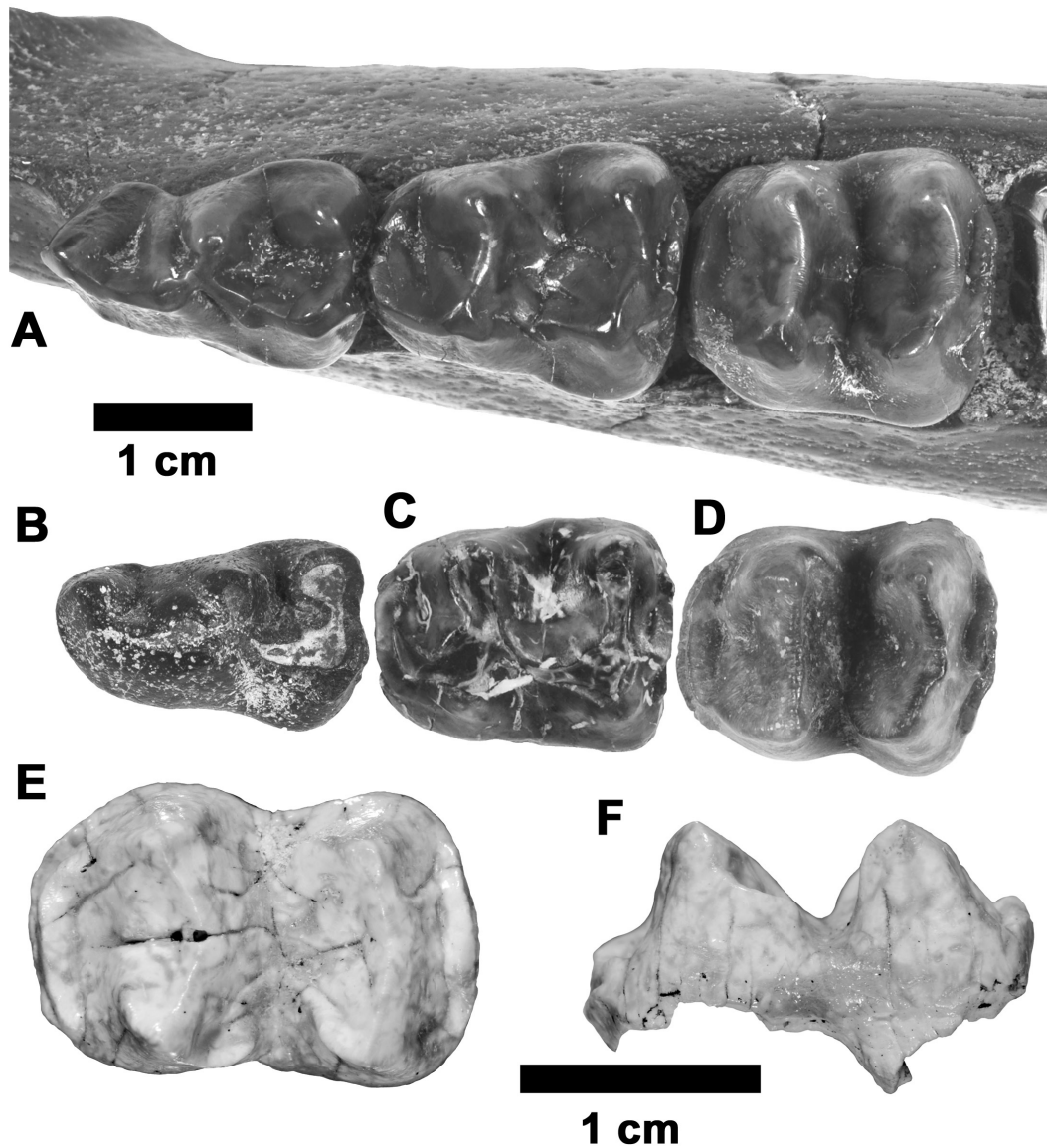
Figure 19. Lower premolars of *Tapirus* sp. indet. from Florida in occlusal (**A-E**) and lingual (**F**) views. **A**, UF 124191, left partial mandible with p2-p4 from Whidden Creek Site, Fort Meade Mine, Polk County, Florida, very late Hemphillian; **B**, UF 51249, left p2 from Kissimmee River 6; **C**, UF/TRO 1489 right p3 (reversed) from Walden Pit 1; **D**, UF/TRO 1469 right p4 (reversed) from Sommers Pit; **E**, occlusal and **F**, lingual, views of UF 249089, left dp3 from Hubbard Pit. The Blancan teeth in B-F are too small to be referred to *Tapirus lundeliusi* or *Tapirus haysii*, but are instead within the size range of an undescribed, small species from the late Hemphillian of Florida. Upper scale bar applies to A-D; lower scale bar to E-F.

and Tennessee (Hulbert et al. 2009), and are most similar to those of the larger, unnamed Palmetto Fauna tapir, especially UF 223991 (L = 19.9; AW = 13.0; PW = 13.2).

Given the close proximity of Sommers Pit and Walden Pit 1 and their equivalent geologic age, it is reasonable to assume that UF/TRO 1469 and UF/TRO 1489 represent the same species. It is statistically improbable that they represent *Tapirus lundeliusi* (recall that UF/TRO 1476 from nearby Walden Pit 2 falls within the OR of *T. lundeliusi*). Of the two species of *Tapirus* known from the late Hemphillian of Florida, overall they are more similar in size to the unnamed, relatively larger species than they are to *Tapirus polkensis* (Fig. 19). The same applies to UF 249089. The p2 from Kissimmee River 6 and the teeth from the US 19 Bridge Site show similarities to both late Hemphillian species, but they too more favor the unnamed, relatively larger species rather than *T. polkensis*. The two postcranial elements from the US 19 Bridge Site are significantly smaller than the same bones in *T. lundeliusi*. Other than size, no preserved morphologic features favor assignment to one of these Hemphillian species over the other. Another alternative is that they represent a completely different species, one not present in the Hemphillian, as equivalence in tooth size is not proof that two samples of *Tapirus* are conspecific. At the present all of these hypotheses are viable. Whatever the case, this small tapir, added to *Tapirus haysii* and *T. lundeliusi*, brings the total number of species of *Tapirus* in Florida during the early late Blancan to three.

PHYLOGENETIC RELATIONSHIPS

Figures 20–21 show the results of cladistic analyses to investigate the evolutionary relationships between *Tapirus lundeliusi* sp. nov. and other New World species of *Tapirus* (Appendix 3). The analyses differ in the presence/absence of the recently described late Miocene Chinese species *Tapirus hezhengensis* Deng et al. 2008. Given that it is only known from three relatively incomplete specimens, most characters for *T. hezhengensis* must be scored as missing. But the relative antiquity of this species,
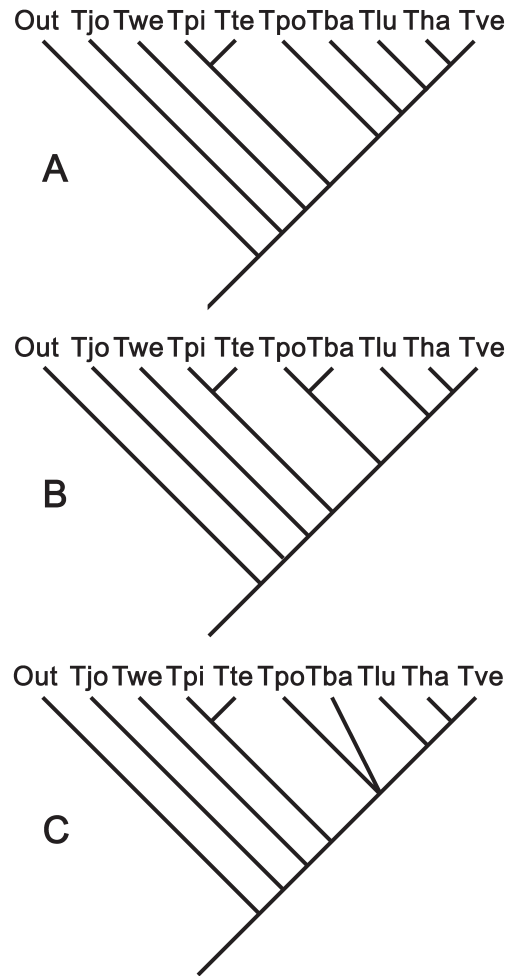
Figure 20. Cladograms of the two equally most parsimonious arrangements of North American fossil species and extant Neotropical species of *Tapirus* (**A** and **B**), and the strict consensus tree (**C**). Multi-state characters treated as unordered; confidence index = 0.68. Characters and character state matrix in Appendices 2 and 3. Taxon abbreviations: Out, outgroup; Tjo, *T. johnsoni*; Twe, *T. webbi*; Tpi, *T. pinchaque*; Tte, *T. terrestris*; Tpo, *T. polkensis*; Tba, *T. bairdii*; Tlu, *T. lundeliusi*; Tha, *T. haysii*; and Tve, *T. veroensis*.

along with its geographic position intermediate between North America and Europe suggest that it is likely to be phylogenetically informative with regards to tapir evolution. Recovery of additional specimens of *T. hezhengensis* to allow scoring of additional characters would likely help resolve inconsistencies in the analyses.

In a cladistic analysis using all of the taxa in Appendix 3 with the exception of *Tapirus hezhengensis*, ordered and unordered multi-state characters produced the same relationships among in-group taxa (Fig. 20). With unordered characters, there are two most parsimonious cladograms, each with an overall consistency index of 0.68 and retention index of 0.74. The analyses strongly support a monophyletic clade comprised of *T. lundeliusi*, *Tapirus haysii*, and *Tapirus veroensis* (i.e., the subgenus *Helicotapirus*), and that *T. lundeliusi* is the sister group to *T. haysii* plus *T. veroensis*. The interrelationships of *Tapirus bairdii* and *Tapirus polkensis* with *Helicotapirus* are unresolved, but there is strong support that they are more closely related to *Helicotapirus* than to other species of *Tapirus*. Synapomorphies of *T.* (*Helicotapirus*) are concave lateral surface of lacrimal (character 30 in Appendix 2); anterior projection of ascending ramus of mandible (39); increased depth of horizontal ramus below molars (40); enlarged parastyles on upper molars (55); loss of posterolabial cingula on upper cheekteeth (56); and increased relative length of the p2 (69). Synapomorphies of *T. haysii* and *T. veroensis* relative to *T. lundeliusi* are delayed fusion of interparietal with occipital (9); relatively short nasal bone (10); absence of a maxillary flange (26); increased length of lacrimal (29); taller metaloph on P2 (51); and reduced p3 cristid obliqua (73). The clade consisting of *Helicotapirus*, *T. bairdii*, and *T. polkensis* is supported by seven unambiguous synapomorphies: broad dorsal table of frontal (4, reversed in *T. lundeliusi*); triangular interparietal (8); meatal fossa on nasal deep (14) and approaches midline of skull (15); meatal fossa on frontal extensive with a distinct posterior margin (16, reversed in *T. lundeliusi*); broad and flat posterior lacrimal process (33); and relatively short postcanine diastema (37, reversed in *T. bairdii*). The trichotomy among *Helicotapirus*, *T. bairdii*, and *T. polkensis* is not resolved in this analysis. To date no North American fossil species of *Tapirus* has been described that shares some of the autapomorphic character states of *T. bairdii* such as presence of a broad sagittal table instead of a narrow sagittal crest, nasal notch extending posterior to orbit, loss of descending sigmoid process of nasal bone, greatly expanded maxillary flange, ossification of nasal septum, shortened posterior process of premaxilla, very long postcanine diastema, and small cheektooth dimensions relative to body size (and skull length). The distribution of cranial and dental characters of such a fossil species could resolve the trichotomy.

Addition of *Tapirus hezhengensis* to the analysis does not effect support for the following monophyletic clades: *Tapirus lundeliusi*, *Tapirus haysii*, and *Tapirus veroensis* (and their relative positions); *Tapirus* (*Helicotapirus*), *Tapirus bairdii* and *Tapirus polkensis*; and *Tapirus terrestris* plus *Tapirus pinchaque* (Fig. 21). Two differences are found from the first analysis. The trichotomy between *T.* (*Helicotapirus*), *T. bairdii* and *T. polkensis* is resolved, albeit weakly (Bremer support of 1), with *T. bairdii* sharing a closer relationship with *T.* (*Helicotapirus*) than does *T. polkensis*. Second, the possibility of a close relationship between *Tapirus webbi* from the late Miocene Florida with the two extant South American species, a hypothesis first tentatively proposed by Hulbert (1995; then using the name *Tapirus simpsoni* for the samples later named *T. webbi*), is revived (Fig. 21A). A late Miocene dispersal of *T. webbi* or a closely related form into South America, followed by in situ evolution that produced *T. terrestris* and *T. pinchaque* is congruent with molecular evidence of a relative ancient (pre-Pliocene) divergence time between *T. bairdii* and the clade formed by *T. terrestris* and *T. pinchaque* (Ashley et al. 1996; Norman & Ashley 2000). More recently, Rincón et al. (2009) noted the resemblance between some fragmentary tapirid material from the late Pliocene or early Pleistocene of Venezuela and *T. webbi*. Although their geologic and chronologic evidence remains controversial, Campbell and co-authors have persistently proposed a late Miocene dispersal to South America of a few North American ungulates, including a tapir (Campbell et al. 2000, 2006, 2010), coeval with the well accepted first dispersal of ground sloths from South America to North America (e.g., Morgan 2005). A much later
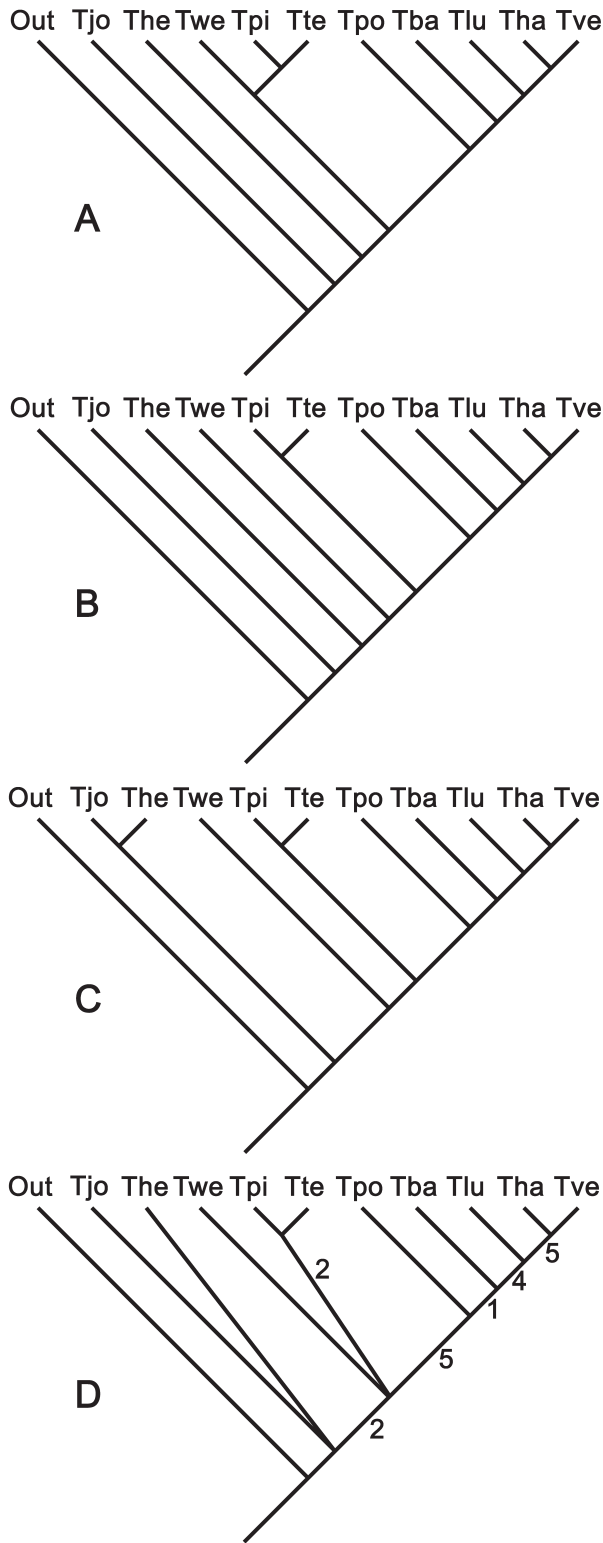
(Pleistocene) dispersal of tapirs into South America appears less likely, as no known North American Pliocene or Pleistocene species is closely related to *T. terrestris* and *T. pinchaque*. This scenario would have to involve an as yet undiscovered taxon or clade of tapirids that persisted isolated in Central America from the late Miocene to the Pleistocene.

DISCUSSION

Nineteenth century paleontologists noted that they could not distinguish the smaller fossil teeth of Pleistocene *Tapirus* found in North America from that of the extant lowland tapir of South America (e.g., Carpenter 1846; Leidy 1859, 1889; Cope 1871), and, in one of the rare instances of taxonomic conservatism on their part, failed to name it as a new species. It took the discovery of a skull to provide convincing evidence that the North American form was a distinct species, *Tapirus veroensis*, differing in many ways from each of the modern species of tapir (Sellards 1918; Simpson 1945; Lundelius & Slaughter 1976). Likewise, if the Blancan remains here named *Tapirus lundeliusi* consisted of only jaw fragments, isolated teeth, and postcranial elements, then they could not be easily differentiated from *T. veroensis* (Tables 3, 4, 6, 7). Fortunately, that is not the case, as the combined sample of skeletons from the Haile 7C and 7G sites make it one of the best known fossil species of tapir, second only to *Tapirus polkensis* (Hulbert et al. 2009).

One of the interesting observations of the large sample of skulls of *Tapirus polkensis* from the Gray Fossil Site in Tennessee was the unexpected

Figure 21. Cladograms of the three equally most parsimonious arrangements of North American fossil species and extant Neotropical species of *Tapirus* (abbreviations as in Fig. 20) and the Miocene species *Tapirus hezhengensis* (The) from China (**A**, **B**, and **C**), and the strict consensus tree (**D**). Multi-state characters treated as unordered; confidence index = 0.67. Numbers on D indicate Bremer support values.

degree of intraspecific variation in a number of features that show greater consistency in extant species and *Tapirus veroensis*, for example in the form of the sagittal crest and number of lacrimal foramina (Hulbert et al. 2009). Such is not the case with the Haile 7G sample of *Tapirus lundeliusi*, which is almost as numerous as the Gray Site sample; once ontogenetic variation is factored, its intraspecific variation in cranial morphology is similar to that observed in extant species of *Tapirus*. Characters that present a high degree of variation in the Haile 7G population, e.g. shape of the nasal bone and development of the lingual cusp and transverse loph on the P1, are also variable in large samples of all species of *Tapirus*. However, many skulls and mandibles from Haile 7G remain to be prepared, so this observation must remain tentative for now.

One of the unusual aspects of the Haile 7C and 7G sample of *Tapirus lundeliusi* is the rarity of old adult individuals. Only one out of 44 individuals that can be aged is in this age class (UF 244600), and it only has very small areas of exposed dentine on its m3, so it barely falls into this category. Tapirs from the old adult wear stage are not uncommon at other Florida fossil localities (pers. obs.) or at the Gray Fossil Site (Hulbert et al. 2009). Indeed, the lone tooth from the Withlacoochee River 1A sample of *T. lundeliusi* is at the old adult stage as is UF/TRO 1476 from Walden Pit 2. It is as yet unclear whether the taphonomic factors causing the very large sample of tapir skeletons at the two Haile 7 sites were acting independent of age ("catastrophically", although not likely a single, rapid event), or were actively biased against older, more experienced individuals. This will probably not be resolved until the cause of the mortality of the Haile tapirs is better understood.

Although there is broad overlap in all tooth dimensions, *Tapirus lundeliusi* is significantly different from *Tapirus veroensis* in 13 out of 37 tooth measurements in the permanent dentition (Table 6) and four out of 19 in the deciduous dentition (Table 7). One consistent dissimilarity is that posterior widths of P4–M3 are all significantly smaller in *T. lundeliusi*. The other difference is the

significantly smaller widths of the p3 (PW only) and p4 (AW and PW) in *T. lundeliusi*. That the m1 of *T. lundeliusi* is significantly longer than that of *T. veroensis* is likely an artifact of the demographics of the two measured samples. The sample of *T. lundeliusi* includes a much greater proportion of juveniles and subadults with unworn and slightly worn m1s which have not lost their anterior and posterior cingulids, while the *T. veroensis* sample contains a greater proportion of full and old adults in which the m1 has worn against the adjacent p4 and m2, reducing its measurable length. Including only unworn or slightly worn m1s from the *T. veroensis* sample produces a population with a mean L of 22.9 mm (N = 12) that is not significantly different from that of *T. lundeliusi*. The greatest differences in the deciduous dentition are the significant smaller AW of DP4 and dp4 in *T. lundeliusi* (Table 7).

In their discussion of the type locality of *Tapirus haysii*, Ray and Sanders (1984) noted that the USNM collection contained specimens of both *T. haysii* and *Tapirus veroensis* from the Neuse River near New Bern, North Carolina. The associated fauna was only briefly noted (Ray & Sanders 1984:293), but resembles mixed Blancan–Rancholabrean faunas in Florida, such as Santa Fe River 1 (compare with MacFadden & Hulbert 2009:table 1). For example the presence of *Nannippus* and *T. haysii* are evidence of a Blancan component, while *Mammuthus*, *Bison*, and *Castoroides* together indicate a Rancholabrean age. Thus the specimens Ray and Sanders (1984) identified as *T. veroensis* may simply be standard Rancholabrean specimens of that taxon. However, given that there is a now a second species of *Tapirus*, of similar size as *T. veroensis*, from the Blancan, then the smaller Neuse River tapir specimens need to be critically compared with *Tapirus lundeliusi*.

Although currently known from a limited geographic range in Florida, it is likely that future discoveries of late Blancan faunas elsewhere in the southeastern United States will produce specimens of *Tapirus lundeliusi*. Fossil species of *Tapirus* tend to have rather broad geographic distributions, as do three of the four extant species. Even if its geographic range is currently small, it has broad implications
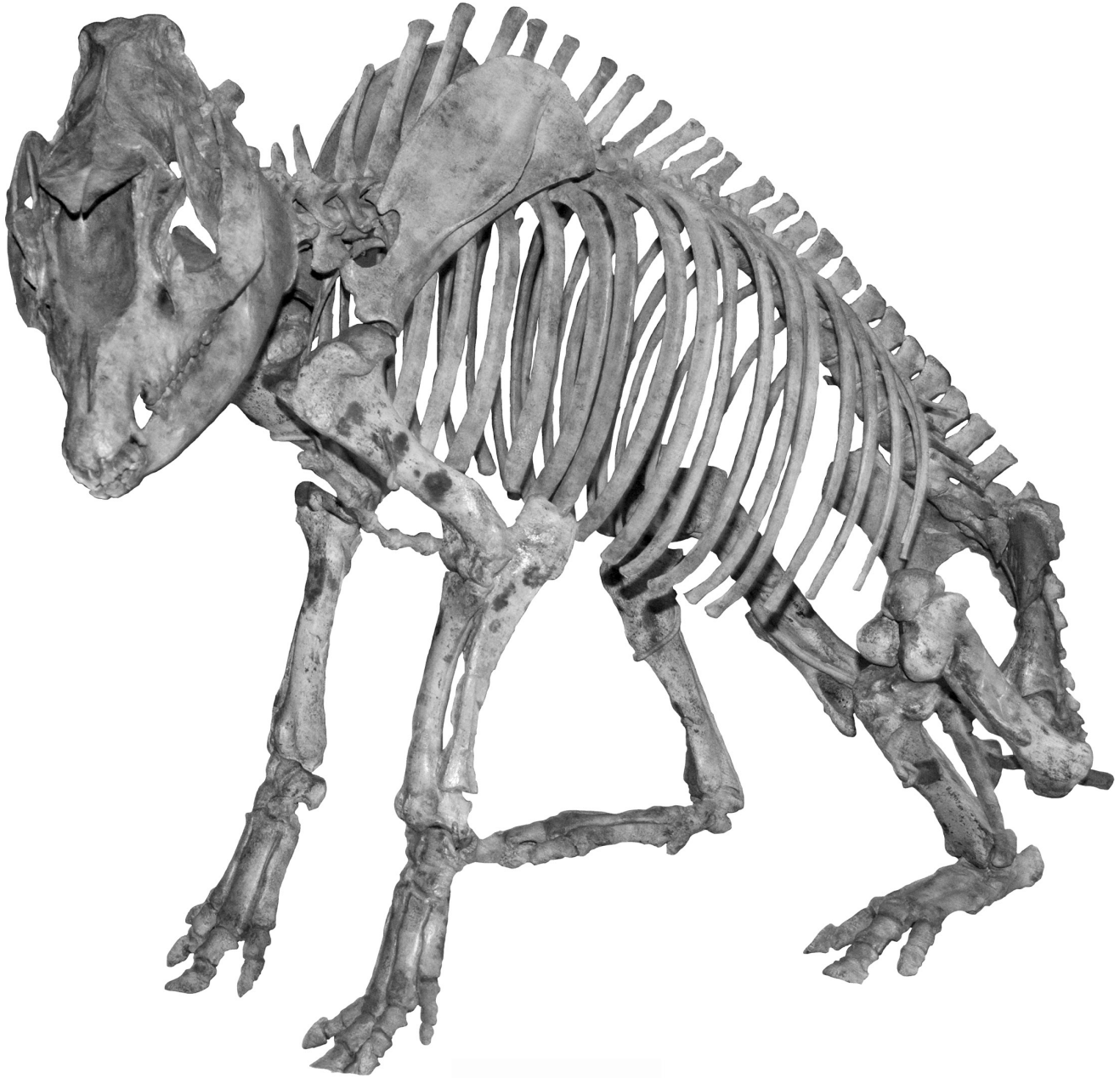
Figure 22. Mounted skeleton of *Tapirus lundeliusi* sp. nov. on public display at the Florida Museum of Natural History. Postcranial skeleton belongs to UF 206878 (with minor restoration). Skull and mandibles (excluding symphysis and incisors) are casts of UF 160715 (with restoration); mandibular symphysis and incisors are a cast of UF 206878 (see Fig. 14A). Skeletal pose designed by Gina Gould; skeleton mounted and casts made and painted by Steve and Sue Hutchens; photography by Jeff Gage.

for the phylogeny of *Tapirus*. The mixture of plesiomorphic character states in *T. lundeliusi* (e.g., presence of maxillary flange, narrow lacrimal, long nasal, early fusion of interparietal) together with apomorphies shared with *Tapirus veroensis* and *Tapirus haysii* (e.g. short postcanine diastema, deep horizontal ramus, absence of posterolabial cingula on upper cheekteeth) allows a better sense of the evolutionary relationships and character state transformations between Miocene species such as *Tapirus johnsoni* and *Tapirus polkensis* and the later Pleistocene species.

CONCLUSIONS

Tapirs are a common component of the large mammalian herbivore guild in Florida during the late Blancan (early Pleistocene). Two named species of *Tapirus* are recognized from this interval, the very large *Tapirus haysii* and the medium-sized *Tapirus lundeliusi* sp. nov. (Fig. 22), plus a smaller, unnamed form making a total of three. But there is only possible one case when more than one species has been found at the same locality (Kissimmee River 6 with *T. haysii* and the small, unnamed species), suggesting some type of ecologic separation or competitive exclusion was the norm. As the Kissimmee River specimens were collected from spoil piles created by dredging, it is not certain that the two taxa are in fact contemporaneous at this locality. *Tapirus lundeliusi* is the best represented late Blancan tapir from Florida, recognized from eleven sites, although complete specimens derive from just two, Haile 7C (the type locality) and Haile 7G. *Tapirus haysii* is rarer and known from only a few Blancan sites in Florida (Fig. 1; Appendix 1). *T. haysii* became more common and widespread in Florida during the early Irvingtonian (Hulbert 1995). In contrast to *T. haysii*, no Irvingtonian records of *T. lundeliusi* are known, with the species apparently becoming extinct near the end of the Blancan. The third late Blancan species, known from Walden Pit 1, Sommers Pit, Hubbard Pit, Kissimmee River 6, and the US 19 Bridge site, is significantly smaller than *T. lundeliusi*, and may represent a holdover of an undescribed species from the late Hemphillian of Florida.

Almost all standard measurements on the skull, mandible, and teeth show considerable overlap between *Tapirus lundeliusi* and the common middle to late Pleistocene species *Tapirus veroensis*. But *T. lundeliusi* retains a number of plesiomorphic features in its skull that are more derived in *T. veroensis* (and *Tapirus haysii*), such as having a maxillary flange and a smaller lacrimal. Formation of the sagittal crest and fusion of the interparietal bone with the occipital and parietals occur earlier in ontogeny in *T. lundeliusi* compared to *T. veroensis* (using tooth eruption sequences to age specimens). *T. lundeliusi* shares with *T. haysii* a much greater relative mandibular condyle height than found in *T. veroensis* or other species of *Tapirus*.

Phylogenetic analysis using 39 characters provides strong support for a North American clade composed of *Tapirus lundeliusi*, *Tapirus veroensis*, and *Tapirus haysii*. *T. lundeliusi* is the sister taxon to the other two. This clade is formally recognized as a new subgenus, *Helicotapirus*. Phylogenetic analysis also strongly supports a clade comprised of *Helicotapirus*, the late Miocene–early Pliocene species *Tapirus polkensis*, and the extant species *Tapirus bairdii*. Many of the synapomorphies of this clade are osteological features of the nasal and frontal bones related to the development of the meatal diverticulum, a soft tissue structure of uncertain function (Witmer et al. 1999). The *Helicotapirus–T. bairdii–T. polkensis* clade most likely diverged from that containing the other two extant New World species (*Tapirus terrestris* and *T. pinchaque*) in the late Miocene.

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LITERATURE CITED

Ashley, M. V., J. E. Norman, & L. Stross. 1996. Phylogenetic analysis of the perissodactylan family Tapiridae using mitochondrial cyto-chrome *c* oxidase (COII) sequences. Journal of Mammalian Evolution 3(4):315–326.

Bader, R. S. 1957. Two Pleistocene mammalian faunas from Alachua County, Florida. Bulletin of the Florida State Museum, Biological Sciences 2(5):53–75.

Bell, C. J., E. L. Lundelius Jr., A. D. Barnosky, R. W. Graham, E. H. Lindsay Jr., D. R. Ruez, Jr., H. A. Semken Jr., S. D. Webb, & R. K. Zakrzewski. 2004. The Blancan, Irvingtonian, and Rancholabrean mammal ages. Pp. 232–314 *in* M. O. Woodburne, ed. Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York.

Boeuf, O. 1991. *Tapirus jeanpiveteaui* nov. sp.,

nouvelle espèce de Tapiridae (Perissodactyla) du Pliocène de Charente (France). Palaeon-tographica, Abteilung A 217:177–194.

Brisson, A. D. 1762. Regnum Animale in Classes IX distributum sive synopsis methodica. Edito altero auctior. Theodorum Haak, Leiden, Netherlands, 294 pp.

Campbell Jr., K. E., C. D. Frailey, & L. Romero-Pittman. 2000. The late Miocene gomphothere *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) from Amazonian Peru: implications for the Great American Faunal Interchange. Instituto Geológico Minero y Metalúrgico, Serie D: Estudios Regionales, Boletín 23:1–152.

Campbell Jr., K. E., C. D. Frailey, & L. Romero-Pittman. 2006. The Pan-Amazonian Ucayali Peneplain, late Neogene sedimentation in Amazonia, and the birth of the modern Amazon River system. Palaeogeography, Palaeoclimatology, Palaeoecology 239:166–219.

Campbell Jr., K. E., D. R. Prothero, L. Romero-Pittman, F. Hertel, & N. Rivera. 2010. Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. Journal of South American Earth Sciences 29:619–626.

Carpenter, W. M. 1846. Remarks on some fossil bones brought to New Orleans from Tennessee and Texas. American Journal of Science, second series 1:244–250.

Colbert, M. W. 2005. The facial skeleton of the early Oligocene *Colodon* (Perissodactyla, Tapiroidea). Paleontologica Electronica 8:12A. Retrieved from http://palaeo-electronica.org/2005_1/colbert12/issue1_05.html

Cope, E. D. 1871. Preliminary report on the Vertebrata discovered in the Port Kennedy bone cave. Proceedings of the American Philosophical Society 12:73–102.

Dalquest, W. W. & Schultz, G. E. 1992. Ice Age Mammals of Northwestern Texas. Midwestern State University Press, Wichita Falls, Texas, 309 p.

Deng, T., W. He, & S. Q. Chen. 2008. A new species of late Miocene tapir (Perissodactyla, Tapiridae) from the Linxia Basin in Gansu, China. Vertebrata PalAsiatica 46(3):190–209. [in Chinese with English summary]

DeSantis, L. G. & MacFadden, B. J. 2007. Identifying forested environments in Deep Time using fossil tapirs: evidence from evolutionary morphology and stable isotopes. Courier Forschung-Institut Senkenberg 258:147–157.

DeSantis, L. R. G. & MacFadden, B. J. 2008. Stable isotopes and REEs of ungulates and xenarthrans from Haile 7G: elucidating the paleoecology of a late Pliocene fossil site from Florida. Journal of Vertebrate Paleontology 28(3, supplement):71A.

Desmarest, A. G. 1819. Tapirs fossils. Pp. 458-461. *In* Nouveau Dictionnaire d'Histoire Naturelle, Nouvelle Edition. Chez Deterville, Paris, vol. 32.

Emslie, S. D. 1992. Two new late Blancan avifaunas from Florida and extinctions of wetland birds in the Plio-Pleistocene. Natural History Museum of Los Angeles County Science Series 36:249–269.

Emslie, S. D. 1998. Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida Peninsula. Ornithological Monographs, No. 50, 113 p.

Ferrero, B. S., & J. I. Noriega. 2007. A new upper Pleistocene tapir from Argentina: remarks on the phylogenetics and diversification of Neotropical Tapiridae. Journal of Vertebrate Paleontology 27(2):504–511.

Gibbard, P. L., M. J. Head, M. J. C. Walker, and the Subcommission on Quaternary Stratigraphy. 2010. Formal ratification of the Quaternary System/Period and the Pleistocene Series/ Epoch with a base at 2.58 Ma. Journal of Quaternary Science 25(2):96-102.

Gill, T. N. 1865. [Description of the genus *Elasmognathus*]. Proceedings of the Academy of Natural Sciences Philadelphia 17:183.

Graham, R. W. 2003. Pleistocene tapir from Hill Top Cave, Trigg County, Kentucky and a review of Plio-Pleistocene tapirs of North America and their paleoecology. Pp. 87–118 *in* B. Schubert, J. I. Mead, & R. W. Graham, eds. Vertebrate Paleontology of Caves. Indiana University Press, Bloomington.

Gray, J. E. 1821. On the natural arrangements of vertebrose animals. London Medical Repository Review, 15:296–310.

Hershkovitz, P. 1954. Mammals of northern Colombia, preliminary report no. 7: tapirs (genus *Tapirus*), with a systematic review of American species. Proceedings of the United States National Museum 103:465–496.

Hulbert Jr., R. C. 1988. A new *Cormohipparion* (Mammalia, Equidae) from the Pliocene (latest Hemphillian and Blancan) of Florida. Journal of Vertebrate Paleontology 7:451–468.

Hulbert Jr., R. C. 1995. The giant tapir, *Tapirus haysii*, from Leisey Shell Pit 1A and other Florida Irvingtonian localities. Bulletin of the Florida Museum of Natural History 37:515–551.

Hulbert Jr., R. C. 1999. Nine million years of *Tapirus* (Mammalia, Perissodactyla) from Florida. Journal of Vertebrate Paleontology 19(3, supplement):53A.

Hulbert Jr., R. C. 2005. Late Miocene *Tapirus* (Mammalia, Perissodactyla) from Florida, with description of a new species, *Tapirus webbi*. Bulletin of the Florida Museum of Natural History 45(4):465–494.

Hulbert Jr., R. C., J. I. Bloch, & A. R. Poyer. 2006. Exceptional preservation of vertebrates from Haile 7G, a new late Pliocene site from Florida. Journal of Vertebrate Paleontology 26(3, supplement):78A–79A.

Hulbert Jr., R. C., & G. S. Morgan. 1993. Quantitative and qualitative evolution in the giant armadillo *Holmesina* (Edentata: Pampatheriidae) in Florida. Pp. 134–177 *in* R. A. Martin & A. D. Barnosky, eds. Morphologic Change in Quaternary Mammals of North America. Cambridge University Press, Cambridge.

Hulbert Jr., R. C., & G. S. Morgan. 2009. Two

new late Blancan vertebrate sites from Florida, with a reassessment of late Pliocene vertebrate biochronology in Florida. Abstract Program, Second Annual Meeting of the Southeastern Association of Vertebrate Paleontology, Virginia Museum of Natural History, Martinsville. Retrieved from http://web.me.com/dooleyclan/SEAVP/SEAVP_files/Abstract%20book.pdf

Hulbert Jr., R. C. & S. C. Wallace. 2005. Phylogenetic analysis of late Cenozoic *Tapirus* (Mammalia, Perissodactyla). Journal of Vertebrate Paleontology, 25(3, supplement):72A.

Hulbert Jr., R. C., S. C. Wallace, W. E. Klippel, & P. W. Parmalee. 2009. Cranial morphology and systematics of an extraordinary sample of the late Neogene dwarf tapir, *Tapirus polkensis* (Olsen). Journal of Paleontology 83(2):238–262.

Jefferson, G. T. 1989. Late Cenozoic tapirs (Mammalia: Perissodactyla) of western North America. Natural History Museum of Los Angeles County Contributions in Science 406:1–21.

Jones, D. S., B. J. MacFadden, S. D. Webb, P. A. Mueller, D. A. Hodell, & T. M. Cronin. 1991. Integrated geochronology of a classic Pliocene fossil site in Florida: Linking marine and terrestrial biochronologies. The Journal of Geology 99(5):637–648.

Kurtén, B., & Anderson, E. 1980. Pleistocene Mammals of North America. Columbia University Press, New York, 442 p.

Leidy, J. 1859. Descriptions of vertebrate fossils. Pp. 99–122 *in* F. S. Holmes, ed. Post-Pleiocene Fossils of South Carolina. Russell and Jones, Charleston.

Leidy, J. 1889. Description of vertebrate remains from Peace Creek, Florida. Transactions of the Wagner Free Institute of Science of Philadelphia 2:19–31.

Louys, W., D. Curnoe, & H. W. Tong. 2007. Characteristics of Pleistocene megafauna extinctions in Southeast Asia. Palaeogeography, Palaeoclimatology, Palaeoecology 243:152–173.

Lundelius, E. L. 1972. Fossil vertebrates from the late Pleistocene Ingleside Fauna, San Patricio County, Texas. Report of Investigation, Bureau of Economic Geology, University of Texas, No. 77, 74 pp.

Lundelius, E. L., & B. H. Slaughter. 1976. Notes on American Pleistocene tapirs. Pp. 226–243 *in* C. S. Churcher, ed. Athlon: Essays in Paleobiology in Honour of Loris Shano Russell. Royal Ontario Museum, Toronto.

MacFadden, B. J., & R. C. Hulbert. 2009. Calibration of mammoth (*Mammuthus*) dispersal into North America using rare earth elements of Plio-Pleistocene mammals from Florida. Quaternary Research 71(1):41–48.

Matthew, W. D., & W. Granger. 1923. New fossil mammals from the Pliocene of Szechuan, China. Bulletin of the American Museum of Natural History 48:563-598.

McKenna, M. C., & S. K. Bell. 1997. Classification of Mammals above the Species Level. Columbia University Press, New York, 631 p.

Merriam, J. C. 1913. Tapir remains from late Cenozoic beds of the Pacific coast region. University of California Publications, Bulletin of the Department of Geology 7:169–175.

Meylan, P. A. 1982. The squamate reptiles of the Inglis 1A fauna (Irvingtonian: Citrus County, Florida). Bulletin of the Florida State Museum 27(1):1–85.

Morgan, G. S. 2005. The Great American Biotic Interchange in Florida. Bulletin of the Florida Museum of Natural History 45(4):271–311.

Morgan, G. S. 2008. Vertebrate fauna and geochronology of the Great American Biotic Interchange in North America. Pp. 93–140 *in* S. G. Lucas, G. S. Morgan, J. A. Spielmann, & D. R. Prothero, eds. Neogene Mammals. New Mexico Museum of Natural History & Science Bulletin 44.

Morgan, G. S., & S. D. Emslie. 2010. Tropical and western influences in vertebrate faunas from the Pliocene and Pleistocene of Florida. Quaternary International 217:143–158.

Morgan, G. S., & R. C. Hulbert Jr. 1995. Overview

of the geology and vertebrate biochronology of the Leisey Shell Pit local fauna, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37:1–92.

Morgan, G. S., & J. A. White. 1995. Small mammals (Insectivora, Lagomorpha, and Rodentia) from the early Pleistocene (early Irvingtonian) Leisey Shell Pit local fauna, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37:397–462.

Norman, J. E., & M. V. Ashley. 2000. Phylogenetics of Perissodactyla and tests of the molecular clock. Journal of Molecular Evolution 50(1):11–21.

Olsen, S. J. 1960. Age and faunal relationships of *Tapiravus* remains from Florida. Journal of Paleontology 34:164–167.

Owen, R. 1848. Description of teeth and portions of jaws of two extinct anthracotheroid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight: with an attempt to develope Cuvier's idea of the classification of pachyderms by the number of their toes. Quarterly Journal of the Geological Society of London 4:103–141.

Petuch, E. J. 1982. Notes on the molluscan paleoecology of the Pinecrest Beds at Sarasota, Florida, with the description of *Pyruella*, a stratigraphically important new genus (Gastropoda, Melongenidae). Proceedings of the Academy of Natural Sciences, Philadelphia 134:12–30.

Ray, C. E. 1964. *Tapirus copei* in the Pleistocene of Florida. Quarterly Journal of the Florida Academy of Sciences 27:59–66.

Ray, C. E. & A. E. Sanders. 1984. Pleistocene tapirs in the eastern United States. Pp. 283–315 *in* H. H. Genoways & M. R. Dawson, eds. Contributions in Quaternary Vertebrate Paleontology: a Volume in Memorial to John E. Guilday. Carnegie Museum of Natural History, Pittsburgh, Special Publication 8.

Ray, C. E., E. Anderson, & S. D. Webb. 1981. The

Blancan carnivore *Trigonictis* (Mammalia: Mustelidae) in the eastern United States. Brimleyana 5:1–36.

Rincón, A. D., G. E. Parra, F. J. Prevosti, M. T. Alberdi, and C. J. Bell. 2009. A preliminary assessment of the mammalian fauna from the Pliocene-Pleistocene el Breal de Orocual locality, Monagas State, Venezuela. Pp. 593–620 *in* L. B. Albright III, ed. Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne. Museum of Northern Arizona Bulletin 65.

Robertson, J. S. 1976. Latest Pliocene mammals from Haile XV A, Alachua County, Florida. Bulletin of the Florida State Museum 20:111–186.

Roulin, X. 1829. Memoir pour servir a l'histoire du tapir; et description dune espece nouvelle appartenant aux hautes regions de la Cordillere des Andes. Annales des Sciences Naturelle Zoologie Paris 17:26–55.

Ruez, D. R. 2001. Early Irvingtonian (latest Pliocene) rodents from Inglis 1C, Citrus County, Florida. Journal of Vertebrate Paleontology 21(1):153–171.

Rustioni, M. 1992. On Pliocene tapirs from France and Italy. Bollettino della Societá Paleontologica Italiana 31(3):269-294.

Sanders, A. E. 2002. Additions to the Pleistocene mammal faunas of South Carolina, North Carolina, and Georgia. Transactions of the American Philosophical Society 92(5):1–152.

Schultz, C. B., L. D. Martin, & R. G. Corner. 1975. Middle and late Cenozoic tapirs from Nebraska. Bulletin of the Nebraska State Museum 10:1–21.

Sellards, E. H. 1918. The skull of a Pleistocene tapir including description of a new species and a note on the associated fauna and flora. Annual Report, Florida Geological Survey 10:57–70.

Shunk, A. J., S. Driese, J. Farlow, R. Hulbert, & M. Whitelaw. 2006. High-resolution stratigraphy and sedimentology of late Miocene-Pliocene paleolacustrine strata deposited in paleosinkhole settings, Eastern U.S.

Abstracts with Programs, Geological Society of America 38(7):85.

Simpson, G. G. 1929. Pleistocene mammalian fauna of the Seminole Field, Pinellas County, Florida. Bulletin of the American Museum of Natural History 56:561–599.

Simpson, G. G. 1945. Notes on Pleistocene and Recent tapirs. Bulletin of the American Museum of Natural History 86(2):33–82.

Smith, K. S., & R. L. Cifelli. 2000. A synopsis of the Pleistocene vertebrates of Oklahoma. Oklahoma Geological Survey Bulletin, No. 147, 36 pp.

Tedford, R. T., X.-M. Wang, & B. E. Taylor. 2009. Phylogenetic systematics of the North American fossil Caninae (Carnivora: Canidae). Bulletin of the American Museum of Natural History 325:1–218.

Tong, H. W. 2005. Dental characters of Quaternary tapirs in China, their significance in classification and phylogenetic assessment. Geobios 38(1):139–150.

Tong, H. W., J. Y. Liu, & L. G. Han. 2002. On fossil remains of early Pleistocene tapir (Perissodactyla, Mammalia) from Fanchang, Anhui. Chinese Science Bulletin 47(7):586–590.

Webb, S. D. 1974. Chronology of Florida Pleistocene mammals. Pp. 5–31 in S. D. Webb, ed. Pleistocene Mammals of Florida. University of Florida Press, Gainesville.

Webb, S. D., R. C. Hulbert Jr., G. S. Morgan, & H. F. Evans. 2008. Terrestrial mammals of the Palmetto Fauna (early Pliocene, latest Hemphillian) from the Central Florida Phosphate District. Pp. 293–312 in X.-M. Wang & L. G. Barnes, eds. Geology and Vertebrate Paleontology of Western and Southern North America, Contributions in Honor of David P. Whistler. Natural History Museum of Los Angeles County Science Series, Number 41.

Webb, S. D., & K. T. Wilkins. 1984. Historical biogeography of Florida Pleistocene mammals. Pp. 370-383 in H. H. Genoways & M. R. Dawson, eds. Contributions in

Quaternary Vertebrate Paleontology: a Volume in Memorial to John E. Guilday. Carnegie Museum of Natural History, Pittsburgh, Special Publication 8.

Witmer, L. M., S. D. Sampson, & N. Solounias. 1999. The proboscis of tapirs (Mammalia: Perissodactyla): a case study in novel narial anatomy. Journal of Zoology 249:249–267.

Wu, X. Z., W. Liu, X. Gao, & G. M. Yin. 2006. Huanglong Cave, a new late Pleistocene hominid site in Hubei Province, China. Chinese Science Bulletin 51(20):2493–2499.

APPENDIX 1

Information on Florida Blancan fossil localities that have produced *Tapirus*. Only approximate location data provided for sites that are still being collected, to protect them from vandalism. Most lack formal stratigraphic names for their sediments, as they are either isolated sinkhole or alluvial deposits.

SITES WITH *TAPIRUS LUNDELIUSI* SP. NOV.

1. Haile 7C (type locality). UF locality AL109, 6 km northeast of Newberry, Alachua County, Florida (Morgan & Hulbert 1995:68–69; Emslie 1998). SE¼ of section 24, T. 9 S., R. 17 E. on USGS 7.5′ Newberry Quadrangle; 29.69° N, 82.56° W. Middle late Blancan, ca. 1.9–2.2 Ma.

2. Haile 7G. UF locality AL125, 6 km northeast of Newberry, Alachua County, Florida. SE¼ of section 24, T. 9 S., R. 17 E. on USGS 7.5′ Newberry Quadrangle; 29.69° N, 82.56° W. Middle late Blancan, ca. 1.9–2.2 Ma. Located about 75 m east of Haile 7G. The lacustrine sediments of the two localities are possibly continuous, but they are currently separated by a covered area.

3. Withlacoochee River 1A. UF locality MR060, in channel of Withlacoochee River about 16 km southeast of Dunnellon, Marion County, Florida. SE¼ of section 29, T. 17 S., R. 20 E. on USGS 7.5′ Stokes Ferry Quadrangle; 29.0° N, 82.3° W. Middle late Blancan, ca. 1.9–2.2 Ma. In situ specimens are collected from sandy gray clay that fills pockets in the Eocene limestone bedrock.

4. Waccasassa River 9A. UF locality LV040, in

bank of Waccasassa River about 8 km southeast of town of Otter Creek, Levy County, Florida. SW¼ of section 8, T. 14 S., R. 16 E. on USGS 7.5′ Bronson SW Quadrangle; 29.3° N, 82.7° W. Caloosahatchee Formation (or lateral equivalent), middle late to latest Blancan, ca. 1.6–2.2 Ma. Vertebrate fossils collected interbedded with species of mollusks found in the Caloosahatchee Formation in southern Florida.

5. Inglis 1A. UF locality CI001, 2.5 km southwest of Inglis, Citrus County, Florida. SW¼ of NE¼ of section 9, T. 17 S., R. 16 E. on USGS 7.5′ Yankeetown Quadrangle; 29.0° N, 82.68° W. Latest Blancan, ca. 1.6–1.9 Ma.

6. Inglis 1B. UF locality CI013, 2.5 km southwest of Inglis, Citrus County, Florida. SW¼ of NE¼ of section 9, T. 17 S., R. 16 E. on USGS 7.5′ Yankeetown Quadrangle; 29.0° N, 82.68° W. Latest Blancan, ca. 1.6–1.9 Ma.

7. Inglis 1D. UF locality CI020, 2 km south-southwest of Inglis, Citrus County, Florida. NW¼ of SE¼ of section 10, T. 17 S., R. 16 E. on USGS 7.5′ Yankeetown Quadrangle; 29.01° N, 82.67° W. Latest Blancan, ca. 1.6–1.9 Ma.

8-10. Santa Fe River 8, 8A, and 8C. UF localities CO006B, CO007B, and CO009B, Columbia County, Florida. NW¼ of SE¼ of section 18, T. 7 S., R. 16 E. on USGS 7.5′ Fort White Quadrangle; 29.88° N, 82.67° W. Middle late to latest Blancan, ca. 1.6–2.2 Ma.

11. Walden Pit 2. UF locality SA050, 8 km east-northeast of Fruitville, Sarasota County, Florida. NE¼ of section 23, T. 36 S., R. 19 E. on USGS 7.5′ Old Myakka Quadrangle; 27.35° N, 82.37° W. Pinecrest Formation; early late Blancan, ca. 2.3–2.6 Ma.

SITES WITH *TAPIRUS HAYSII*

12–13. Santa Fe River 1 and 1B. UF localities CO003B and CO038B, Columbia County, Florida. NE¼ of NW¼ of section 34, T. 7 S., R. 16 E. on USGS 7.5′ High Springs SW Quadrangle; 29.84° N, 82.70° W. Early late Blancan, ca. 2.3–2.6 Ma. (UF 177841, 177842, 213920, and 224631).

14. Kissimmee River 2. UF locality OB002, 18 km west of Okeechobee, Okeechobee County, Florida. Section 13, T. 37 S., R. 33 E. on USGS 7.5′ Fort Basinger Quadrangle; 27.25° N, 80.97° W. Pinecrest Formation; early late Blancan, ca. 2.3–2.6 Ma. (UF 51250).

15. Kissimmee River 6. UF locality OB006, 18 km west of Okeechobee, Okeechobee County, Florida. Section 21, T. 36 S., R. 33 E. on USGS 7.5′ Fort Basinger Quadrangle; 27.33° N, 81.03° W. Pinecrest Formation; early late Blancan, ca. 2.3–2.6 Ma. (UF 52601). This stretch of the river also produced UF 51249, a p2 of *Tapirus* sp. indeterminate.

16. Inglis 1C. UF locality CI019, 2 km south-southwest of Inglis, Citrus County, Florida. NW¼ of SE¼ of section 10, T. 17 S., R. 16 E. on USGS 7.5′ Yankeetown Quadrangle; 29.01° N, 82.67° W. Latest Blancan, ca. 1.6–1.9 Ma. (UF 177844).

17. De Soto Shell Pit 5. UF locality DE018, 17 km south of Arcadia, De Soto County, Florida. NW¼ of SE¼ of section 33, T. 39 S., R. 25 E. on USGS 7.5′ Arcadia SE Quadrangle; 27.04° N, 81.82° W. Caloosahatchee Formation, latest Blancan, ca. 1.6–1.9 Ma. (UF 223920, 232075). Neither specimen was collected in situ, and these two specimens could be Irvingtonian rather than Blancan, as this mine also contained sediments from the early Irvingtonian Bermont Formation.

18. Devil's Elbow 2. UF locality PU005B, submerged locality on St. Johns River near East Palatka, Putnam County, Florida. Section 38, T. 10 S., R. 27 E. on USGS 7.5′ Hastings Quadrangle; 29.65° N, 81.61° W. Nashua Formation, early late Blancan, ca. 2.3–2.6 Ma. (UF 177843).

SITES WITH *TAPIRUS* SPECIES INDETERMINATE

19. Sommers Pit. UF locality SA029, 8 km east-northeast of Fruitville, Sarasota County, Florida. NE¼ of section 23, T. 36 S., R. 19 E. on USGS 7.5′ Old Myakka Quadrangle; 27.34° N, 82.37° W. Pinecrest Formation; early late Blancan, ca. 2.3–2.6 Ma. (UF/TRO 1469).

20. Walden Pit 1. UF locality SA049, 8 km east-northeast of Fruitville, Sarasota County, Florida. NE¼ of section 23, T. 36 S., R. 19 E. on USGS 7.5′ Old Myakka Quadrangle; 27.35° N, 82.37° W.

Pinecrest Formation; early late Blancan, ca. 2.3–2.6 Ma. (UF/TRO 1489).

21. De Soto Shell Pit 2. UF locality DE009, 16 km south of Arcadia, De Soto County, Florida. NW¼ of SW¼ of section 27, T. 39 S., R. 25 E. on USGS 7.5′ Arcadia SE Quadrangle; 27.05° N, 81.81° W. Caloosahatchee Formation, latest Blancan, ca. 1.6–1.9 Ma. (UF 177836).

22. Lehigh Acres Pit. UF locality LE003, 5.2 km south of Alva, Lee County, Florida. NE¼ of section 10, T. 44 S., R. 27 E. on USGS 7.5′ Alva Quadrangle; 26.67° N, 81.60° W. Caloosahatchee Formation, late Blancan, ca. 2–2.6 Ma. (UF 162666).

23. Haile 15A. UF locality AL032, 4.7 km northeast of Newberry, Alachua County, Florida. NW¼ of SW¼ of section 24, T. 9 S., R. 17 E. on USGS 7.5′ Newberry Quadrangle; 29.67° N, 82.57° W. Early late Blancan, ca. 2.3–2.6 Ma. (UF 17468).

24. US 19 Bridge Site. UF locality GI008, north of bridge over Suwannee River, Gilchrist County, Florida. SW¼ of SW¼ of section 20, T. 10 S., R. 14 E. on USGS 7.5′ Fanning Springs Quadrangle; 29.6° N, 82.9° W. Early late Blancan, ca. 2.3–2.6 Ma. (UF 247180, 248788, 248789, 255357, 255358). This previously unpublished local fauna also includes *Trachemys platymarginata*, *Pseudemys* sp., *Sternotherus* sp., *Macroclemys* sp., *Apalone ferox*, *Hesperotestudo* sp., *Alligator* sp., *Dasypus bellus*, the small morph of *Holmesina floridanus*, *Paramylodon garbanii*, *Nannippus peninsulatus*, *Odocoileus virginianus*, and *Capromeryx arizonensis*.

25. Hubbard Pit. UF locality OR003, abandoned clay and sand quarry, Orange County, Florida. SW¼ of NW¼ of section 6, T. 22 S., R. 29 E. on USGS 7.5′ Orlando West Quadrangle; 28.6° N, 81.5° W. Late early or early late Blancan, ca. 2.9–2.5 Ma. (UF 249089). This quarry produced two fossiliferous horizons with abundant marine invertebrates and vertebrates. The younger bed, which also produced a few terrestrial vertebrate specimens, is of Blancan age based on the presence of *Nannippus peninsulatus* and molluscan species characteristic of bed 11 from Macasphalt Shell Pit near Sarasota (R. Portell, pers. comm.). In addition

to *N. peninsulatus* and *Tapirus*, fossils of *Equus* sp. and *Dasypus bellus* were also recovered from this locality.

APPENDIX 2

List of characters and character states used in the phylogenetic analyses. They are adapted from a larger character set originally developed by Hulbert and Wallace (2005), with phylogenetically uninformative characters for the group of species under study here deleted. Original numbering scheme of characters is retained to maintain consistency between publications.

3. temporal crests meet to form sagittal crest: (0) at or posterior to frontal-parietal suture; (1) anterior to frontal-parietal suture.

4. dorsal table of frontal. (0) relatively narrow or small; (1) relatively broad.

6. nasal-frontal lateral profile: (0) nasals and frontal on same plane; (1) nasals notably stepped down from frontals.

7. size of interparietal bone: (0) large; (1) small.

8. shape of interparietal bone: (0) typically polygonal (hexagonal or diamond shaped); (1) typically triangular.

9. interparietal fusion with occipital: (0) occurs early in ontogeny (before loss of DP4); (1) occurs late in ontogeny (after eruption of P4).

10. nasal length: (0) long, longer than width of combined nasals; (1) short, shorter than width of combined nasals.

14. fossa for meatal diverticulum on nasal: (0) shallow and without distinct margins; (1) deep and with distinct margins.

15. fossa for meatal diverticulum on posterior dorsal surface of nasal: (0) not extensive, does not near midline; (1) very extensive, approaches midline.

16. development of fossa for meatal diverticulum on dorsal table of frontal: (0) very limited; (1) broad exposure with distinct posterior margin.

18. posterodorsal process of maxilla widely

exposed dorsal above the orbit, forming base of trough for meatal diverticulum: (0) yes; (1) no.

20. orientation of lambdoidal crests in adults: (0) mostly posterior with little or no outward flair; (1) posterolateral orientation, with notable lateral flair.

22. location of infraorbital foramen relative to the cheekteeth: (0) dorsal to P4; (1) dorsal to P3 or P2.

25. anteromedial process of maxilla: (0) well exposed in lateral view dorsal to premaxilla; (1) covered by premaxilla, not visible in lateral view or barely so.

26. dorsal maxillary flange: (0) absent; (1) slight; (2) extensive.

27. length of posterior process of premaxilla: (0) long, terminates posterior to P1; (1) terminates dorsal to or just in front of P1; (2) ends about midway over C-P1 diastema; (3) very short, terminates well anterior to midway point of diastema.

28. width of maxillary bar between infraorbital foramen and lacrimal: (0) narrow, usually less than 5 mm; (1) wide, more than 5 mm.

29. shape of lacrimal: (0) narrow, much taller than long; (1) broad, about as long as it is high.

30. facial surface of lacrimal: (0) flat or convex; (1) concave.

31. anterior lacrimal process(es): (0) absent or very weak; (1) present, well developed.

33. posterior process of lacrimal: (0) broad and flat; (1) slender, pointed or knobby.

34. typical number of large lacrimal foramen: (0) two; (1) one.

37. relative diastema length: (0) short (ldl/p2m3L < 0.40); (1) medium (0.40 ≤ ldl/p2m3L < 0.50); (2) long (ldl/p2m3L ≥ 0.50).

38. location of mental foramen: (0) anterior to the p2; (1) directly ventral to the p2.

39. orientation of anterior margin of ascending ramus of mandible in lateral view: (0) projects vertically and posteriorly, not anteriorly (does not overlie the m3); (1) projects anteriorly as well as vertically below the coronoid process, often lies dorsal to m3.

40. depth of horizontal ramus below m3: (0) shallow (m3depth < 18% mandL); (1) moderate (m3depth between 18 and 19% of mandL); (2) deep (m3depth between 19 and 20% of mandL); (3), very deep (m3depth > 20% of mandL).

41. relative crown height of cheek teeth: (0) short, relatively brachydont; (1) taller.

43. P1 with: (0) single, small posterolingual cusp (=hypocone of some) and lingual cingulum, but no cross lophs or other cusps; (1) large posterolingual cusp, sometimes with accessory cusps and often with some development of a transverse loph; (2) large posterolingual cusp with strong, complete transverse loph; (3) no distinct posteriorlingual cusp, only a cingulum.

45. P2 AW/PW ratio: (0) on average, less than or equal to 0.85; (1) on average, greater than 0.85.

47. transverse lophs on P2-P4 and p2-p4: (0) poorly separated; 1; well separated.

48. P2 protoloph: (0) does not reach ectoloph; (1) just reaches to base of ectoloph; (2) merges midway or higher onto ectoloph.

49. P3 protoloph: (0) does not reach ectoloph; (1) just reaches to base of ectoloph; (2) merges midway or higher onto ectoloph.

51. P2 metaloph: (0) does not reach ectoloph; (1) just reaches to base of ectoloph; (2) merges midway or higher onto ectoloph.

55. parastyle development on P3-M3: (0) moderate; (1) strong; (2) very strong.

56. labial cingulum on posterior half of upper cheek teeth: (0) present on half or more of P3-M3; (1) absent or very rare on P3-M3.

67. i1 morphology and size: (0) i1 slightly larger than i2, not procumbent; (1) i1 larger than i2, slightly procumbent; (2) i1 much larger than i2, very procumbent and spatulate.

69. length of p2 relative to p3: (0) short, (p2 L)/(p3 L) less than 1.1; (1) long, this ratio greater than 1.1.

72. relative height of unworn protolophid and hypolophid (or hypoconid/entoconid if no hypolophid) on premolars: (0) protolophid

distinctly taller than hypolophid; (1) the two are approximately equal in height.

73. cristid obliqua on p3: (0) strong, blocks interlophid valley labially; (1) very weak or absent.

APPENDIX 3.

Character state matrix used in phylogenetic analyses. Character numbers in top row correspond to those in Appendix 2. A "?" indicates a unknown or non applicable character state.

	3	4	6	7	8	9	10	14	15	16	18	20	22	25	26	27	28	29	30	31
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
T. hezhengensis	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	?	?	?	?	?
T. johnsoni	0	0	0	0	0	?	0	0	0	0	0	1	0	1	1	1	1	0	0	0
T. webbi	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	1	1	0	0	?
T. polkensis	0	1	0	0	1	1	0	1	1	1	0	1	1	0	1	1	1	0	0	0
T. lundeliusi	1	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	0	0	1	0
T. haysii	0	1	0	0	1	1	1	1	1	1	0	1	1	0	0	2	0	1	1	0
T. veroensis	0	1	0	0	1	1	1	1	1	1	0	1	1	0	0	1	0	1	1	0
T. bairdii	?	1	1	0	1	0	0	1	1	1	1	1	1	0	1	3	0	0	0	0
T. terrestris	1	0	1	1	?	?	0	0	0	0	0	0	1	1	0	2	1	0	0	1
T. pinchaque	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	2	1	0	0	1

	33	34	37	38	39	40	41	43	45	47	48	49	51	55	56	67	69	72	73
Outgroup	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
T. hezhengensis	?	?	?		?	?	0	0	0	1	1	1	1	0	0	?	?	?	?
T. johnsoni	1	0	1	0	0	2	0	1	0	0	1	1	1	0	0	1	0	0	0
T. webbi	1	0	1	1	0	0	1	1	1	1	0	1	1	1	0	2	0	1	0
T. polkensis	0	1	0	1	0	1	1	0	1	1	1	2	1	1	0	2	0	1	0
T. lundeliusi	0	1	0	1	1	3	1	1	1	1	1	2	1	2	1	2	1	1	0
T. haysii	0	1	0	1	1	3	1	2	1	1	1	2	2	2	1	2	1	1	1
T. veroensis	0	0	0	1	1	2	1	1	1	1	1	2	2	2	1	2	1	1	1
T. bairdii	0	?	2	1	0	1	1	0	1	1	1	2	1	1	0	2	0	1	?
T. terrestris	1	0	1	1	0	1	1	1	1	1	1	2	1	1	1	2	0	1	1
T. pinchaque	1	0	1	1	0	0	1	0	1	1	0	1	1	1	0	2	0	1	0

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