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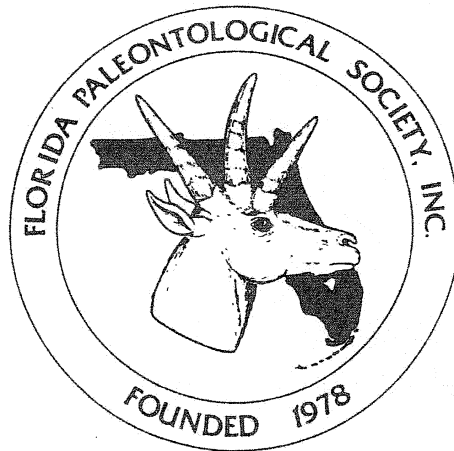
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TAPIRUS VEROENSIS SELLARDS, 1918

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Fossil Species of Florida is a publication of the Florida Paleontological Society, Inc. (FPS), and is intended to provide basic information about common or important fossil species found in the state. For vertebrates, it will supplement information provided in the book *The Fossil Vertebrates of Florida* published by the University Press of Florida for the FPS in 2001. It is anticipated that several issues will be produced each year. The earlier issues in the series will primarily cover vertebrate species, but eventually it will encompass all taxonomic groups and include articles on fossil plants, invertebrate animals, and microfossils. Planned forthcoming issues will be on the rhino *Aphelops mutilus*, and the tortoise *Hesperotestudo incisa*. The editor of *Fossil Species of Florida* is Dr. Richard C. Hulbert, Jr., Vertebrate Paleontology Collections Manager, Florida Museum of Natural History, Dickinson Hall, Gainesville (e-mail: rhulbert@flmnh.ufl.edu). Contact Dr. Hulbert for suggestions as to species we should cover or if you are interested in authoring an article in the series. Do not submit unsolicited manuscripts.

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Tapirs are moderately large herbivores that together with rhinoceroses and horses form the perissodactyl group of mammals. Their barrel-shaped bodies are supported by relatively slender, short limbs. The tapir's most distinguishing facial feature is a short proboscis or trunk. The single living genus *Tapirus* includes four extant species, one in southeastern Asia and three in the subtropical to tropical regions of the Americas. The northernmost of the latter lives in southern Mexico, so tapirs are currently not native to the U.S.

Fossil evidence that tapirs were once wide-spread in the U.S. gradually accumulated through the 1800s (Hatcher, 1896). The first, brief reports in the scientific literature of fossil tapirs from Florida were by Joseph Leidy of Philadelphia, the preeminent vertebrate paleontologist of his day. He noted their presence in Levy County at Mixson's Bone Bed (Leidy, 1885) and from "Peace Creek" (= Peace River of current usage) near Arcadia in De Soto County (Leidy, 1889). By that time, Leidy had long recognized that two different sizes of fossil tapirs were found in the eastern U.S., a larger species he named *Tapirus haysii* in 1859 based on a lower premolar from North Carolina, and a smaller species whose teeth he could not tell from those of the living Brazilian tapir (*Tapirus terrestris*). Leidy assigned the Peace River fossils to the smaller form.

The practice of assigning Pleistocene tapirs from the eastern U.S. to *Tapirus haysii* if they were large and to *Tapirus terrestris* if they were small continued through the early

1900s (e.g., Sellards, 1916). This all changed with the discovery of the first skull of a Pleistocene tapir from North America (Fig. 1) near Vero Beach, Florida in late October 1916. Elias H. Sellards, then the head of the Florida Geological Survey, used this skull and other Vero specimens as the basis for naming a new species, *Tapirus veroensis*. It was "... the first species of North American Pleistocene tapir to be founded on fully satisfactory, confidently diagnostic material and it retains this distinction" (Ray and Sanders, 1984:287). Sellards (1918) suggested that fossil tapirs from the eastern U.S. previously identified as *T. terrestris* probably also belonged to his new species. Subsequently collected fossil tapir skulls from Florida, South Carolina, Tennessee, Missouri, and Texas, although not as complete as the Vero skull, have proven Sellards was almost certainly correct in this assertion.

Although generally rare elsewhere, fossils of tapirs are relatively common at Miocene through Pleistocene fossil sites in Florida. However, they are usually found in fewer numbers than those of ungulate mammals that lived in groups or herds, such as horses, deer, llamas, peccaries, rhinos, or mammoths. The more commonly found specimens are isolated teeth, parts of jaws, and the more durable bones of the skeleton, such as the astragalus and other carpal and tarsal bones, metapodials, phalanges, and distal ends of the tibia and radius. Skulls, mandibles, and associated skeletons are rare, but of much greater scientific importance.

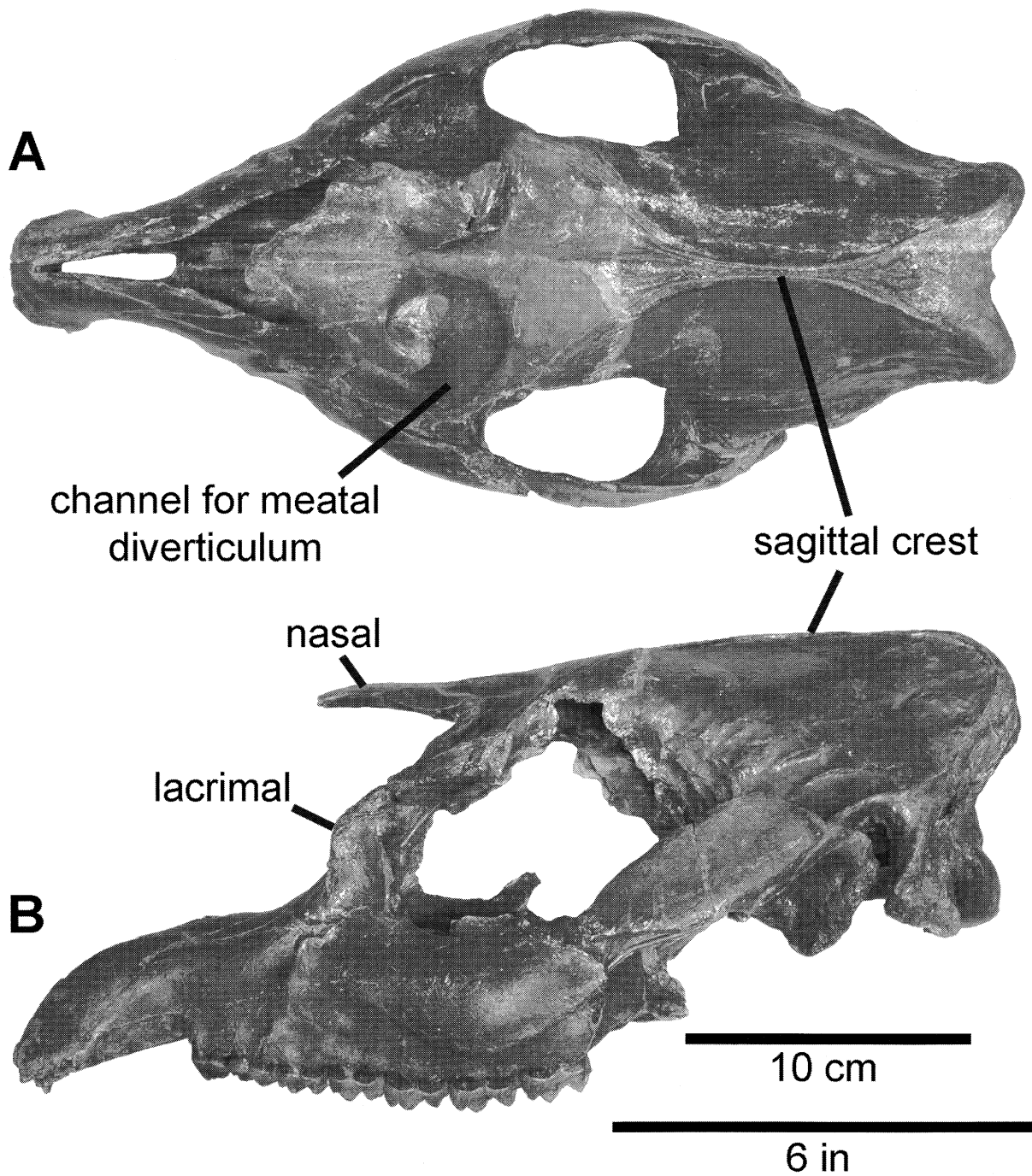


FIGURE 1. A, dorsal, and B, left lateral views of UF/FGS 277, the holotype skull of *Tapirus veroensis*. Collected at the Vero Site, Indian River County, Florida in 1916, it remains the most complete skull ever found of this species. The large, deep channel for the meatal diverticulum on the nasal and frontal bones is characteristic of this species and its close relative *Tapirus haysii*. Similarly, the anatomy of the lacrimal bone and the sagittal crest are also distinctive for this pair of species.

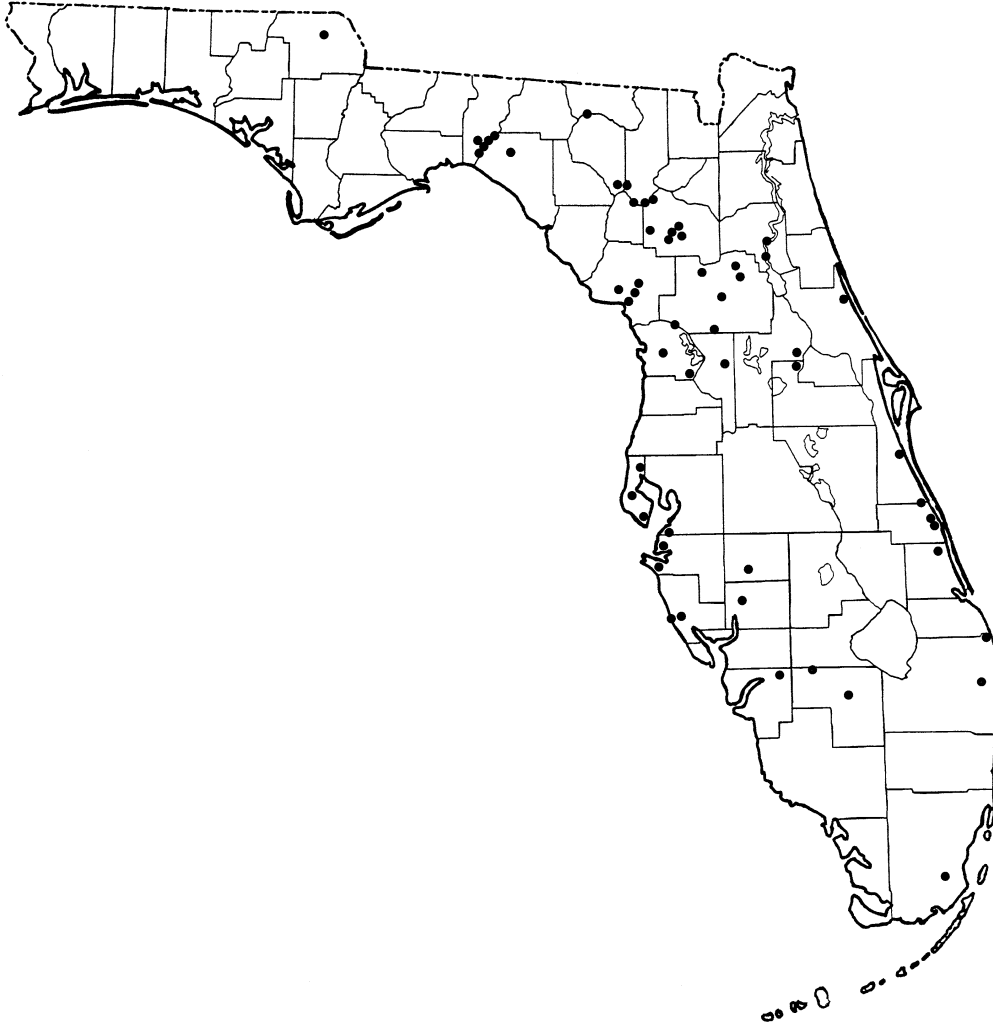


FIGURE 2. Map of Florida showing localities (black circles) where fossils of *Tapirus veroensis* have been found.

**VERTEBRATA
TETRAPODA
MAMMALIA
PERISSODACTYLA
TAPIRIDAE
TAPIRUS VEROENSIS**

Taxonomic History-Sellards (1918) described *Tapirus veroensis* on the basis of fossils from Vero Beach, Florida (late Pleistocene). Simpson (1929) separated *T. veroensis* into two subspecies in Florida, *T. veroensis veroensis* for Atlantic Coast specimens and *T.*

veroensis sellardsi for Gulf Coast specimens. Additional specimens and statistical analysis later convinced Simpson (1945) that this separation was completely unjustified and no one has subsequently used Simpson's (1929) subspecific designations. Relatively large individuals of *T. veroensis* have been erroneously referred to *T. haysii* on numerous occasions, but all modern authorities agree that *T. veroensis* is the valid species name for the common late Pleistocene tapir of the eastern and central U.S. (Lundelius and Slaughter, 1976; Ray and Sanders, 1984; Hulbert, 1995).

Chronologic Range—The geologic age of all definite records of *Tapirus veroensis* (i.e., skulls) is late middle to very late Pleistocene, about 500,000 to 10,000 years ago. Older records can not be conclusively identified until more completely preserved specimens are collected. A few teeth resembling those of *T. veroensis* in both size and shape are known from the middle Pleistocene (McLeod Lime-rock Pit) and latest Pliocene (Inglis 1B) of Florida. However, the vast majority of late Pliocene to early Pleistocene tapirs from Florida belong instead to either *Tapirus haysii* or an undescribed species hereafter referred to as *Tapirus* n.sp.

Geographic Range—*Tapirus veroensis* was widely distributed throughout Florida (Fig. 2). Most records of the species are from the southeastern U.S., but it ranged as far north as New York and Pennsylvania and as far west as Nebraska and Texas (Simpson, 1945; Schultz et al., 1975; Ray and Sanders, 1984).

Key Florida Specimens¹—Vero, Indian River County: UF/FGS 277, skull (holotype). Aucilla River, Taylor County: UF 18947, partial skull; UF 162830, maxilla; UF 14834, 47929, 135772, and 180216, USNM 336258, dentaries. Ichetucknee River, Columbia County: UF 14064, associated partial skull, mandible, and partial postcranial skeleton; UF 11328, maxilla. Branford 1A, Suwannee County: UF 14056, associated juvenile skull and partial postcranial skeleton. Hornsby Springs, Alachua County: UF 885, 886, 888, and 56944, maxillae; UF 3270, juvenile dentary. Arredondo 2A, Alachua County: UF 2560, associated maxilla, mandible, and partial postcranial skeleton. Paynes Prairie, Alachua County: UF 14025, associated maxilla, mandible, and partial postcranial skeleton. Rock Springs, Orange County: UF 18702, UF/FGS 4388, maxillae; UF/FGS 4390, UF 121941, dentaries. Seminole Field, Pinellas County: AMNH

23492, maxilla; AMNH 23493, dentary. Melbourne, Brevard County: USNM 239811, USNM 239813 dentaries. Tri-Britton Site, Hendry County: UF 210878-210880, maxillae; UF 210886-210888, nasals; UF 210890, dentary. Florida City, Dade County: UF 1539, three teeth (southernmost record in the state).

MORPHOLOGY

Skull—The most common cranial remains of *Tapirus veroensis* are the maxilla, sometimes with sutured portions of adjoining skull elements such as the premaxilla, lacrimal, jugal, or palatine. The connection between these relatively sturdy elements and the dorsal skull table and occipital region is thin, weak, and rarely preserved. Unfortunately, many of the scientifically most informative regions of the skull are those most rarely found as fossils. Among the cranial features distinctive of *T. veroensis* are (Fig. 1): lacrimal bone large and deeply concave; channel or groove on the dorsal surface of the nasal and frontal bones to house the meatal diverticulum (terminology of Witmer et al., 1999) extensive and deep; frontal convex and moderately inflated posterior to the meatal diverticular groove; sagittal crest low, narrow, and flat; and interparietal bone large, triangular, and not fused with parietals and supraoccipital until or after the eruption of the M3.

The mandibular symphysis is solidly fused with a deeply concave dorsal surface. A single, large mental foramen is located on the lateral surface of the dentary below the p2 (Fig. 3). The ventral surface of the dentary is slightly bowed or convex in lateral view. Most fossil dentaries are broken just posterior to the last cheek tooth. The few more complete specimens, such as UF 2560, bear deep fossae on both the lateral and medial surfaces of the ascending ramus for attachment of jaw muscles, have a strongly inflected angle, and the ascending ramus projects anteriorly in lateral view such that it partially overhangs the m3.

¹ UF, Florida Museum of Natural History; UF/FGS, Florida Geological Survey; AMNH, American Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution.

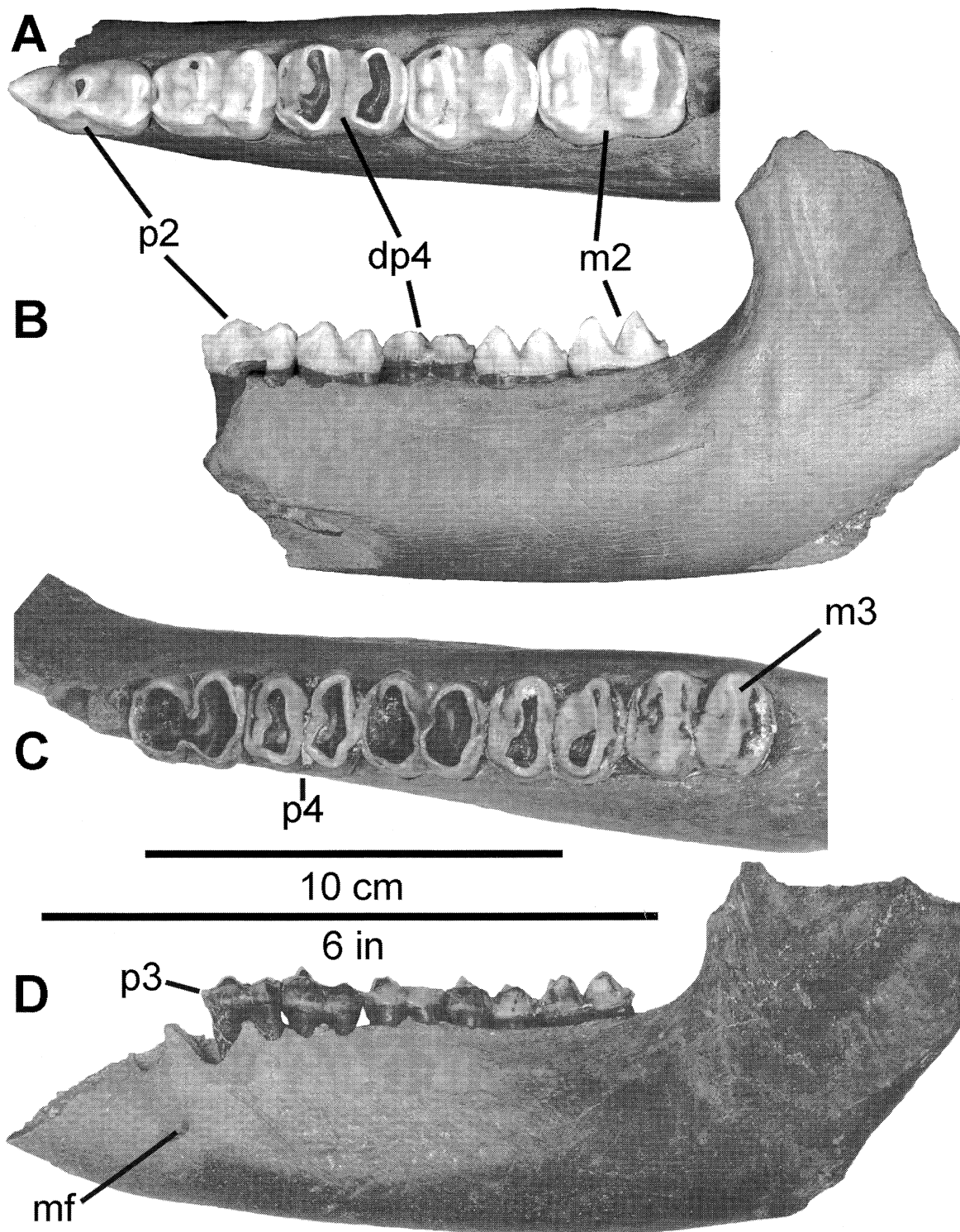


FIGURE 3. Mandibles of *Tapirus veroensis* from Florida. **A**, occlusal, and **B**, lateral views of UF 121941, partial left dentary with p2-p3, dp4, m1-m2; from Rock Springs, Orange County. **C**, occlusal, and **D**, lateral views of UF 210890, partial right dentary with p3 through m3, digitally reversed; from Tri-Britton Site, Hendry County. Note mental foramen (**mf**) below the alveoli for the p2 and that the mandible depth of the subadult UF 121941 and the full adult UF 210890 are essentially the same. Scale bars are for B and D only; A and C are at about natural size (1X).

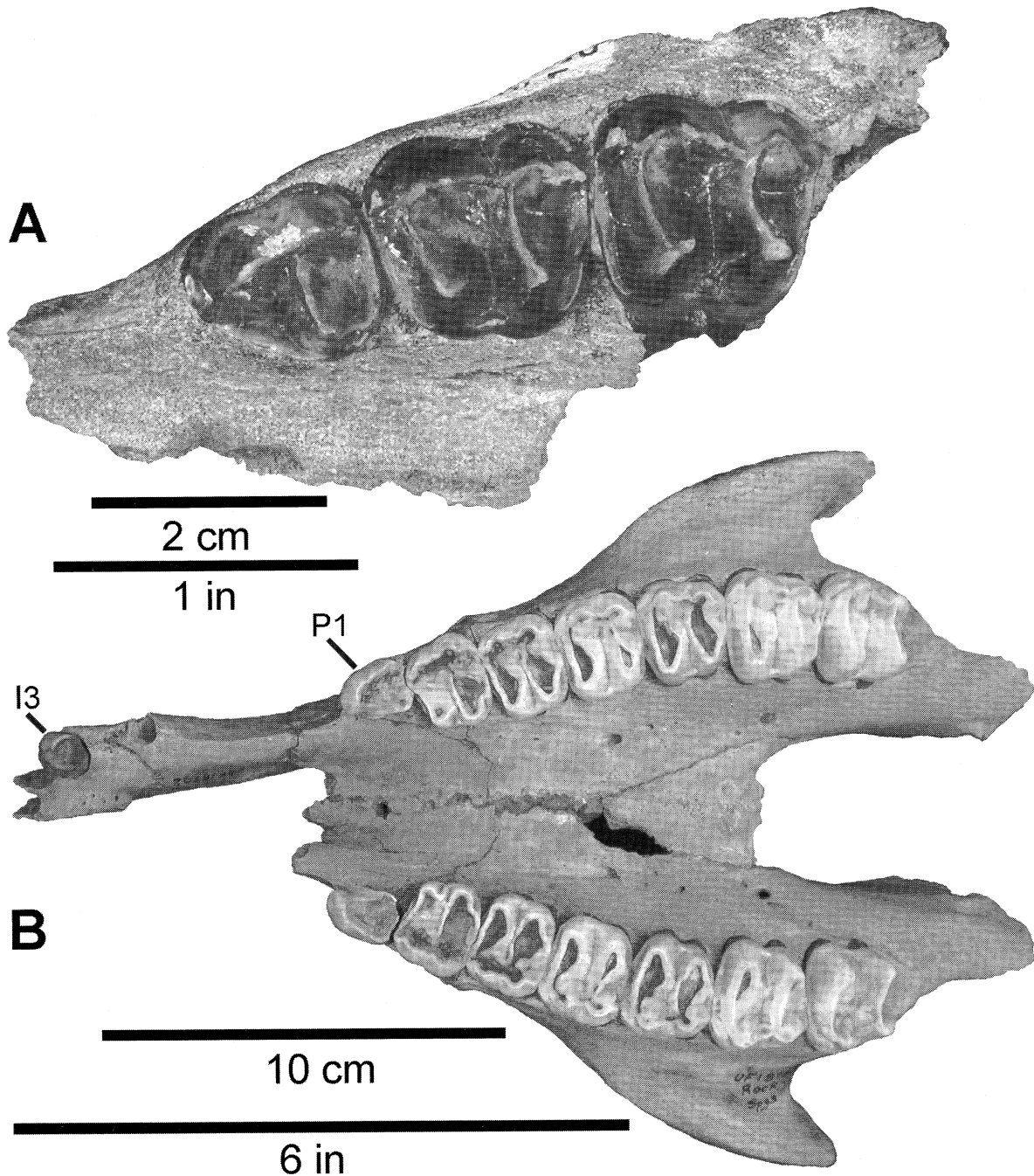


FIGURE 4. Occlusal views of upper dentitions of *Tapirus veroensis* from Florida. A, UF 210879, juvenile right maxilla with DP1-DP3, digitally reversed so that it appears to be from the left side; from Tri-Britton Site, Hendry County. B, UF 18702, palate with right P1-M3 and left I3, P1-M3; from Rock Springs, Orange County.

Dentition² -The dental formula for *Tapirus veroensis* is the same as all other members of the genus: three upper and lower incisors; an upper and lower canine; four upper and three

lower premolars; and three upper and lower molars. The lower third incisor (i3) is greatly reduced in size, but the upper third incisor (I3) is enlarged, conical, and has functionally replaced the canine (it occludes with the lower canine). The true upper canine is one half to a

²Dental terminology follows Hulbert (2001)

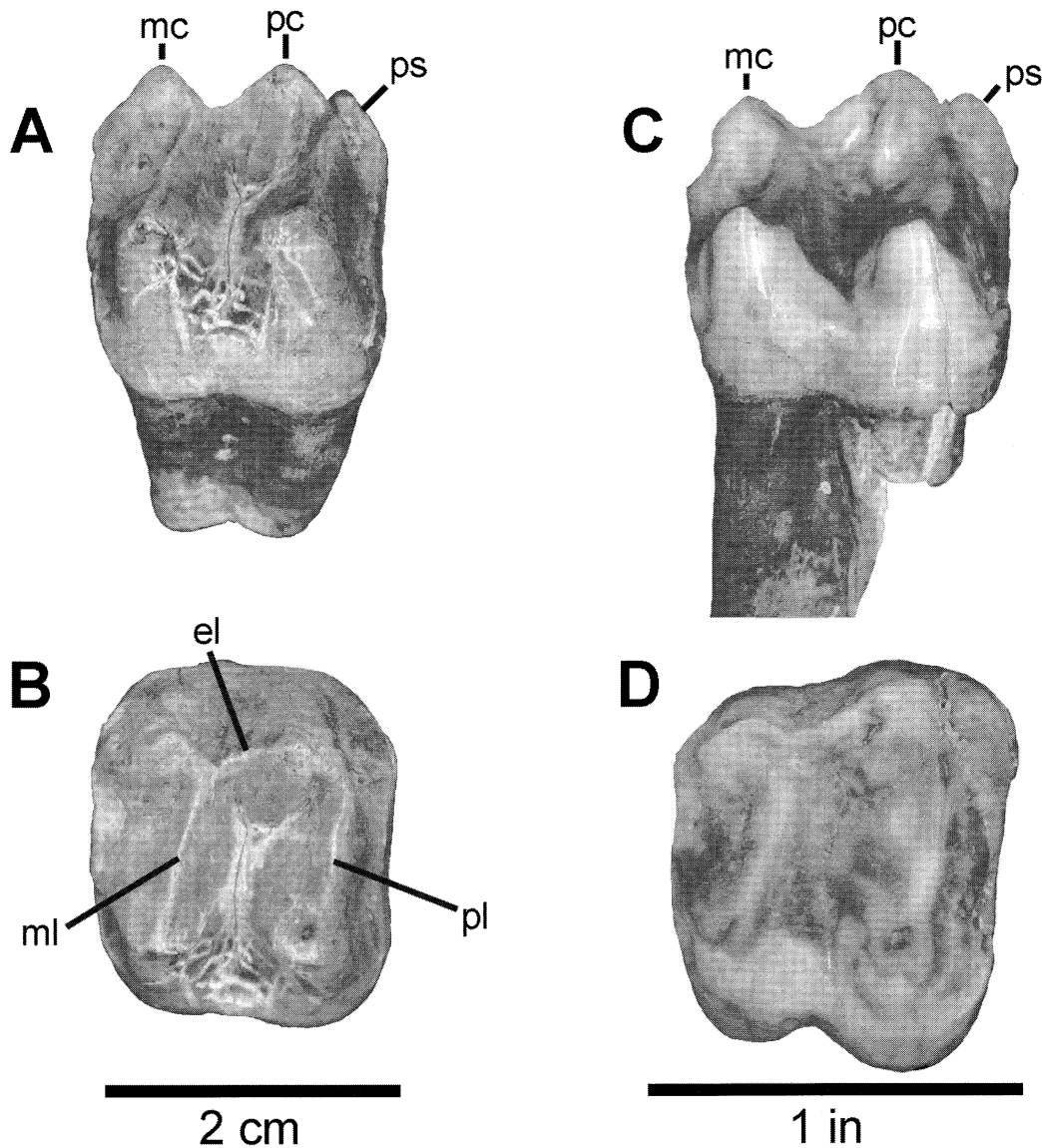


FIGURE 5. Upper teeth of *Tapirus veroensis* from Florida. A, occluso-lingual, and B, occlusal views of UF 162832, right P4; from Rocky Creek, Taylor County. C, occluso-lingual, and D, occlusal views of UF 2560, right M2; from Arredondo 2A, Alachua County. Abbreviations: el, ectoloph; mc, metacone; ml, metaloph; pc, paracone; pl, protoloph; ps, parastyle.

quarter of the size of the I3 and separated from it by a short diastema. The crowns of the first and second incisors are shovel-shaped in the lowers and scoop-like in the uppers.

The low-crowned (brachyodont) cheek teeth are separated from the canines by moderately long diastemata (Figs. 3-5). Tapirs are unusual among mammals, although not

unique, in that the first deciduous premolar (DP1) is replaced by a permanent tooth, the P1. The P1 is triangular in occlusal view, with a sharp labial loph and a single lingual cusp, and has three roots. The remaining upper cheek teeth have four roots (the two lingual roots are typically fused) and crowns bearing two prominent transverse lophs, the protoloph

and metaloph (Fig. 5B). These connect with the labial ectoloph which in unworn and slightly worn teeth can be seen to link three distinct cusps, the parastyle, paracone, and metacone (Fig. 5A, C). In the DP4 and true molars, the paracone is clearly the largest and tallest labial cusp. In the P2, P3, and P4, the metacone is largest or the metacone and paracone are about subequal in size and height. Subtle changes in tooth proportions and shape allow isolated cheek teeth to be identified with some confidence, although not always with certainty. In occlusal view, the P2 is trapezoidal in outline, the width of the crown across the anterior half of the tooth is less than across the posterior half, and the protoloph is relatively low and poorly formed. The P3 and P4 are similar and cannot always be distinguished. The P3 is usually more square while the P4 is more rectangular (wider than long). In the P3, the anterior and posterior halves of the tooth are about equally wide; anterior width of P4 tends to be slightly greater than its posterior width. Upper molars have larger paracones and parastyles than premolars, and their posterior widths are distinctly less than anterior widths (Fig. 5C-D). The first molar (M1) is smaller than the M2 or M3, but similar in shape to the M2 so isolated specimens can be hard to distinguish if intermediate in size. M3s can be distinguished from M2s by their relatively much narrower posterior width; also, the posterior surface of the crown will lack a wear facet that is present on the M2. The DP1 and DP2 are similar in shape to their permanent replacements, but are lower crowned, have thinner enamel, and shallow roots. The DP3 and DP4 are shaped like the molars, but are relatively narrower and lower crowned (Fig. 4A).

Of the six lower cheek teeth, the anteriormost, the second premolar (p2) is most distinctive as its anterior end narrows to a point instead of being squared-off with a well developed cingulum (Fig. 3A). The posterior transverse lophid (the hypolophid) is complete on the p2, but it lacks the anterior protolophid

found on the other lower cheek teeth. Instead, two conjoined central cusps, the protoconid and metaconid, make up the middle of the tooth, and strong, anteroposteriorly directed, labial lophids connect the hypoconid to the protoconid-metaconid complex and the protoconid with the anterior paraconid. These labial lophids are weaker but still evident on the p3 but are essentially lost on the remaining lower cheek teeth. The p3 is also distinctive in that its anterior width is slightly less than its posterior width. The p4 is larger than the p3 and has approximately equal anterior and posterior widths. The molars have narrower posterior widths than anterior widths. As in the uppers, the m1 is essentially a smaller version of the m2, m2 and m3 are similar in size, and the posterior width of the m3 is relatively less than that of the m2. The m2 and m3 can also be differentiated by the posterior deflection of the posterior roots on the m3 and the absence of a wear facet on the posterior surface of the crown in well worn m3s. The latter feature can only be used successfully for teeth showing moderate to heavy wear, as slightly worn m2s will also lack a posterior wear facet. The dp2 is similar in size and form to the p2, but lower crowned; the dp3 and dp4 are shaped like molars. Except for the three-rooted p2 and dp2, the lower cheek teeth have four roots, although the anterior pair fuse together as do the posterior pair.

The tooth eruption sequence in *Tapirus* is fairly normal but the eruption of the fourth premolars and third molars is somewhat delayed. This means that fossils bearing the anterior permanent premolars, the deciduous fourth premolar, and the first two molars are fairly common (e.g., UF 11328, 121941; Fig. 3A) as are those with all of the permanent cheek teeth in wear except for the unerupted third molar (e.g., UF/FGS 4390, UF 14064). Such specimens are fully adult in size.

Postcranial Skeleton-Examples of *Tapirus veroensis* postcrania are shown in Figures 6-9. Each digit, four on the front foot and three on

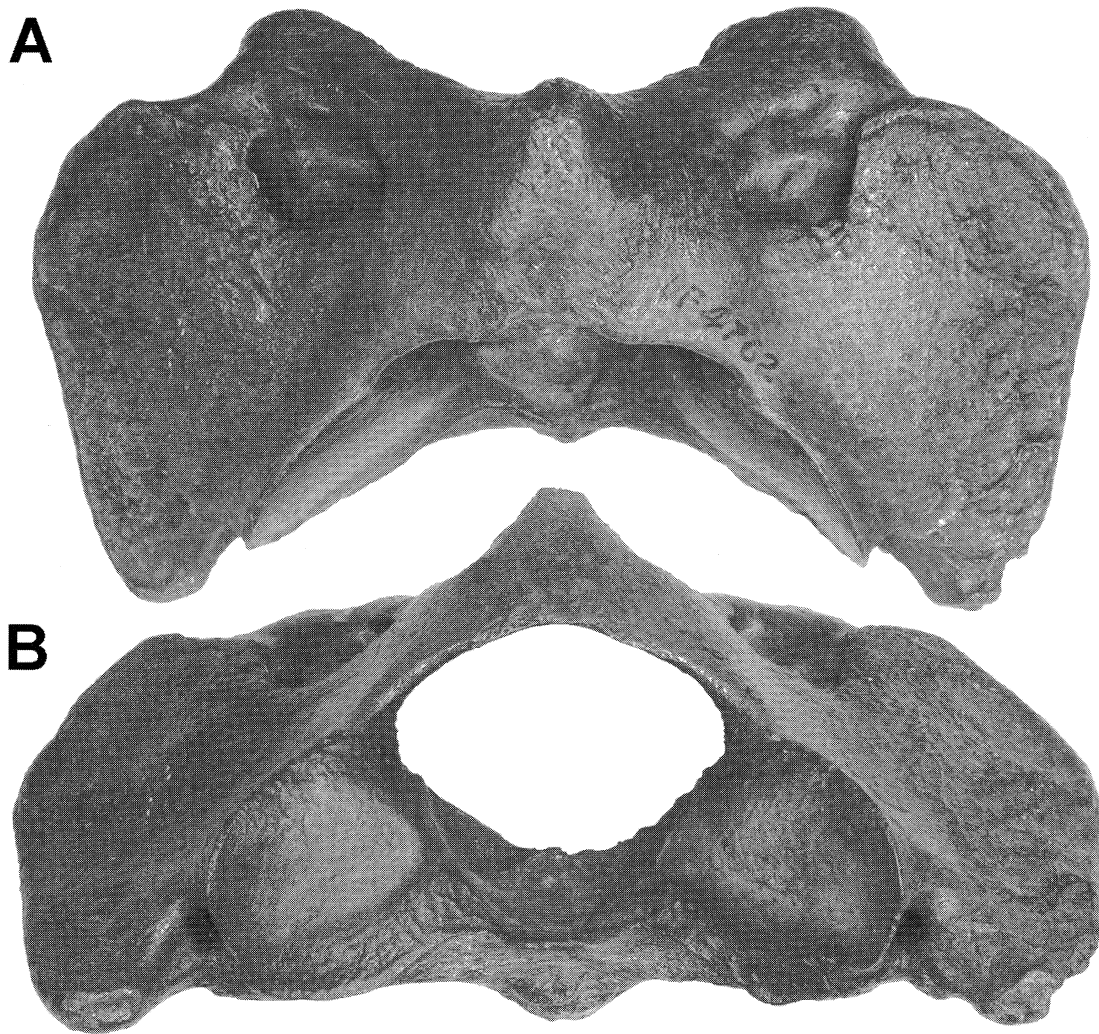


FIGURE 6. **A**, dorsal, and **B**, posterior views of UF 4762, atlas (first cervical) vertebra of *Tapirus veroensis* from Bradenton 51st Street Site, Manatee County, Florida. About natural size (1X).

the hind, bears three phalanges, including the terminal phalanx that forms the core of the hoof. The lateralmost digit of the front foot, homologous with the fifth digit in five-toed mammals, is reduced in size compared to the others and did not bear weight except when the animal walked or ran over a soft substrate. The distal ulna is fused with the radius in adults, but the fibula normally remains separate from the tibia. The lateral side of the femur bears a large third trochanter for muscle attachment (Fig. 8C), a characteristic of perissodactyls. The astragalus (Fig. 9A) also re-

sembles those of other perissodactyls, such as the horse *Equus*, but compared to the latter, the dorsal ridges for articulation with the tibia are shorter and the intervening valley is shallower.

KEYS TO SPECIFIC IDENTIFICATION

Identification to the species level of fossils of *Tapirus* from Florida depends on which element(s) are represented, their completeness, and their geologic context. *Tapirus* lived nearly continuously in Florida between the late Miocene and the end of the Pleis-

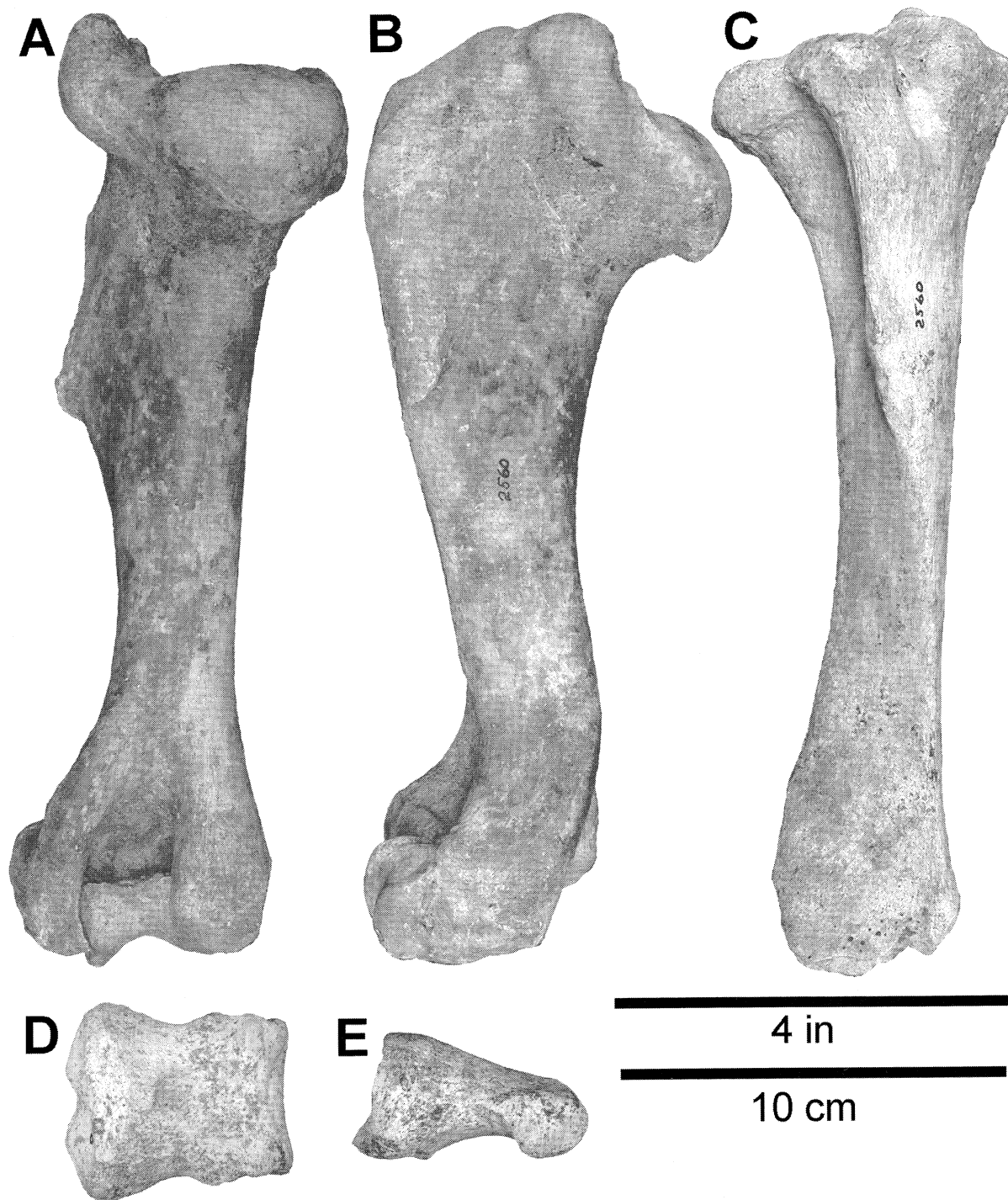


FIGURE 7. Limb bones of *Tapirus veroensis* from Florida. **A**, posterior, and **B**, lateral views of left humerus of UF 2560. **C**, anterior view of UF right tibia of 2560. UF 2560 is a partial skeleton collected at Arredondo 2A, Alachua County. **D**, anterior, and **E**, lateral views of UF 3576, proximal phalanx of digit 3; from Ray House Quarry, Alachua County. Scale bars are for A-C only; D and E are at natural size (1X).

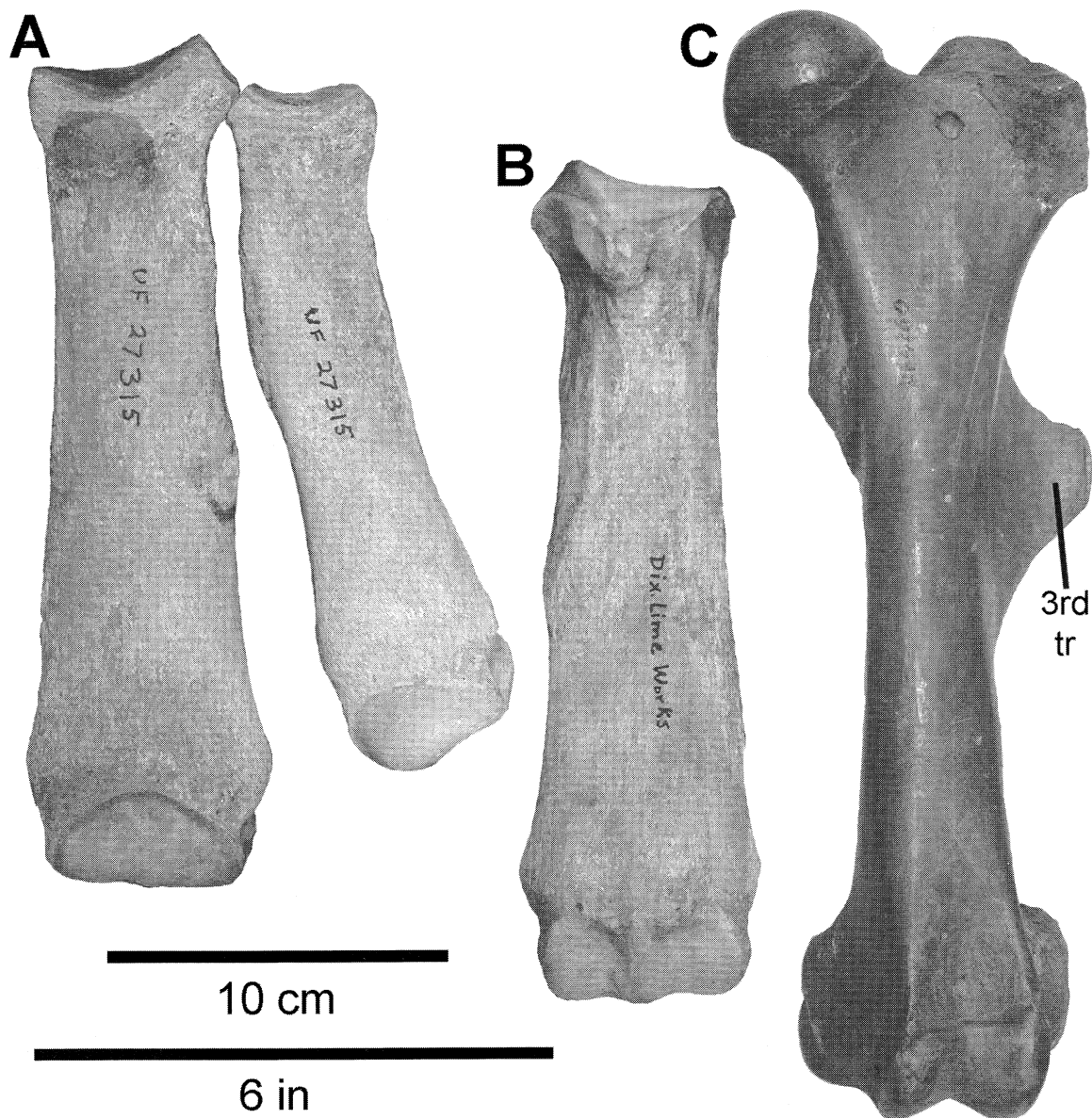


FIGURE 8. Limb bones of *Tapirus veroensis* from Florida. **A**, anterior view of UF 27315, left metacarpals 3 and 4; from Coleman 2A, Sumter County. **B**, posterior view of left metacarpal 3 of UF 27315. **C**, anterior view of UF 4760, left femur from Bradenton 51st Street Site, Manatee County. Note large third trochanter (**3rd tr**). Scale bars are for C only; A and B are at natural size (1X).

tocene, an interval of about 9 million years, and a minimum of five species are known (Hulbert, 2001). All evidence to date suggests that *Tapirus veroensis* was the only species present in Florida between 500,000 to 10,000 years ago (late middle to late Pleistocene). Thus, even relatively incomplete specimens from this interval are *T. veroensis*. Such speci-

mens are usually found associated with *Holmesina septentrionalis*, *Glyptotherium floridanum*, *Megalonyx jeffersoni*, *Equus*, *Bison*, *Mammuthus columbi*, *Tremartus floridanus*, *Panthera onca*, and *Canis dirus*.

In contexts where the geologic age of the specimen is uncertain, as is often the case with specimens from Florida's rivers, or is known

to be older than 500,000 years old, then specific identification of even relatively complete specimens is not always possible. *Tapirus haysii* was the common early Pleistocene tapir in Florida (Hulbert, 1995) and was also present in the late Pliocene. Its cranial features are similar to those of *Tapirus veroensis*. On average, the teeth of *T. veroensis* are 10 to 20 percent smaller than those of *T. haysii*, however larger individuals of the former overlap in size with smaller specimens of *T. haysii*. Also, the first molars of *T. haysii* are about the same size as second molars of *T. veroensis*, making isolated molars in this size range impossible to identify to species. Other than size, a few characters are helpful in distinguishing *T. veroensis* from *T. haysii*. The P1 of *T. haysii* is relatively wider than that of *T. veroensis* and usually has a transverse loph extending from the lingual cusp towards the ectoloph (absent or weaker in *T. veroensis*). The difference in anterior and posterior widths across the P2 is usually less in *T. haysii*, making the tooth squarer and less trapezoidal. The size difference between the postcranial elements of *T. veroensis* and *T. haysii* is apparently less than those between the dentition and skull, but more specimens of both species are needed to confirm this trend.

The common late Pliocene tapir in Florida is *Tapirus* n.sp. A number of important fossil collecting sites in the state, such as the Santa Fe and St. Johns rivers, produce mixed assemblages of late Pliocene and late Pleistocene specimens, resulting in possible commingling of *Tapirus veroensis* and *Tapirus* n.sp. The size difference is slightly less than that between *T. veroensis* and *Tapirus haysii*, except in this case *T. veroensis* is the larger of the two species. A few dental characters separate the two. The protoloph and metaloph on the P2 and the hypolophid on the p2 are weaker in *Tapirus* n.sp., and the anterior width of the p4 is less than the posterior width (compared to about equal in *T. veroensis*). Skulls show significant differences in the lacrimal (narrow with one posterior foramen in

Tapirus n.sp.; broad with two posterior foramina in *T. veroensis*); width of the nasal aperture (wider in *T. veroensis*); height of sagittal crest (slightly taller in *Tapirus* n.sp.); and timing of fusion of the interparietal to the parietals and supraoccipital (before full eruption of M2 in *Tapirus* n.sp.; until eruption of M3 in *T. veroensis*). Postcrania of *Tapirus* n.sp. average much smaller than those of *T. veroensis*.

PALEOECOLOGY

Very little scientific investigation has been done on the paleoecology of fossil tapirs, primarily because of their rarity. All four modern species of *Tapirus* have similar diets, life histories, and social behavior, and these have been assumed to apply to fossil members of the genus. The low-crowned teeth of tapirs and their diet of leaves, twigs, fruit, nuts, and aquatic vegetation fits the classic association of browsing diets with brachyodont teeth and grazing diets with hypsodont teeth.

For fossils 7 million years old and younger, this correspondence can be directly tested using stable carbon isotopes in tooth enamel. Different chemical pathways during photosynthesis cause grasses and some related plants to have a different proportions of carbon-12 and carbon-13 than other plants. This proportional difference is transferred to the tissues of animals that eat the plants, including their tooth enamel. Enamel is analyzed because it usually does not change chemically during the fossilization process, unlike bone. The proportion of carbon isotopes in the enamel of a tooth of *Tapirus veroensis* from the Ichetucknee River resembles that found in modern browsers, with no significant amounts of grass in its diet (MacFadden and Cerling, 1996). This was also true of older fossils of *Tapirus*.

EXTINCTION

Tapirus veroensis survived until the latest Pleistocene, about 11 thousand years ago. Among its youngest records in the state are

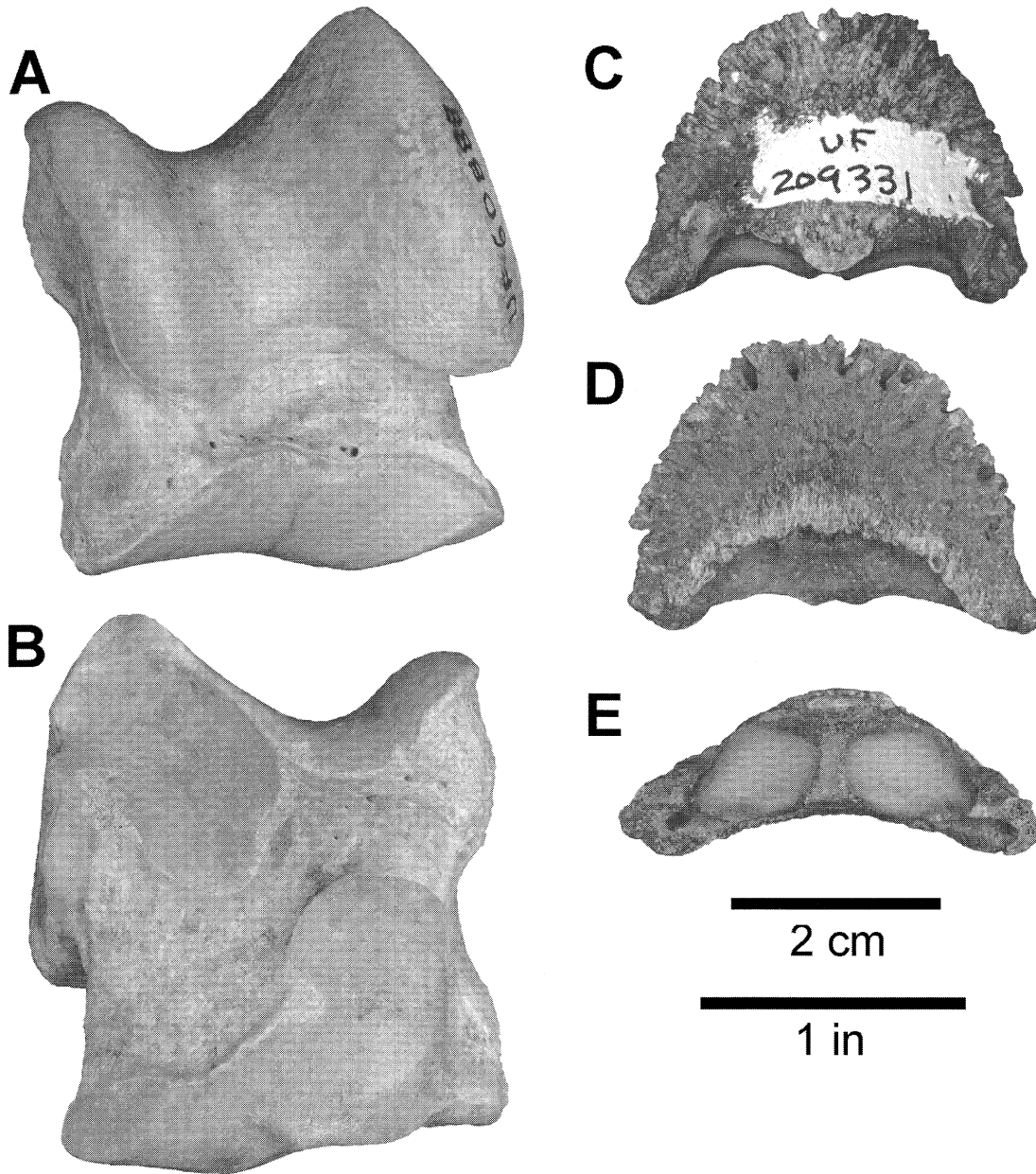


FIGURE 9. **A**, anterior, and **B**, posterior views of UF 60888, left astragalus of *Tapirus veroensis* from Branford 1A, Suwannee County, Florida. **C**, dorsal, **D**, ventral, and **E**, proximal views of UF 209331, distal phalanx (hoof core) of digit 3; from Tri-Britton Site, Hendry County, Florida.

specimens from the Aucilla, Oklawaha, and Wacissa rivers in northern Florida and from Vero, Seminole Field, Melbourne, and the Peace River in the southern half of the state. There is no direct evidence of interaction

between the state's first humans, the Paleo-Indians, and *T. veroensis*. But indigenous people of both South America and Asia hunt and eat tapirs today. The habit of tapirs of seeking refuge in water is not usually an effective

strategy with human hunters.

The extinction of *Tapirus veroensis* occurred more or less simultaneously with that of many other large mammals in North America, including mammoths, mastodon, horses, llamas, ground sloths, pampathere, dire wolf, sabertooth cats, lion, and short-faced bears. This extinction event also included a few reptiles and birds, most notably large tortoises of the genus *Hesperotestudo* and the largest flying bird of the time, the teratorn. The two major scientific hypotheses to explain this extinction event are human overhunting and rapid climatic change leading to disruption of ecosystems and breeding cycles (Martin and Klein, 1984). Which of these, if either, was the proximate cause of the extinction of *T. veroensis* is not known. Tapirs survived in North America only in the jungles of Central America in the form of *Tapirus bairdii*. It does not have a fossil record, although some fossils from the western U.S. are possibly related to it. *T. veroensis* is not ancestral to *T. bairdii*, nor any of the other modern species. Thus, its extinction was the termination for a lineage of species that had lived in the Southeast since the Pliocene. Modern tapirs are currently facing a new wave of extinction with three of the four living species regarded as endangered or highly threatened due to hunting and habitat loss.

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