

# LATE MIOCENE *TAPIRUS* (MAMMALIA, PERISSODACTYLA) FROM FLORIDA, WITH DESCRIPTION OF A NEW SPECIES, *TAPIRUS WEBBI*

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*Tapirus webbi* n. sp. is a relatively large tapir from north-central Florida with a chronologic range of very late Clarendonian (Cl3) to very early Hemphillian (Hh1), or ca. 9.5 to 7.5 Ma. It is about the size of extant *Tapirus indicus* but with longer limbs. *Tapirus webbi* differs from *Tapirus johnsoni* (Cl3 of Nebraska) by its larger size, relatively shorter diastema, thicker nasal, and better developed transverse lophs on premolars. *Tapirus webbi* is more similar to *Tapirus simpsoni* from the late early Hemphillian (Hh2, ca. 7 Ma) of Nebraska, but differs in having narrower upper premolars and weaker transverse lophs on P1 and P2. *Tapirus webbi* differs from North American Plio-Pleistocene species such as *Tapirus veroensis* and *Tapirus haysii* in its polygonal (not triangular) interparietal, spicular posterior lacrimal process, relatively narrow P2-M3, and lack of an extensive meatal diverticulum fossa on the dorsal surface of the nasal.

In Florida, Hh2 *Tapirus* is known only from relatively incomplete specimens, but at least two species are represented, both of significantly smaller size than *Tapirus webbi* or *Tapirus simpsoni*. One appears to be the dwarf *Tapirus polkensis* (Olsen), previously known from the very late Hemphillian (Hh4) in Florida and the Hemphillian of Tennessee (referred specimens from Nebraska need to be reexamined). Previous interpretations that the age of *T. polkensis* is middle Miocene are incorrect; its chronologic range in Florida is Hh2 to Hh4 based on direct association with biochronologic indicator taxa such as *Neohipparion eurystyle*, *Dinohippus mexicanus* and *Agriotherium schneideri*. The second species of Hh2 *Tapirus* from Florida is of moderate size and similar in some respects to *Tapirus haysii* and *Tapirus veroensis* (e.g., triangular interparietal), but it retains some primitive dental character states, such as a labial cingulum and small parastyles on the upper cheek teeth.

Key Words: Perissodactyla; Tapiridae; *Tapirus*; Miocene, late; new taxon; Florida

## INTRODUCTION

Among the large terrestrial mammals that inhabited North America during the Neogene, tapirids are perhaps the least studied, particularly those of the late Miocene and early Pliocene. In the introduction to their review of Pleistocene *Tapirus* in the eastern United States, Ray and Sanders (1984:283) noted, "the widespread and fairly abundant fossil material is generally inadequate for rigorous specific identification, and it must be understood that our concept of the number of species in the Pleistocene of North America and of their geographic and temporal distribution remains very insecurely founded." What then must the situation be for the late Neogene, which covers a much longer interval of time than the Pleistocene and for which fossils of *Tapirus* and other tapirids are much less abundant? To date, only three small regions in North America have produced late Miocene or early Pliocene samples of

tapirids that include crania, mandibles, postcrania, and abundant teeth: the Xmas-Kat Channels Fauna of north-central Nebraska (Skinner & Johnson 1984), the Gray Fossil Site in eastern Tennessee (Parmalee et al. 2002; Wallace et al. 2002; Wallace & Wang 2004), and the Archer Fauna of north-central Florida (Webb & Hulbert 1986). No published study has described any of these samples in detail until now. All are of importance in understanding tapirid biogeography and phylogeny during the late Neogene.

Tapirids apparently became relatively rare in North America after the Arikareean Land Mammal Age (early Miocene), in contrast to their much greater abundance and diversity in older faunas (Wortman & Earle 1893; Albright 1998; Colbert & Schoch 1998). They are absent or exceedingly scarce in all large, well sampled Hemingfordian through middle Clarendonian faunas, such as Sheep Creek, Lower Snake Creek, Devils Horse Gulch, Burge, and Minnechaduzza from Nebraska, the Burkeville, Lapara Creek, and Clarendon from Texas, and Thomas Farm from Florida. Although reduction of

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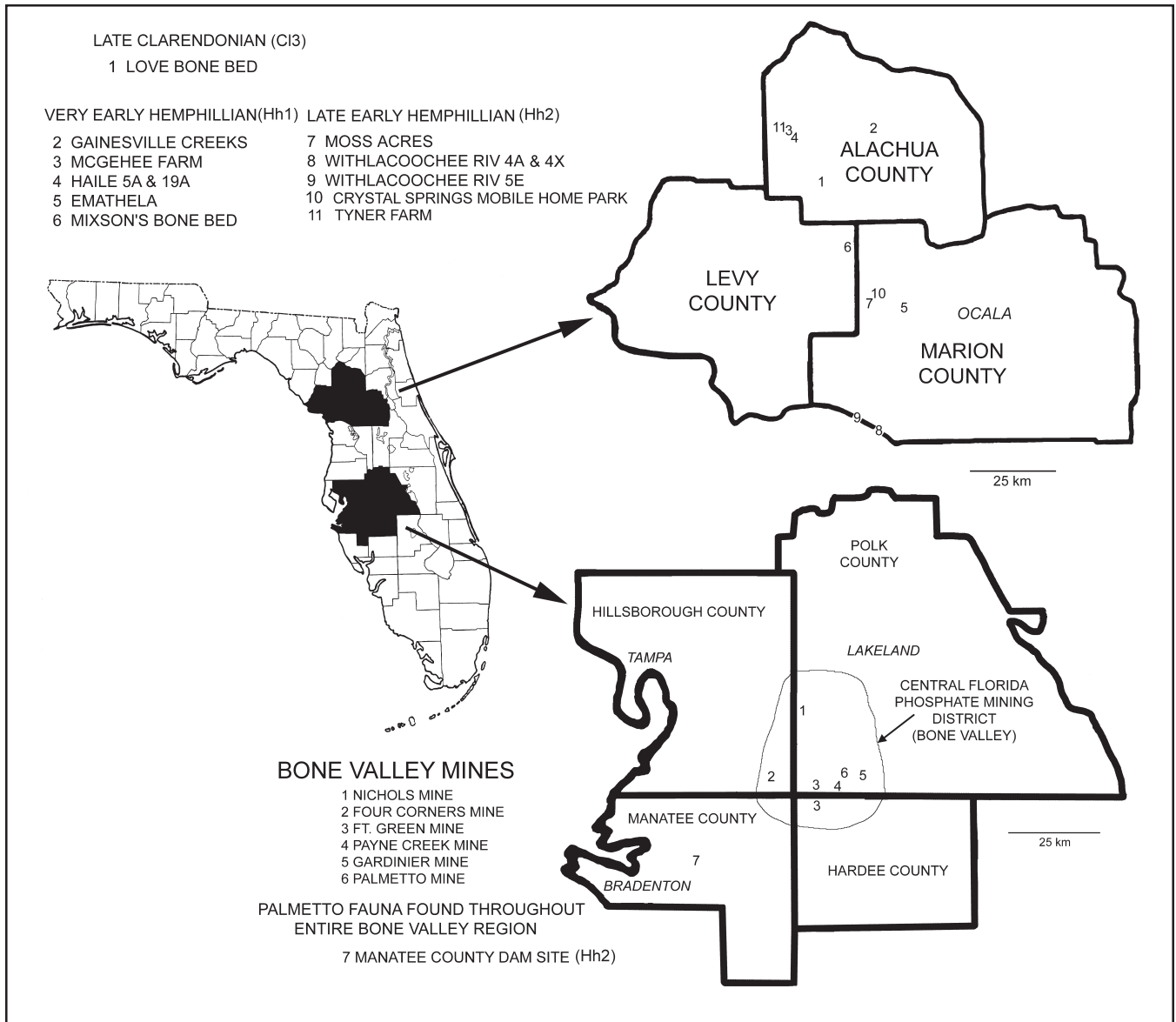


Figure 1. Map of late Clarendonian and Hemphillian vertebrate fossil localities in Florida mentioned in this study.

mesic forested habitats is commonly cited as the reason for this decline (e.g., Colbert & Schoch 1998), this argument is less persuasive in the Gulf Coastal Plain where this environmental change either did not occur or was much less severe than in the Great Plains. Nevertheless, there are no known tapirids from either coastal Texas or Florida during the Hemingfordian, Barstovian, and early Clarendonian Land Mammal Ages, despite recovery of medium- to large-sized mammals at many localities. In sharp contrast to their earlier rarity, tapirids suddenly became abundant near the end of the Clarendonian,

at about 9.5 Ma. This occurred almost simultaneously in Nebraska (Xmas-Kat Channels Fauna, Cherry County) and Florida (Love Site, Alachua County; Fig. 1). Unlike older records, the taxa involved in both regions can be confidently referred to the extant genus *Tapirus* (as defined below). *Tapirus* persisted in both the Great Plains and Gulf Coastal Plain into the Pleistocene, being consistently much more common in the latter region.

The late Clarendonian (C13; Tedford et al. 2004) representative of *Tapirus* in the Great Plains is *Tapirus*

*johnsoni*. Originally described from rather limited material, more complete specimens, including two skulls, of *T. johnsoni* from the Xmas-Kat Channels Fauna are housed at the American Museum of Natural History. It is relatively small and brachydont compared to most other species of *Tapirus*. Other apparently plesiomorphic states in *T. johnsoni* include an anteriorly located mental foramen and poorly developed transverse lophs on premolars. No specimens of *T. johnsoni* have been recovered from Florida.

In an unpublished masters thesis, Yarnell (1980) studied the extensive sample of *Tapirus* from the Archer Fauna (Love, McGehee Farm, and Mixson's sites in north-central Florida; Webb & Hulbert 1986). She recognized that it was not conspecific with *T. johnsoni* because it was significantly larger in size and differed in some aspects of its cranial and dental morphology. Yarnell (1980) referred the Archer Fauna sample of *Tapirus* to *Tapirus simpsoni*. Schultz et al. (1975) described this species on a palate and two isolated teeth from the Hh2 Ft-40 locality in Frontier County, Nebraska. Yarnell's (1980) allocation of the Florida specimens to *T. simpsoni* was followed by Webb et al. (1981), Becker (1985), MacFadden and Hulbert (1990), Hulbert (1995), Colbert and Schoch (1998), and Hulbert et al. (2001). The topotypic sample of *T. simpsoni* is about 1 to 2.5 million years younger than Yarnell's (1980) referred Florida specimens. With few exceptions, when they have genera in common, Ft-40 and Love Site/McGehee Farm mammals differ at the species level. Examples of this pattern include the nimravid *Barbourofelis*, rhinocerotids *Aphelops* and *Teleoceras*, equids *Nannippus*, *Neohipparion*, and *Calippus*, camelid *Hemiauchenia*, dromomerycid *Pediomeryx*, and gomphothere *Amebelodon*. The extensive sample of *Tapirus* teeth from the Love Site allows a good assessment of intraspecific variation. Several dental features on the holotype of *T. simpsoni* are outside of the range of variation observed in the Archer Fauna sample of *Tapirus*. Also, study of Pleistocene and extant *Tapirus* has demonstrated that features of the premaxillary, maxillary, nasal, frontal, parietal, interparietal, and lacrimal bones of the skull are extremely important to properly diagnose and characterize species in this genus, generally more important than the dentition (Simpson 1945; Hershkovitz 1954; Ray & Sanders 1984). While many phylogenetically significant cranial characters can be observed in the late Miocene sample of *Tapirus* from Florida, this is not true of *T. simpsoni* from Nebraska. For these rea-

sons I have elected to formally designate the Florida samples as a new species instead of including them in *T. simpsoni*. Increased, more complete samples of the latter are necessary to fully compare the two species and to test whether they are distinct.

The purpose of this study is to describe fossils of *Tapirus* from the late Miocene (Cl3-Hh2) of north-central Florida, and to compare them with other species in the genus. All specimens were re-measured and described independently of Yarnell (1980), following the methods of Ray and Sanders (1984) and Hulbert (1995). Postcranial elements, which were not studied by Yarnell (1980), were measured and examined for phylogenetically important characters. This is the first of four planned descriptive papers on significant late Neogene samples of *Tapirus*. The others will describe a new late Blancan species from Florida, *Tapirus johnsoni* from Nebraska, and *Tapirus polkensis* from eastern Tennessee. These will be followed by a comprehensive, species-level phylogenetic analysis of North American *Tapirus*, which will permit interpretations of its biogeography, determination of relationships between fossil and extant species, and analysis of character evolution in the genus *Tapirus* from the Miocene to the present.

The definition of *Tapirus* used here is the taxon comprised of *Tapirus terrestris* and all species that share a more recent common ancestor with *T. terrestris* than with the type species of the remaining genera in the family Tapiridae as defined and used by Colbert (2005). This stem-based definition allows fossil species to be placed in the genus even if phylogenetic analysis places them outside of crown-clade *Tapirus*. This is a more inclusive definition than that of Colbert (2005), who limited the genus to only members of the crown-clade. Boundaries for Neogene North American Land Mammal Ages and their subdivisions follow the recent revision by Tedford et al. (2004); biochronology of Florida vertebrate fossil localities follows Webb and Hulbert (1986) and Hulbert (2001).

#### ABBREVIATIONS

Institutional Abbreviations.—AMNH, vertebrate paleontology collection, American Museum of Natural History, New York; ChM PV, vertebrate paleontology collection, Charleston Museum, South Carolina; ETMNH, vertebrate paleontology collection, East Tennessee Museum of Natural History, Johnson City; F:AM, Frick fossil mammal collection, AMNH; MCZ, Museum

of Comparative Zoology, Harvard University, Cambridge, Massachusetts; SCSM, South Carolina State Museum, Columbia; UF, vertebrate paleontology collection, Florida Museum of Natural History, Gainesville; UF(M), mammalogy collection, Florida Museum of Natural History; UF/FGS, Florida Geological Survey collection, now housed with the UF collection; UNSM, vertebrate paleontology collection, University of Nebraska State Museum, Lincoln; USNM, vertebrate paleontology collection, National Museum of Natural History, Washington, D.C.; USNM(M), mammalogy collection, National Museum of Natural History.

Morphological Abbreviations.—IOF, infraorbital foramen; L, greatest length; DL, 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; 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).

Statistical Abbreviations.—*x*, sample mean; *s*, sample standard deviation; OR, observed range of a sample; *n*, sample size; *CV*, sample coefficient of variation.

Chronological Abbreviations.—Cl, Clarendonian Land Mammal Age; Hh, Hemphillian Land Mammal Age; Ma, meganna, millions of years before present.

#### COMPARATIVE MATERIAL EXAMINED

*Tapirus johnsoni* Schultz, Martin, and Corner 1975.—A cast of the holotype mandible UNSM 1096, plus an associated skeleton with skull and mandible (F:AM 37302), a juvenile skull (F:AM 37362), and numerous maxillae, mandibles, and isolated teeth from the Merritt Dam Member of the Ash Hollow Formation, Nebraska, including F:AM 37303, 37307, 37320-37324, 37326-37328, 37346, 37352, 37258, 37366, 37367, 37374, and 37385.

*Tapirus simpsoni* Schultz, Martin, and Corner 1975.—A plaster cast of the holotype palate UNSM 45106 in the UF collection.

*Tapirus polkensis* (Olsen) 1960.—The UF and UF/FGS sample from the Central Florida Phosphate Mining Region (informally known as Bone Valley), southwestern Polk and adjacent counties (Fig. 1), including the holotype and paratype. Also the extensive sample of skulls, mandibles, and postcrania from the Gray Fos-

sil Site, eastern Tennessee in the ETMNH collection (Wallace et al. 2002; Wallace & Hulbert 2005).

*Tapirus haysii* Leidy 1859.—The UF sample from Florida listed by Hulbert (1995) plus a newly recovered, undescribed sample in the UF collection from the Irvingtonian SR138 Spring Site, Gilchrist County, Florida, which includes a nearly complete left nasal (UF 217536). From the private collection of Barbara Fite in Tampa, Florida, a relatively complete although reconstructed skull from Leisey Shell Pit.

*Tapirus veroensis* Sellards 1918.—The holotype skull UF/FGS 277, three partial associated skeletons from Florida (UF 2560, 14025, and 14064) that include both cranial and postcranial elements, a skull from South Carolina (ChM PV 4257; Ray & Sanders 1984:figs. 4, 7), and numerous other partial crania, mandibles, teeth, and postcrania from Florida, Georgia, and South Carolina in the UF, UF/FGS, USNM, ChM, SCSM, MCZ, and AMNH collections.

*Tapirus (Megatapirus) augustus* Matthew and Granger 1923.—The AMNH sample listed by Colbert and Hooijer (1953), including AMNH 18433 and 18748

Extant *Tapirus*.—For the four extant species of *Tapirus*, *T. (Tapirus) terrestris* Linnaeus 1758, *T. (Tapirella) bairdii* (Gill) 1865, *T. (Pinchaqus) pinchaque* Roulin 1829, and *T. (Acrocodia) indicus* Desmarest 1819, I examined and measured skulls, mandibles, and postcrania in the USNM(M) and UF(M) collections. Other measurements were taken from the literature, including Simpson (1945) and Hooijer (1947).

Comments and descriptions of all other species were based on published accounts, and appropriate literature citations are provided in these cases.

#### SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen 1848

Family TAPIRIDAE Burnett 1830

Genus *TAPIRUS* Brünnich 1771

#### *TAPIRUS WEBBI* n. sp.

*Tapiravus* sp.: Hirschfeld and Webb (1986:247-249).

*Tapirus simpsoni* Schultz, Martin and Corner 1975: Webb et al. (1981:521-538); MacFadden and Hulbert (1990:339, 344, 350-352); Hulbert (1995:545-549, fig. 6B, D); Colbert and Schoch (1998:577), in part, Florida records only; Hulbert et al. (2001:297, fig. 14.26).

Holotype.—UF 11005, fragmented partial skull that includes portions of right and left maxillae and nasals; right I1, I3, and P2-P3; and left C and P1-M2. A right



p2 catalogued with the same UF number appears to belong to the same individual as the skull based on similarities in wear-stage and preservation, and it occludes well with the right P2; therefore it is regarded as part of the holotype specimen. An additional upper right premolar with the catalogue number UF 11005 has much less wear on its occlusal surface than any of the other teeth assigned to UF 11005, and is most likely extra P3. For these reasons, this tooth is excluded from the holotype of *Tapirus webbi*. A third of the crown of this extraneous premolar was sampled for stable carbon isotope analysis and the results of this analysis were published by MacFadden and Cerling (1996) under the UF 11005 catalogue number. The holotype was collected in 1964 by R. R. Allen and S. D. Webb.

**Type Locality.**—The holotype was collected at the McGehee Farm Site, 4 km north of Newberry in western Alachua County, Florida (Fig. 1; UF locality AL027). Age is late Miocene, Hh1, about 8.5 Ma. Primarily references on this locality are Brodkorb (1963), Hirschfeld and Webb (1968), Webb (1969), and Olson (1976).

**Paratypes.**—From the McGehee Farm Site: UF 11117, fragmented partial juvenile skull that includes partial right nasal, portions of right and left frontals, parietals, jugals, and squamosals, right DP2-M1, left DP1-M1, and portions of mandible with right dp2-dp4 and left dp4; UF 11007, associated partial maxillae with right P1-P3 and left P1-P4; and UF 11009, left maxillary fragment with M1-M2. From the Love Site: UF 26179, associated maxillae with right P1-M2 and left P2-P4; and UF 26191, nearly complete mandible with right and left i1-i2, c, p2-m3.

**Distribution.**—In addition to the type locality, *Tapirus webbi* is known from two other late Miocene vertebrate fossils sites in north-central Florida, the Hh1 Mixson's Bone Bed, Levy County, and the CI3 Love Site, Alachua County.

**Referred Specimens.**—McGehee Farm, Alachua County (in addition to the holotype and paratypes listed above): UF 10986, fragmented posterior portion of skull with supraoccipital, interparietal, squamosals, and exoccipital; 11004, maxillary fragments with right and left P1 and portions of other premolars; 27005, left maxillary fragment with P3-P4; 27070, associated right and left P1-P4; 11137, left maxillary fragment with M1; 16620, right dentary fragment with partial m2; 27006, right partial dentary with dp3-dp4; 211277, left I1; 211278-211279, two left I3s; 177829, right DP2; 19234, 211276, two left DPs; 32054, right DP3; 177830, left DP3; 16625, right

M1; 32058, right M2; 211280, partial i1; 211281-211282, two lower canines; 27007, p4; 11124, 111125, two scapulae; 10977, 10994, 32057, three humeri; 11100, 11126, 11134, 16674, 32060, 32061, 177817, seven radii; 11121, 11125, 32059, three ulnae; 32067-32070, four metacarpal 2s; 16635, 32071, 32072, three metacarpal 3s; 32073, 177818, 177818, 177821, four metacarpal 4s; 32074, metacarpal 5; 11120, femur; 10943-10944, 11006, 16612 four tibiae; 9531, 9543, 10948, 32078, eight astragali; 9514, 10978, 11015, 11122, 32079, 32080, six calcanea; 16635, 28005, five metatarsal 3s.

Love Site, Alachua County (in addition to the paratypes listed above): UF 26163, partial cranium with right and left P4-M3, ascending process of maxilla, and squamosal; 26171, partial skull with right C-P1 and left P2-M3; 26164, crushed partial palate with right lacrimal, P4, and M2-M3 and left M2-M3; 26160-26162, 26165-26168, 26174, 26177-26178, 26185, 32083, 13 maxillae; 26169, 26182, 26183, three associated upper dentitions; 26175, 26176, 26662, three occipitals; 211184-211202, 19 I3s; 211203-211204, two Cs; 211205, DP2; 211206-211208, three DP3s; 211209-211210, two DP4s; 27087-27096, 211211, 11 P1s; 27097-27102, 211212-211213, nine P2s; 211214-211223, ten P3s; 211224-211233, ten P4s; 211234-211244, 11 M1s; 211245-211251, seven M2s; 211252-211257, six M3s; 26172, 26193, 27280, three mandibular symphyses; 26187, 26195, 26197, 28013, 32081, five associated right and left dentaries; 26173, 26180, 26186, 26188-26190, 26192, 26194, 26196, 26198, 26202, 26207, 26209, 26210, 26212-26216, 26218-26222, 28014, 32082, 14 dentaries; 211268, 211275, two i1s; 211258-211265, eight lower canines; 27071, dp2; 211266, dp4; 27072-27076, five p2s; 27077-27080, four p3s; 27082, 27084-27086, 211267, 211269-211271 nine p4s; 27242-27243, 27247-27248, 27250, 211272-211274, eight m1s; 26184, 27245, two m2s; 27244, 27246, two m3s; 26199, 26733-26735, four atlases; 26200, 26203, 26287-26291, seven axes; 26224-26226, 26228-26230, 26234-26243, 26264, 26267, 26281-26284, 32085, 24 humeri; 26320, 27279, 27282, 27283, 39816, 39817, six radio-ulnae; 26244-26246, 26250, 26251, 26253-26261, 26263-26268, 26732, 27310, 27311, 39807-39811, 39813-39815, 39818, 32 radii; 26269-26278, 27309, 39819, 12 ulnae; 26455-26461, 26483-26488, 26728, 32089, 32090 16 metacarpal 2s; 26462-26478, 26666, 26667, 32087, 32088 21 metacarpal 3s; 26440, 26441, 26443-26454, 27313, 15 metacarpal 4s; 26545-26550, 26560-26565, 12 metacarpal 5s; 26292-26308, 32091, 32092, 19 femora; 26309-26319, 26321, 26323-26334, 26336-

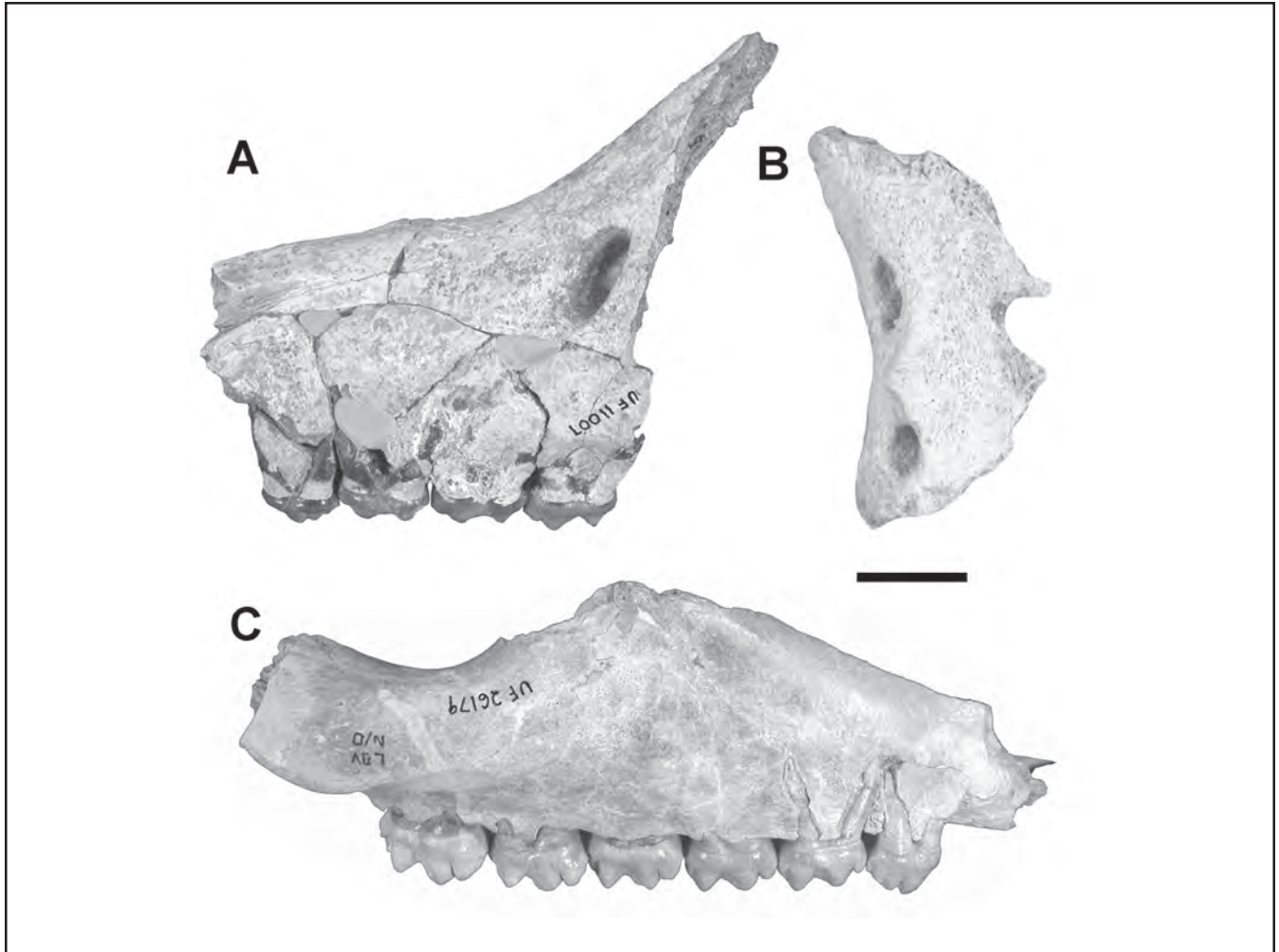


Figure 2. Cranial material of *Tapirus webbi* n. sp., from the late Miocene of Florida. A, lateral view of UF 11007 (paratype), partial left maxilla with P1-P4, McGehee Farm Site. Note location of IOF dorsal to P4 and terminus of suture for premaxilla dorsal to P1. B-C, Love Site. B, posterolateral view of UF 26164, posterior portion of right lacrimal. Note small posterior process that does not obstruct view of either lacrimal foramen. C, lateral view of UF 26179, left partial maxilla and jugal with P1-M2 (see Fig. 8A for occlusal view of teeth). IOF location relative to tooth row is between the P3 and P4. Scale bar = 2.4 cm for A and C, = 1 cm for B.

26339, 26341-26343, 26345, 26665, 26731, 27284-27286, 27308, 32093, 32094, 39825-39830, 46 tibiae; 26344, fibula; 26792-26825, 27272, 27273, 27314, 39824, 38 astragali; 26826-26860, 32095, 32458, 32612, 38 calcanea; 26551-26559, 26566-26571, 26726, 26727, 26729, 26730, 19 metatarsal 2s; 26489-26523, 26724, 26725, 27271, 38 metatarsal 3s; 26524-26544, 26721-26723, 27270, 32096, 26 metatarsal 4s. The Love Site sample also includes numerous carpals, tarsals, and phalanges.

Mixson's Bone Bed, Levy County: F:AM 37403, associated upper dentition; 37404, right DP2; 37402, subadult mandible with incisors, p2-p3, dp4, m1-m2;

37408-37409, 2 distal tibiae. Also uncatalogued F:AM material, including an astragalus, metapodials, carpals, and phalanges.

Diagnosis.—Large, long-limbed species of *Tapirus*; smaller than *Tapirus augustus*, *Tapirus merriami*, or *Tapirus haysii*; larger than *Tapirus johnsoni*, *Tapirus polkensis*, *Tapirus arvernensis*, *Tapirus jeanpiveteaui*, *Tapirus terrestris*, *Tapirus pinchaque*, or *Tapirus bairdii*. Differs from *Tapirus indicus*, *T. augustus*, *T. haysii*; *T. veroensis*, *T. polkensis*, and *T. bairdii* in having a relatively longer, thicker nasal without an extensive, deep fossa for the

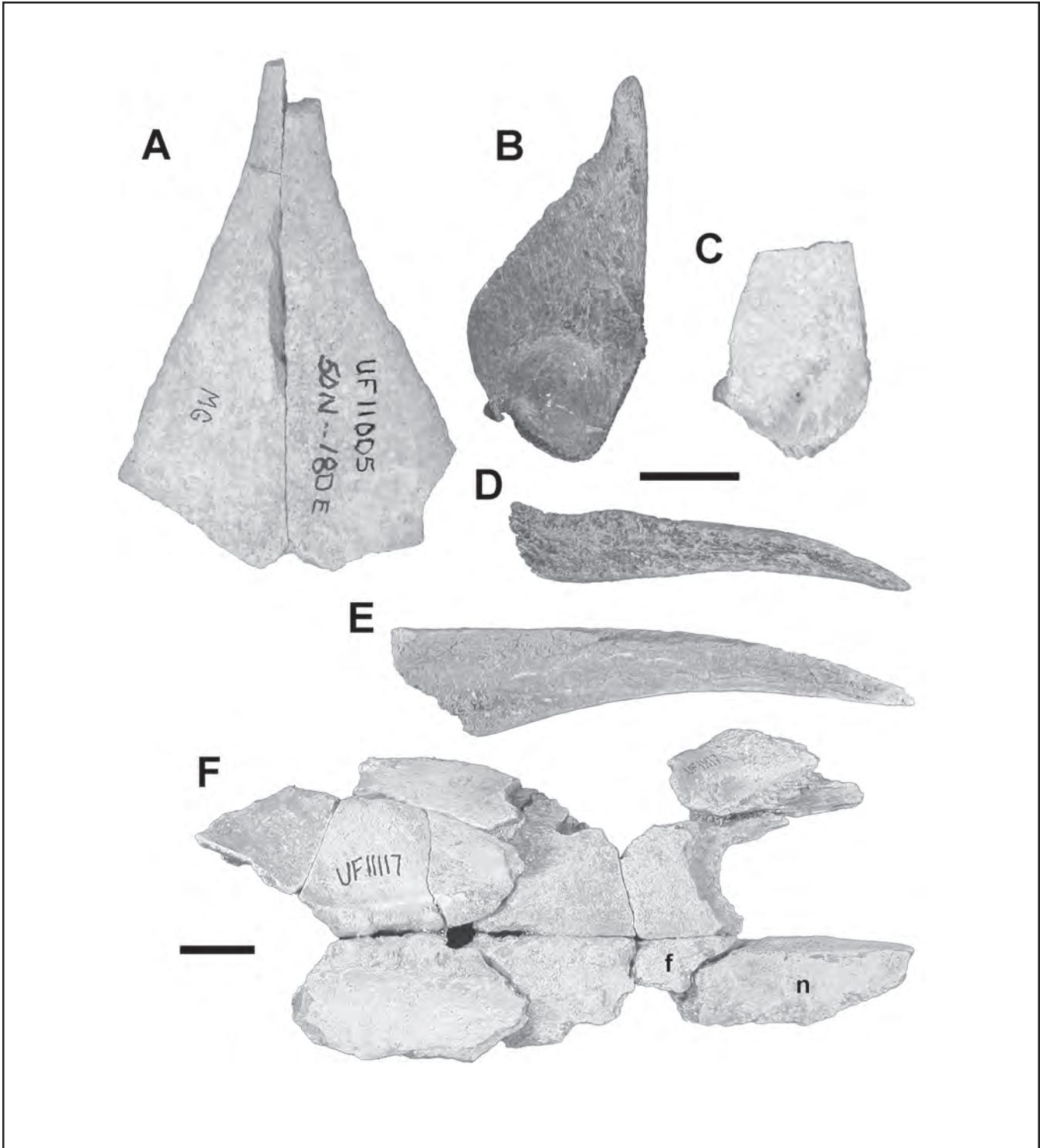


Figure 3. Dorsal skull bones of *Tapirus* from Florida. A, C, and E-F are *Tapirus webbi* n. sp., from the McGehee Farm Site. B and D are *Tapirus veroensis*, middle Pleistocene, Tri-Britton Site, Hendry County. A, dorsal view of UF 11005 (holotype), partial right and left nasals. B, dorsal, and D, medial views of UF 210888, left nasal. C, dorsal view of UF 177816, posterior half of juvenile left nasal. E, medial view of left nasal of UF 11005. F, dorsal view of UF 11117 (paratype), partial juvenile cranium including partial right nasal (n), frontals (f), and parietals. Scale bars = 2 cm; upper scale bar for A-E, lower bar for F only.

meatal diverticulum. Differs from all other New World species in having articular contact between the first and fourth metatarsals. Differs from *T. simpsoni* in having narrower upper premolars (both absolutely and relatively) and more weakly developed transverse lophs on P1 and P2. Differs from *T. terrestris* in having a lower sagittal crest, larger interparietal, and posterolabial cingulum common on P2-M3. Differs from *T. pinchaque* in having a broader P1, a more rectangular P2, and a longer posterior process of the premaxilla.

**Etymology.**—The species name honors S. David Webb, both for his contributions to Florida vertebrate

paleontology and biochronology, including spearheading excavations at both McGehee Farm and the Love Site, and to understanding the Great American Biotic Interchange, of which *Tapirus* was a prominent participant.

**Description.**—All tapirid crania from the Love and McGehee Farm sites are fragmented and incomplete (Figs. 2-4). However, many critical cranial features can be discerned in a piecemeal fashion. The posterior process of the premaxilla terminates in an acute point at a level dorsal to the P1 (UF 11007, 26171; Fig. 2A). A broad anterodorsal projection of the maxilla lies medial to the posterior process of the premaxilla and is visible

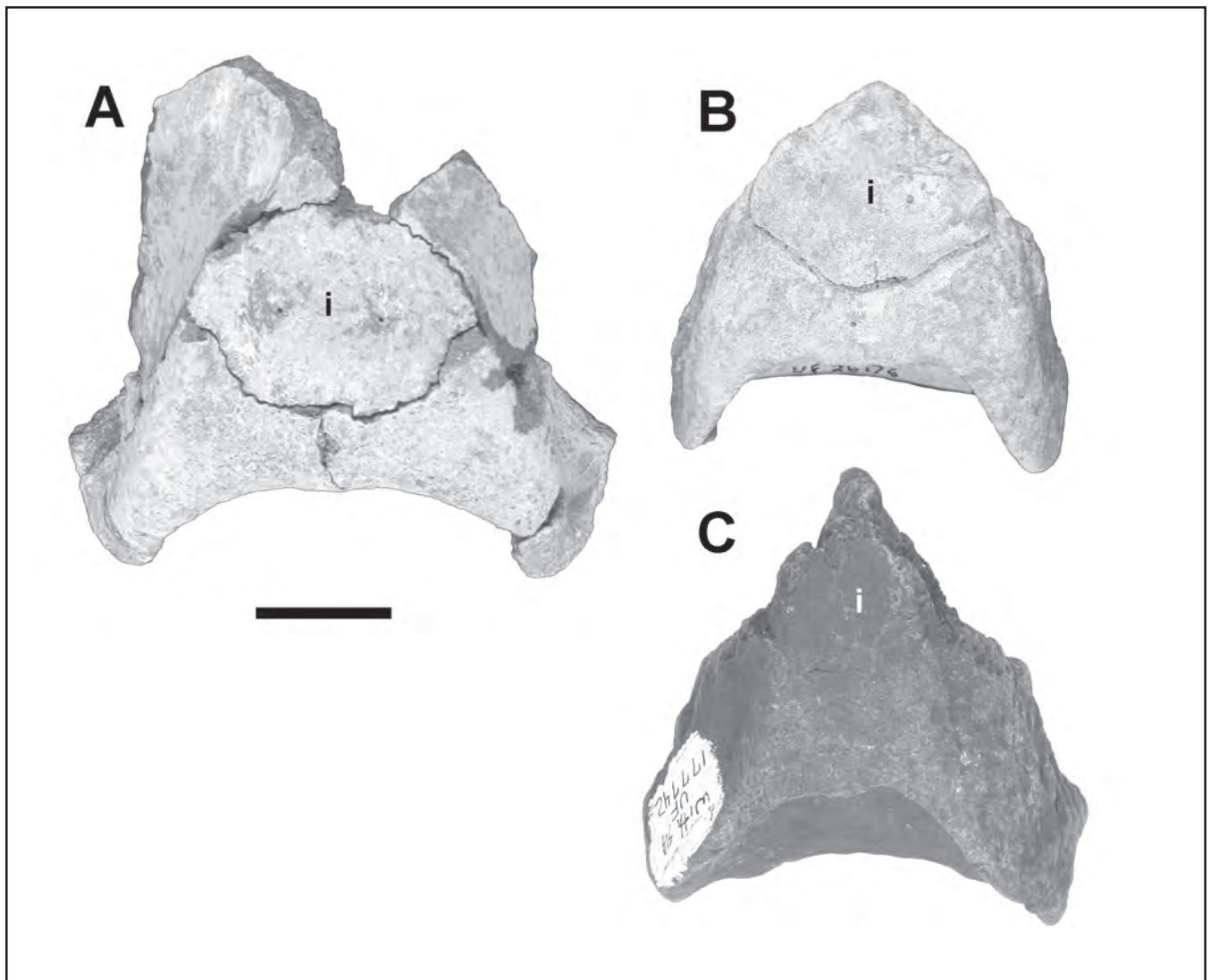


Figure 4. Dorsal views of occipital regions of skulls of *Tapirus* from the late Miocene of Florida. A and B are *Tapirus webbi* n. sp.; C is *Tapirus* sp. A, UF 10986, McGehee Farm Site. B, UF 26176, Love Site, juvenile. C, UF 17742, Withlacoochee River Site 4A. The shape of the interparietal bone (i) is polygonal with 5 or 6 sides in *T. webbi*, and triangular in *Tapirus* sp. Scale bar = 2 cm.



in lateral view; its medial border is slightly thickened dorsoventrally but lacks a distinct flange for enclosing the mesethmoid. The upper diastema, 40.7 mm between the C and P1 alveoli, is relatively short for a *Tapirus* of this size, but is preserved in only one specimen, UF 26171. The posterodorsal ascending process of the maxilla bears a distinct groove in some specimens that begins just dorsal to the IOF and widens posteriorly to form the channel for the meatal diverticulum. This groove is well developed on UF 11005, 11117, and 26160, but much fainter on UF 11007, and absent in UF 26963. In the latter, the flat to slightly convex surface of maxilla posterodorsal to the IOF changes gradually to a concave trough dorsal to the lacrimal. The channel or trough widens and deepens slightly dorsal to the orbit, as it crosses the frontal-maxillary contact. The IOF is located dorsal to the anterior half of the P4 or the posterior half of the P3 (Fig. 2A, C); a wide (10 to 17 mm) strut or bar of the maxilla separates the IOF from the lacrimal. UF 26164 includes the only known lacrimal, and only the posterior and central portions of the bone are preserved (Fig. 2B). The lacrimal has two large foramina on the margin of the orbit, one dorsal to the posterior lacrimal process and one ventral to the process. The posterior lacrimal process is a small spike directed posterolaterally which does not obscure the visibility of either lacrimal foramina in lateral view. The

lateral preorbital surface of the lacrimal is rough and slightly concave. Although broken anteriorly, it appears that the original height of the lacrimal was much greater than its length.

The dorsal table of the frontal is relatively short anteroposteriorly (about 70.5 mm in UF 26171), with a relatively flat, smooth surface that is slightly convex transversely; the dorsomedial continuation of the supraorbital diverticular groove on the dorsal table is shallow and lacks a distinct posterior border. The dorsal table of the frontal is in the same general plane as the nasals and sagittal crest, lacking any notable swelling. There is a short, blunt projection of the frontals between the nasals. Portions of the nasals are preserved in one adult, UF 11005, and two juveniles, UF 11117 and 177816. UF 11005 is the most complete, containing both right and left sides (Fig. 3A), and is missing only the posterolateral corners and the anterior tip. The nasals are very long (length would have exceeded 106 mm along the midline), taper very gradually, and are arched anteroposteriorly; medially the nasals are very thick (> 22 mm at the posteriormost preserved portion; Fig. 3E), but they thin to sharp lateral margins. There is no indication of a fossa for the meatal diverticulum on the dorsal surface of the nasals of UF 11005, meaning that it must be limited to the posterolateral region of the nasals. This is confirmed by UF 177816, which preserves

Table 1. Comparative mandibular measurements of late Miocene *Tapirus*. Numbers in parentheses after measurements are the corresponding number for von den Driesch's (1976) mandibular measurements of *Equus*.

|                | <i>Tapirus webbi</i> n. sp. |             |          |          |             |          | <i>Tapirus johnsoni</i> |          |             |          |
|----------------|-----------------------------|-------------|----------|----------|-------------|----------|-------------------------|----------|-------------|----------|
|                | UF<br>26191                 | UF<br>28013 | <i>x</i> | <i>s</i> | OR          | <i>n</i> | <i>x</i>                | <i>s</i> | OR          | <i>n</i> |
| Condylar L (2) | 332.0                       | 326.5       | 329.5    | 3.89     | 326.5-332.0 | 2        | 298.0                   | 9.54     | 288.0-307.0 | 3        |
| Muzzle W (16)  | 47.0                        | 50.5        | 50.0     | 4.21     | 46.6-55.7   | 4        | 42.7                    | 2.14     | 40.4-44.6   | 3        |
| Symphysis L    | 98.6                        | —           | —        | —        | —           | 1        | 83.2                    | 0.78     | 82.3-83.8   | 3        |
| i3-p2 DL (15)  | 71.5                        | 70.2        | 71.9     | 1.79     | 70.0-74.8   | 6        | 73.1                    | 2.71     | 70.8-76.1   | 3        |
| c-p2 DL        | 58.7                        | 55.2        | 58.1     | 1.96     | 55.2-61.2   | 6        | 58.1                    | 5.20     | 52.5-64.2   | 4        |
| p2-m3 L (6a)   | 143.4                       | —           | 143.1    | 4.14     | 137.5-147.5 | 4        | 128.6                   | 4.41     | 122.0-136.0 | 11       |
| p2-p4 L (8a)   | 66.3                        | 66.2        | 65.6     | 1.87     | 62.1-68.3   | 8        | 59.7                    | 2.44     | 55.8-63.0   | 13       |
| m1-m3 L        | 76.9                        | —           | 76.6     | 2.42     | 72.2-79.4   | 6        | 69.4                    | 2.48     | 66.0-73.6   | 12       |

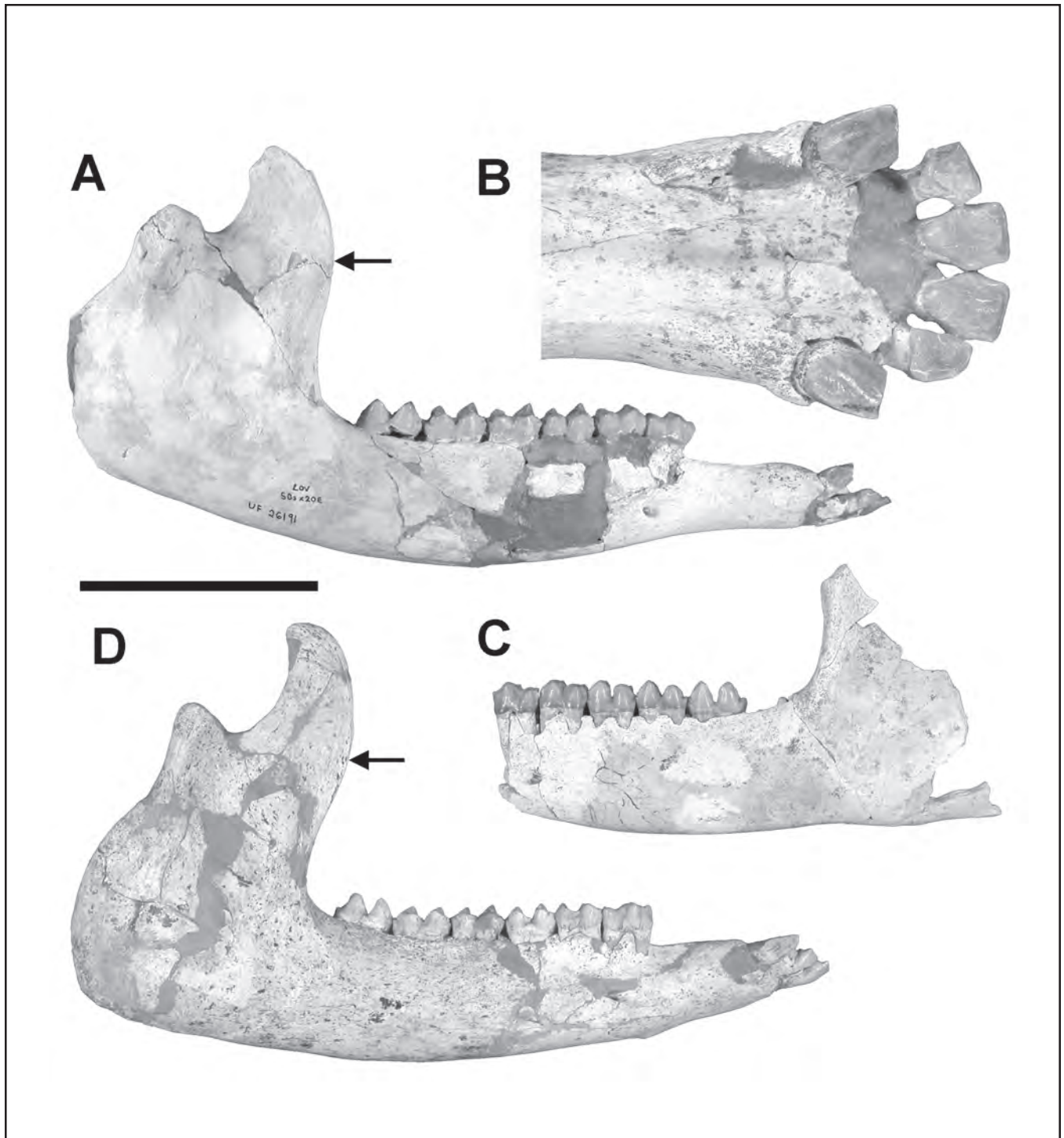


Figure 5. Mandibles of *Tapirus webbi* n. sp., from the Love Site (A-C) compared to that of a younger *Tapirus* from Florida (D). A, lateral view of right dentary of UF 26191 (paratype, see Fig. 10A for occlusal view of teeth). B, occlusal view of symphysis of UF 26191 with right and left i1-i2 and c. C, lateral view of UF 28014, partial left dentary with p2-m2 (m3 beginning to erupt, see Fig. 10B for occlusal view of teeth). D, lateral view of UF 206878, right dentary of an undescribed late Pliocene species from Haile 7C, Alachua County. UF 206878 has the morphology typical of Plio-Pleistocene *Tapirus* from Florida, with a short diastema, deep ramus, and the anterior border of the ascending ramus projecting anteriorly in lateral view to overlie the m3 (indicated by arrow). In contrast, *T. webbi* has a longer diastema, shallower ramus with a more deeply convex ventral margin, and a near vertical anterior margin of the ascending ramus that does not overlie the m3. Scale bar = 10 cm for A, C-D, = 4 cm for B.

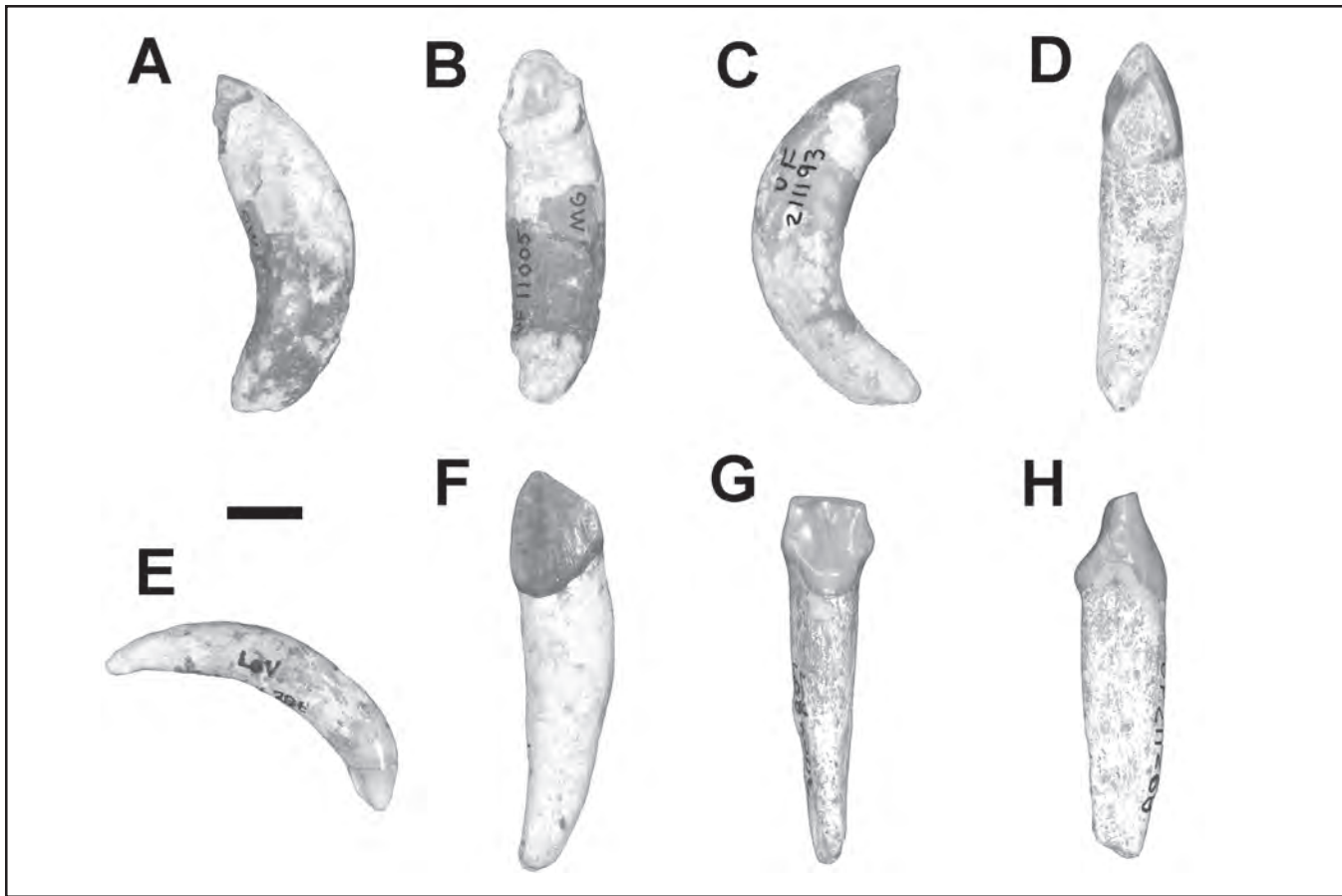


Figure 6. Incisors and canines of *Tapirus webbi* n. sp., from the late Miocene of Florida. A, medial, and B, occlusal views of UF 11005 (holotype), right I3, McGehee Farm Site. C-H from the Love Site. C, medial view of UF 211193, left I3. D, occlusal view of UF 211201, left I3. Note large posterior wear facet for c and smaller anteromedial facet for i2 and i3. E, lateral view of UF 211203, right C. F, medial view of UF 211262, left c. G, occlusal, and H, lateral views of UF 211268, right i1. Scale bar = 1 cm.

the entire posterior half of the left nasal (Fig. 3C). Almost none of the dorsal surface of the nasal housed the meatal fossa; instead the fossa is very shallow, without a pronounced margin, and limited to the posterolateral corner of the nasal, far from the midline. The nasal of UF 11117, although less complete and not well preserved (Fig. 3F), confirms that the meatal diverticulum fossa on the nasal did not approach the midline of the skull.

The dorsal portion of the parietals is only preserved in the juvenile UF 11117 (slight wear on DP4, M1 unworn); the temporal crests converge rapidly behind the frontoparietal suture and consist of low, wide, rugous ridges (Fig. 3F). The distance across the ridges reaches a minimum of about 15.5 mm at a point 25 mm posterior to the frontal suture. Posterior to this point the temporal crests diverge rapidly, forming the boundaries of the dorsal table of the occipital. The interparietal is a discrete ele-

ment in all four specimens preserving the occipital region, even in the relatively large UF 10986 and 26175. The interparietal is wider than it is long (41 by 23.5 mm in UF 10986; 34 by 29 mm in the juvenile UF 26176), relatively large in size, and polygonal in shape with five or six sides (Fig. 4A-B). The lambdoidal crests are large, thick, and project mostly posteriorly with slight lateral flair. The posterior region of the occiput, between the lambdoidal crests and dorsal to the foramen magnum, is strongly slanted anterodorsally-posteroventrally. Thus the foramen magnum is located much more posteriorly than is the akrocranium. In lateral view, the external auditory meatus is about 20 mm in diameter (UF 10986) and widely open ventrally as there is only a very slight posterior projection on the postglenoid process and the mastoid process of the squamosal lacks an anterior process.

The mandible of *T. webbi* is generally like those of

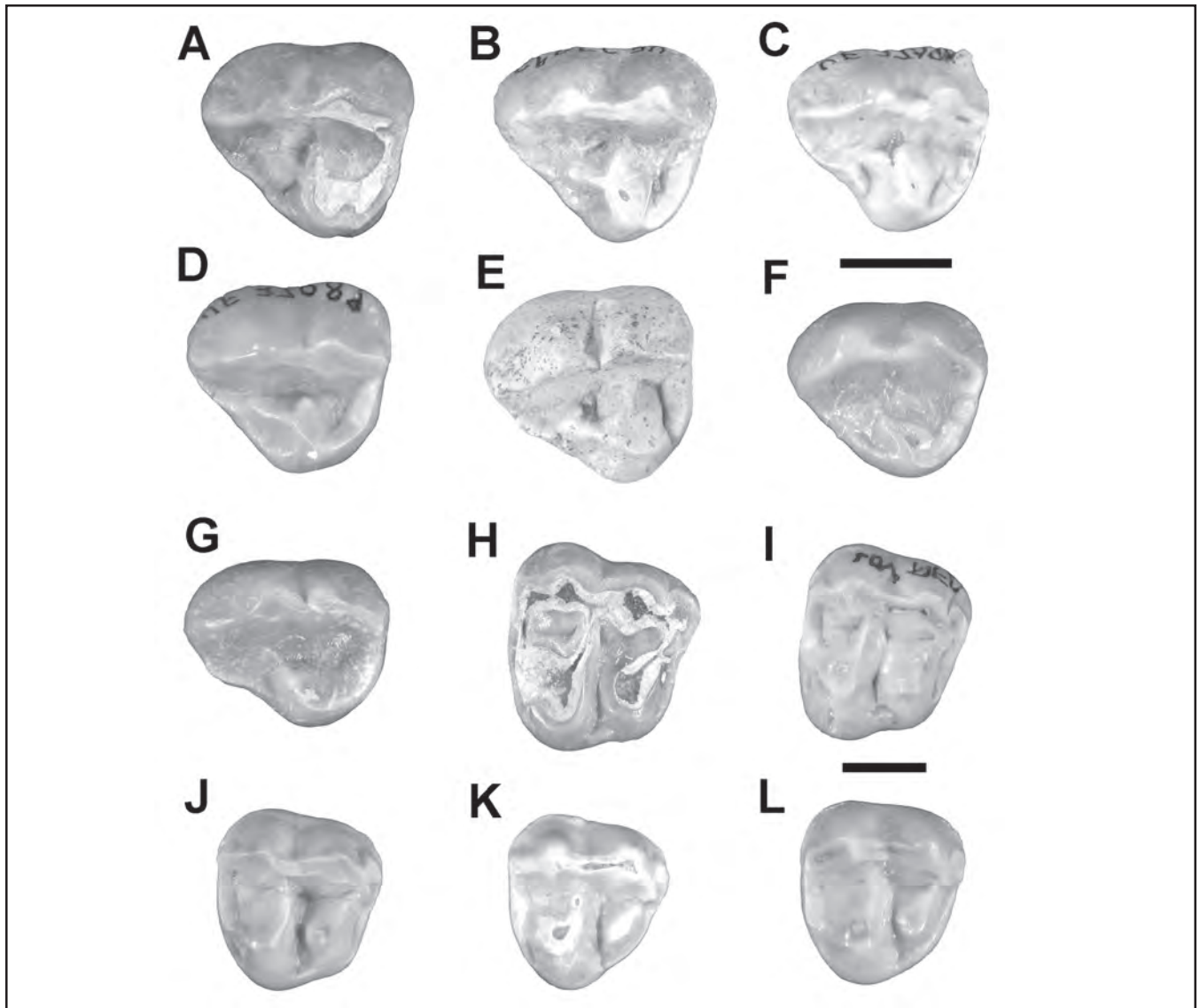


Figure 7. Variation in anterior upper premolars of *Tapirus webbi* n. sp., from the late Miocene of Florida. A and H from the McGehee Farm Site, all others from the Love Site. A-G, occlusal views of P1; right P1s reversed so as to appear to be lefts. A, UF 11005 (holotype). B, UF 27092. C, UF 27090. D, UF 27089. E, UF 26160. F, UF 26169. G, UF 26183. H-L, occlusal views of P2; left P2s reversed. H, UF 11005 (holotype). I, UF 27101. J, UF 27099. K, UF 27100. L, UF 26169. Scale bars = 1 cm; upper scale bar for A-G, lower for H-L.

other species of *Tapirus*, but with a relatively short diastema and shallow horizontal ramus (Fig. 5; Table 1). The ventral margin of the ramus is very bowed. The large mental foramen is located ventral to the p2, the circular masseteric fossa is found high on the ascending ramus. The anterior border of the ascending ramus rises vertically (in lateral view), then curves posteriorly to form the coronoid process; it does not project anteriorly to overlie the m3 (Fig. 5A). The posteroventral angle of the ramus is slightly inflected and its margin is not greatly

thickened. The mandibular foramen is located at a level equal to or slightly dorsal to the cheek teeth. Dorsoventral height of the ramus, from angle to articular condyle is relatively low.

As in all *Tapirus*, the cheek teeth of *T. webbi* are brachydont and bilophodont. Tables 2 and 3 list measurements taken on individual teeth while Table 4 presents summary statistics. The CV for teeth of *T. webbi* ranges between 2.5 and 7.5 for all but one dental parameter, P1 width (Table 4). The magnitude of the CVs



Table 2. Measurements on individual upper cheek teeth of the holotype, paratypes, and key referred specimens of *Tapirus webbi* n. sp. from the late Miocene of Florida. Locality abbreviations: LOV, Love Site; MCG, McGehee Farm Site; and MIX, Mixson's Bone Bed. In tooth locus column, R indicates a tooth from the right side and L indicates a left.

|            | Locality | Locus | L    | AW   | PW    | Comments |
|------------|----------|-------|------|------|-------|----------|
| UF 11005   | MCG      | LP1   | 20.0 | —    | 18.5  | Holotype |
| UF 11005   | MCG      | RP2   | 23.1 | 21.9 | 25.2  | "        |
| UF 11005   | MCG      | RP3   | 22.6 | —    | 26.5  | "        |
| UF 11005   | MCG      | LP4   | 22.6 | 26.7 | 26.3  | "        |
| UF 11005   | MCG      | LM1   | 23.8 | 27.4 | 23.7  | "        |
| UF 11005   | MCG      | LM2   | 27.3 | 29.4 | 26.0  | "        |
| UF 11007   | MCG      | LP1   | 18.0 | —    | 15.1  | Paratype |
| UF 11007   | MCG      | LP2   | 21.1 | 19.1 | 22.4  | "        |
| UF 11007   | MCG      | LP3   | 20.7 | 23.7 | 24.8  | "        |
| UF 11007   | MCG      | LP4   | 21.7 | 26.8 | 25.8  | "        |
| UF 11009   | MCG      | LM1   | 23.7 | 26.1 | 24.1  | "        |
| UF 11009   | MCG      | LM2   | 27.2 | 28.4 | 26.8  | "        |
| UF 11117   | MCG      | LDP1  | 20.0 | —    | 16.5  | "        |
| UF 11117   | MCG      | RDP2  | 22.1 | 19.4 | 20.6  | "        |
| UF 11117   | MCG      | RDP3  | 22.0 | 21.2 | 20.7  | "        |
| UF 11117   | MCG      | RDP4  | 23.2 | 24.3 | 21.5  | "        |
| UF 11117   | MCG      | RM1   | 24.0 | 25.7 | 22.6  | "        |
| UF 26171   | LOV      | RP1   | 19.5 | —    | 15.7  | "        |
| UF 26171   | LOV      | LP3   | 21.3 | 24.2 | 24.3  | "        |
| UF 26171   | LOV      | LM3   | 25.4 | 28.6 | 23.6  | "        |
| UF 26179   | LOV      | RP1   | 18.1 | —    | 16.6  | "        |
| UF 26179   | LOV      | RP2   | 19.6 | 18.9 | 21.9  | "        |
| UF 26179   | LOV      | RP3   | 20.4 | 23.2 | 22.9  | "        |
| UF 26179   | LOV      | RP4   | 20.8 | 24.3 | 23.8  | "        |
| UF 26179   | LOV      | RM1   | 21.6 | 24.3 | 21.6  | "        |
| UF 26179   | LOV      | RM2   | 25.1 | 26.7 | 24.0  | "        |
| F:AM 37403 | MIX      | LP1   | 18.4 | —    | 14.1  |          |
| F:AM 37403 | MIX      | LP2   | 21.3 | 20.7 | 23.2  |          |
| F:AM 37403 | MIX      | LP3   | 22.7 | 25.6 | 25.8  |          |
| F:AM 37403 | MIX      | LM1   | 22.8 | 26.0 | 23.3  |          |
| F:AM 37403 | MIX      | LM2   | 26.4 | 28.8 | 25.7  |          |
| F:AM 37403 | MIX      | LM3   | 24.8 | 28.0 | 22.6  |          |
| F:AM 37404 | MIX      | RDP2  | 21.7 | 18.9 | 19.6  |          |
| UF 211276  | MCG      | LDP1  | 19.6 | —    | 16.7  |          |
| UF 211205  | LOV      | LDP2  | 19.7 | 16.7 | 18.5  |          |
| UF 177829  | MCG      | RDP2  | 20.9 | 17.2 | 18.3  |          |
| UF 19234   | MCG      | LDP2  | 21.9 | 18.2 | 20.4  |          |
| UF 177830  | MCG      | LDP3  | 20.2 | 18.6 | 18.4  |          |
| UF 211206  | LOV      | LDP3  | 21.3 | 20.7 | 19.75 |          |
| UF 211210  | LOV      | LDP4  | 23.3 | 24.4 | 22.1  |          |
| UF 211209  | LOV      | RDP4  | 22.4 | 24.6 | 21.3  |          |
| UF 26166   | LOV      | LDP4  | 23.6 | 24.8 | 21.9  |          |
| UF 11004   | MCG      | LP1   | 18.4 | —    | 15.2  |          |
| UF 27101   | LOV      | LP2   | 20.6 | 21.5 | 24.5  |          |
| UF 26169   | LOV      | RP2   | 20.2 | 18.9 | 22.8  |          |
| UF 27070   | MCG      | RP3   | 21.4 | 25.3 | 25.8  |          |
| UF 27070   | MCG      | RP4   | 23.3 | 27.9 | 27.4  |          |
| UF 11137   | MCG      | LM1   | 24.1 | 26.7 | 23.8  |          |
| UF 32058   | MCG      | LM3   | 25.1 | 27.2 | 23.3  |          |

Table 3. Measurements on individual lower cheek teeth of the holotype, paratypes, and key referred specimens of *Tapirus webbi* n. sp. from the late Miocene of Florida. Locality abbreviations: LOV, Love Site; MCG, McGehee Farm Site; and MIX, Mixson's Bone Bed. In tooth locus column, R indicates a tooth from the right side and L indicates a left.

|            | Locality | Locus | L     | AW    | PW   | Comments |
|------------|----------|-------|-------|-------|------|----------|
| UF 11005   | MCG      | R p2  | 24.1  | —     | 17.2 | Holotype |
| UF 26191   | LOV      | R p2  | 22.6  | 12.0  | 13.8 | Paratype |
| UF 26191   | LOV      | R p3  | 21.2  | 15.0  | 16.5 | "        |
| UF 26191   | LOV      | R p4  | 21.0  | 17.9  | 17.4 | "        |
| UF 26191   | LOV      | R m1  | 22.8  | 17.9  | 16.3 | "        |
| UF 26191   | LOV      | R m2  | 26.5  | 19.2  | 18.0 | "        |
| UF 26191   | LOV      | R m3  | 27.7  | 19.2  | 17.5 | "        |
| UF 11117   | MCG      | R dp2 | 26.6  | 11.9  | 13.8 | "        |
| UF 11117   | MCG      | R dp3 | 23.3  | 13.9  | 14.4 | "        |
| UF 11117   | MCG      | L dp4 | 24.5  | 16.0  | 15.6 | "        |
| F:AM 37402 | MIX      | R p2  | 25.5  | —     | 17.3 |          |
| F:AM 37402 | MIX      | R p3  | 24.5  | 16.9  | 20.0 |          |
| F:AM 37402 | MIX      | R dp4 | 24.5  | 16.9  | 17.0 |          |
| F:AM 37402 | MIX      | R m1  | 25.3  | 18.9  | 18.7 |          |
| F:AM 37402 | MIX      | L m2  | 29.4  | 20.85 | 20.8 |          |
| UF 27071   | LOV      | R dp2 | 24.2  | 11.35 | 12.8 |          |
| UF 27006   | MCG      | R dp3 | 22.8  | 14.6  | 14.9 |          |
| UF 26216   | LOV      | R dp3 | 20.5  | 12.3  | 13.2 |          |
| UF 26188   | LOV      | L dp3 | 22.8  | 13.5  | 15.8 |          |
| UF 26188   | LOV      | L dp4 | 24.4  | 15.6  | 16.2 |          |
| UF 26216   | LOV      | R dp4 | 21.9  | 14.3  | 14.3 |          |
| UF 27006   | MCG      | R dp4 | 25.0  | 16.8  | 16.0 |          |
| UF 26192   | LOV      | L dp4 | 23.50 | 15.40 | 15.6 |          |
| UF 211266  | LOV      | L dp4 | 23.30 | 15.30 | 15.4 |          |
| UF 26216   | LOV      | R m1  | 23.0  | 16.5  | 15.6 |          |
| UF 26188   | LOV      | L m1  | 25.2  | 18.2  | 17.5 |          |
| UF 26186   | LOV      | L m1  | 24.0  | 19.4  | 18.1 |          |
| UF 28013   | LOV      | R m1  | 23.3  | 18.1  | 17.3 |          |
| UF 28013   | LOV      | R m2  | 25.7  | 19.6  | 18.7 |          |
| UF 26186   | LOV      | L m2  | 26.2  | 20.5  | 19.2 |          |
| UF 26190   | LOV      | R m2  | 27.4  | 19.4  | 18.3 |          |
| UF 26195   | LOV      | L m2  | 26.6  | 18.6  | 16.9 |          |
| UF 26195   | LOV      | L m3  | 27.2  | 19.4  | 17.1 |          |
| UF 26186   | LOV      | L m3  | 26.9  | 19.6  | 17.2 |          |
| UF 26213   | LOV      | R m3  | 24.7  | 18.8  | 17.2 |          |
| UF 32082   | LOV      | L m3  | 26.8  | 20.0  | 17.2 |          |
| UF 27244   | LOV      | L m3  | 25.8  | 18.0  | 16.2 |          |
| UF 26187   | LOV      | R m3  | 27.5  | 19.3  | 17.9 |          |
| UF 27246   | LOV      | R m3  | 27.8  | 19.0  | 17.3 |          |

Table 4. Statistical comparison of upper and lower cheek tooth measurements of fossil *Tapirus*. Sample of *Tapirus webbi* composed of specimens from the Love, McGehee Farm, and Mixson's sites, late Miocene of Florida. Measurements of UNSM 45106, holotype of *Tapirus simpsoni*, late Miocene of Nebraska taken from Schultz et al. (1975). Sample of *Tapirus johnsoni* composed of specimens from the Xmas-Kat Channel Fauna and stratigraphic equivalents, late Miocene of Nebraska (Skinner & Johnson 1984). Sample of *Tapirus veroensis* composed of specimens from the late Pleistocene of Florida, Georgia, and South Carolina.

|       | <i>Tapirus webbi</i> n. sp. |       |      |      | <i>Tapirus simpsoni</i> | <i>Tapirus johnsoni</i> |       |      |      | <i>Tapirus veroensis</i> |       |      |      |
|-------|-----------------------------|-------|------|------|-------------------------|-------------------------|-------|------|------|--------------------------|-------|------|------|
|       | n                           | x     | s    | CV   |                         | n                       | x     | s    | CV   | n                        | x     | s    | CV   |
| P1 L  | 20                          | 18.82 | 0.83 | 4.38 | 19.7                    | 5                       | 17.26 | 0.40 | 2.34 | 37                       | 18.80 | 1.06 | 5.64 |
| P1 W  | 20                          | 16.64 | 1.53 | 9.20 | 20.0                    | 5                       | 16.04 | 0.72 | 4.49 | 37                       | 16.47 | 1.54 | 9.37 |
| P2 L  | 16                          | 20.66 | 0.92 | 4.46 | 20.6                    | 8                       | 19.32 | 1.56 | 8.06 | 36                       | 19.87 | 1.00 | 5.05 |
| P2 AW | 16                          | 20.08 | 1.02 | 5.07 | 23.8                    | 7                       | 20.34 | 1.36 | 6.69 | 36                       | 21.32 | 1.00 | 4.69 |
| P2 PW | 16                          | 23.09 | 0.91 | 3.94 | 25.9                    | 7                       | 22.74 | 0.77 | 3.39 | 32                       | 23.60 | 1.24 | 5.24 |
| P3 L  | 22                          | 21.28 | 0.79 | 3.71 | 21.1                    | 7                       | 19.70 | 1.04 | 5.28 | 33                       | 20.55 | 0.95 | 4.61 |
| P3 AW | 18                          | 24.32 | 0.77 | 3.16 | 27.8                    | 7                       | 24.27 | 0.85 | 3.51 | 33                       | 24.79 | 1.16 | 4.70 |
| P3 PW | 18                          | 24.69 | 0.96 | 3.88 | 27.6                    | 7                       | 24.14 | 0.50 | 2.08 | 32                       | 24.79 | 1.19 | 4.79 |
| P4 L  | 18                          | 22.33 | 0.74 | 3.31 | 21.8                    | 7                       | 19.91 | 1.00 | 5.01 | 40                       | 21.55 | 1.26 | 5.86 |
| P4 AW | 19                          | 26.47 | 1.05 | 3.97 | 29.5                    | 7                       | 25.09 | 0.93 | 3.71 | 41                       | 26.93 | 1.48 | 5.48 |
| P4 PW | 19                          | 26.01 | 1.09 | 4.17 | 28.3                    | 7                       | 24.76 | 0.62 | 2.52 | 41                       | 26.33 | 1.51 | 5.72 |
| M1 L  | 23                          | 23.41 | 1.04 | 4.43 | 22.2                    | 6                       | 21.30 | 1.08 | 5.07 | 46                       | 22.79 | 1.21 | 5.29 |
| M1 AW | 21                          | 25.54 | 1.17 | 4.57 | 27.0                    | 6                       | 25.58 | 0.53 | 2.08 | 44                       | 26.50 | 1.22 | 4.60 |
| M1 PW | 21                          | 23.13 | 0.85 | 3.66 | 24.0                    | 6                       | 22.28 | 0.34 | 1.54 | 45                       | 24.13 | 1.08 | 4.47 |
| M2 L  | 16                          | 26.06 | 1.13 | 4.32 | 26.3                    | 5                       | 23.87 | 1.32 | 5.52 | 49                       | 25.00 | 1.18 | 4.72 |
| M2 AW | 15                          | 27.70 | 1.09 | 3.94 | 30.5                    | 5                       | 26.93 | 1.16 | 4.31 | 48                       | 28.87 | 1.50 | 5.19 |
| M2 PW | 14                          | 24.92 | 0.96 | 3.86 | 26.5                    | 5                       | 23.98 | 0.89 | 3.72 | 46                       | 25.86 | 1.23 | 4.75 |
| M3 L  | 14                          | 25.76 | 1.06 | 4.13 | 26.2                    | 9                       | 24.03 | 1.14 | 4.73 | 44                       | 24.95 | 1.26 | 5.05 |
| M3 AW | 14                          | 27.97 | 0.72 | 2.57 | 28.7                    | 9                       | 26.83 | 0.95 | 3.53 | 41                       | 28.74 | 1.60 | 5.55 |
| M3 PW | 14                          | 23.18 | 0.94 | 4.04 | 23.7                    | 8                       | 21.94 | 0.70 | 3.21 | 42                       | 24.30 | 1.35 | 5.54 |
| p2 L  | 14                          | 23.54 | 0.85 | 3.61 | —                       | 12                      | 20.72 | 1.07 | 5.18 | 37                       | 23.60 | 1.14 | 4.84 |
| p2 PW | 14                          | 14.31 | 1.03 | 7.21 | —                       | 12                      | 14.32 | 0.86 | 6.02 | 36                       | 14.89 | 1.21 | 8.12 |
| p3 L  | 21                          | 22.38 | 1.01 | 4.50 | —                       | 11                      | 19.56 | 1.06 | 5.41 | 44                       | 21.42 | 1.24 | 5.78 |
| p3 AW | 21                          | 15.35 | 0.78 | 5.09 | —                       | 11                      | 15.94 | 0.71 | 4.45 | 45                       | 15.94 | 1.16 | 7.31 |
| p3 PW | 21                          | 17.21 | 0.98 | 5.69 | —                       | 10                      | 17.67 | 0.83 | 4.67 | 45                       | 17.97 | 1.37 | 7.64 |
| p4 L  | 23                          | 22.32 | 1.09 | 4.86 | —                       | 13                      | 20.11 | 0.97 | 4.84 | 46                       | 22.28 | 1.28 | 5.73 |
| p4 AW | 23                          | 17.86 | 0.85 | 4.77 | —                       | 13                      | 17.87 | 0.84 | 4.69 | 45                       | 18.98 | 1.29 | 6.81 |
| p4 PW | 23                          | 18.42 | 0.89 | 4.83 | —                       | 13                      | 18.96 | 0.76 | 4.01 | 44                       | 20.34 | 1.50 | 7.39 |
| m1 L  | 23                          | 23.71 | 0.89 | 3.77 | —                       | 15                      | 21.20 | 1.03 | 4.85 | 42                       | 22.48 | 1.08 | 4.82 |
| m1 AW | 23                          | 17.93 | 0.95 | 5.29 | —                       | 14                      | 17.28 | 0.80 | 4.65 | 40                       | 18.82 | 1.05 | 5.55 |
| m1 PW | 22                          | 16.73 | 0.92 | 5.52 | —                       | 15                      | 16.34 | 0.69 | 4.23 | 41                       | 17.67 | 1.02 | 5.78 |
| m2 L  | 14                          | 26.73 | 1.09 | 4.07 | —                       | 14                      | 23.59 | 0.93 | 3.96 | 57                       | 25.42 | 1.27 | 4.99 |
| m2 AW | 12                          | 19.53 | 0.84 | 4.31 | —                       | 14                      | 18.72 | 0.75 | 4.00 | 56                       | 20.21 | 1.00 | 4.92 |
| m2 PW | 14                          | 18.48 | 1.00 | 5.40 | —                       | 14                      | 17.86 | 0.80 | 4.48 | 56                       | 19.31 | 1.06 | 5.47 |
| m3 L  | 12                          | 26.63 | 1.04 | 3.92 | —                       | 18                      | 24.96 | 1.08 | 4.34 | 59                       | 26.67 | 1.40 | 5.25 |
| m3 AW | 14                          | 19.08 | 0.53 | 2.77 | —                       | 18                      | 18.40 | 0.72 | 3.91 | 58                       | 19.95 | 1.01 | 5.08 |
| m3 PW | 13                          | 17.15 | 0.56 | 3.29 | —                       | 17                      | 17.07 | 0.78 | 4.57 | 59                       | 17.92 | 0.97 | 5.39 |

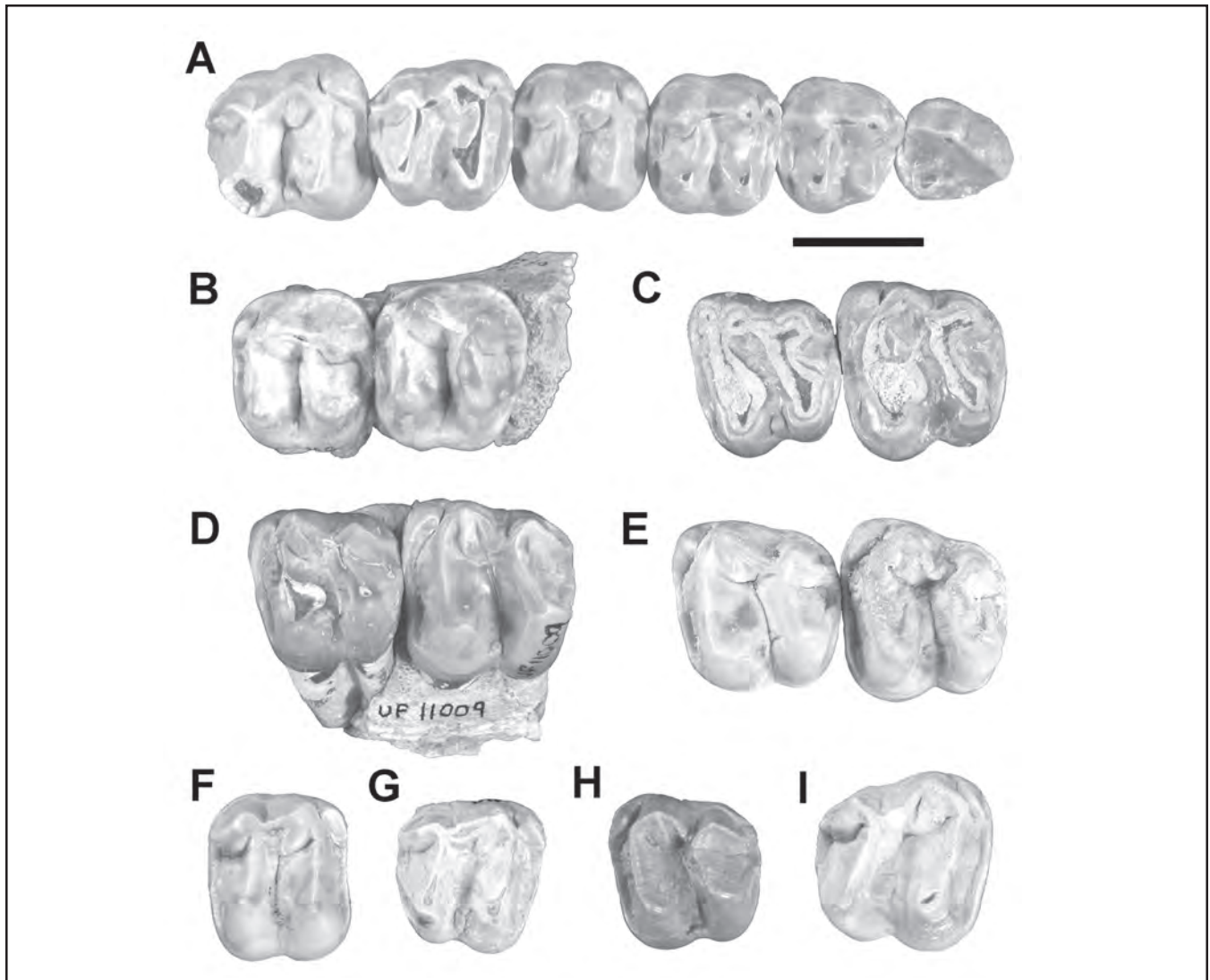


Figure 8. Occlusal views of upper cheek teeth of *Tapirus webbi* n. sp., from the late Miocene of Florida. B-D and G-H from the McGehee Farm Site, all others from the Love Site. A, UF 26179 (paratype), right P1-M2. B, UF 27005, left P3-P4. C, UF 11005 (holotype), left M1-M2. D, UF 11009 (paratype), left M1-M2. E, UF 26182, left M2-M3 (M3 unworn). F, UF 211230, right P4. G, UF 16625, right M1. H, UF 11117, left M1 (paratype, unworn). I, UF 211253, right M3. Scale bar = 2 cm.

for the *T. webbi* sample is the same as in other species of *Tapirus*, such as *T. veroensis* (Table 4) and *T. terrestris* (Simpson 1945).

The arrangement and morphology of the incisors and canines is similar to those of other *Tapirus* (Figs. 5B,6). The I3 is enlarged, caniniform, and much larger than the reduced true canine. The i1 and i2 are spatulate and procumbent, i1 much larger than i2, i3 very small (F:AM 37402 preserves the only known i3), and the large, blade-like lower canine occludes with the posterior edge of the I3.

The development of the cusps and lophs on the P1

and P2 display considerable individual variation (Figs. 7, 8A). The modal morphology of the P1 is represented by UF 26160 and 27092. Length of P1 is slightly greater than width (Tables 2, 4); and the paracone and metacone are subequal in height and located near each other (Fig. 7A-G). A low loph begins at the posterolabial end of the ectoloph and curves anterolingually around the back of the tooth, often connecting with the main lingual cusp. This cusp in its unworn state is about two-thirds the height of the paracone or metacone. In most P1s, a low transverse loph projects from the lingual cusp towards the ectoloph, but it is never long enough to di-



Table 5. Ratio of upper cheek tooth width to length in various species of *Tapirus*. Tooth width is PW for P1, P2, and P3, AW for M1, M2, and M3, and the maximum of AW and PW for P4. Right two columns show the ratio of anterior width (AW) to posterior width (PW) for P2 and M1. Data of *T. terrestris* from Simpson (1945), of *T. indicus* from Hooijer (1947), of *T. simpsoni* from Schultz et al. (1975), and of *T. priscus* and *T. arvernensis* from Guérin and Eisenmann (1994) used to calculate ratios for those taxa; remaining values based on original data. Values are sample means (except mean, minimum, and maximum observed values are listed for *T. webbi* and *T. johnsoni*); sample size is very small for several taxa, especially *T. simpsoni*, *T. priscus*, and *T. pinchaque*, and is generally adequate ( $n > 10$ ) only for *T. webbi*, *T. polkensis*, *T. veroensis*, *T. terrestris*, *T. indicus*, and *T. bairdii*.

|                           | P1  | P2  | P3  | P4  | M1  | M2  | M3  | AW/PW P2 | AW/PW M1 |
|---------------------------|-----|-----|-----|-----|-----|-----|-----|----------|----------|
| <i>T. webbi</i> (minimum) | 77  | 106 | 109 | 112 | 103 | 100 | 103 | 82       | 105      |
| <i>T. webbi</i> (mean)    | 88  | 112 | 116 | 119 | 109 | 106 | 109 | 87       | 111      |
| <i>T. webbi</i> (maximum) | 97  | 119 | 122 | 128 | 117 | 114 | 114 | 93       | 119      |
| <i>T. simpsoni</i>        | 102 | 126 | 132 | 135 | 122 | 116 | 110 | 92       | 112      |
| <i>T. johnsoni</i> (min.) | 89  | 109 | 119 | 119 | 112 | 111 | 105 | 83       | 112      |
| <i>T. johnsoni</i> (mean) | 93  | 118 | 124 | 127 | 120 | 113 | 112 | 89       | 115      |
| <i>T. johnsoni</i> (max.) | 97  | 131 | 129 | 135 | 126 | 116 | 117 | 96       | 116      |
| <i>T. priscus</i>         | 89  | 108 | 115 | 118 | 113 | 114 | 109 | 84       | 112      |
| <i>T. arvernensis</i>     | 92  | 116 | 123 | 124 | 119 | 115 | 118 | 87       | 109      |
| <i>T. augustus</i>        | 88  | 118 | 126 | 128 | 116 | 116 | 112 | 87       | 114      |
| <i>T. polkensis</i>       | 93  | 124 | 127 | 130 | 117 | 116 | 112 | 88       | 115      |
| <i>T. haysii</i>          | 92  | 118 | 120 | 125 | 116 | 117 | 117 | 91       | 110      |
| <i>T. veroensis</i>       | 88  | 119 | 121 | 126 | 116 | 116 | 115 | 90       | 110      |
| <i>T. terrestris</i>      | 93  | 115 | 119 | 124 | 113 | 113 | 115 | 90       | 111      |
| <i>T. pinchaque</i>       | 74  | 106 | 108 | 125 | 105 | 101 | 105 | 90       | 111      |
| <i>T. bairdii</i>         | 85  | 115 | 121 | 123 | 114 | 112 | 112 | 87       | 112      |
| <i>T. indicus</i>         | 77  | 111 | 119 | 130 | 106 | 112 | 110 | 82       | 113      |

rectly connect with the ectoloph (Fig. 7A-E). The height and length of this transverse loph vary greatly. Sometimes another loph or ridge extends anteriorly from the lingual cusp (UF 26160, 27089; Fig. 7D-E), but in other specimens there is instead a distinct, much smaller cusp anterior to the main lingual cusp (UF 11005, 27090; Fig. 7A, C). This anterior loph or cuspule is distinct from the even lower anterior cingulum which also starts from the main lingual cusp and ends before it can connect with the ectoloph. Several P1s in the Love Site sample have a much simpler morphology, with no hint of a transverse loph and a weaker lingual cusp (Fig. 7F-G). A posterolabial cingulum is generally absent on the P1, being present only in UF 27090.

Anterior width of P2 is between 82 and 93 percent of PW with a mean value of 87 ( $n=16$ ; Table 5; Fig. 7H-L). P2 has a weak parastyle; both transverse lophs are low, usually connecting with the base of the ectoloph (protoloph not connected in some P2s); protocone lowest of the four major cusps. While the outline of most P2s is trapezoidal (Fig. 7H-J), it is more triangular in UF 26169 and 27100 (Fig. 7K-L), with a much weaker and

more labially located protocone, protoloph that ends before connecting to the ectoloph, and a much stronger anterior cingulum. In about half of the P2s, and in a similar proportion of the succeeding cheek teeth, a distinct labial cingulum encircles the base of the metacone that usually ends with a very small styler cusp between the paracone and metacone. Other specimens possess the styler cusp but lack the labial cingulum. Despite the variable presence of this cingulum, the PW of the P2 through M3 are not significantly more variable than AW or tooth length (Table 4). The P3 through M3 have strong, complete protolophs and metalophs (Fig. 8).

Deciduous upper premolars (Fig. 9A-C; Table 2) are more brachydont than the permanent dentition and have thinner enamel. The transverse loph from the main lingual cusp on the DP1 is complete, connecting with the ectoloph. The DP2-DP4 are more molariform than their replacements, with well developed, complete protolophs and metalophs. The DP4 has the same general proportions as the M3.

The p2 and p3 have strong paralophs and metalophs; these are weaker on p4-m3 (Fig. 10; Tables

3-4). Unworn and slightly worn p3 through m3 have prominent anterior and posterior cingula (Figs. 9F, 10E-F); these are reduced by interdental wear. The protolophids and hypolophids are well separated on p4 through m3, and in unworn teeth the height of the hypolophid is not distinctly less than that of the protolophid. Lower deciduous premolars (Fig. 9D-F; Table 3) are narrower than their permanent replacements, more brachydont, and the dp3 and dp4 are morphologically and proportionally more like the permanent molars.

Relatively large samples of most major limb elements of *T. webbi* are available (Table 6; Fig. 11). General morphologic similarity with other members of the genus is evident, with three notable exceptions. Size of the limb elements, especially their lengths, relative to the teeth or cranium is large. Also, all metatarsal 4s for which the proximal end is well preserved bear a posterior facet for articulation with the metatarsal 1 (Fig. 12). This facet varies in size, but is consistently present. The muscle scars on the diaphyses of the metapodials are unusually well developed.

Discussion.—The first published record of the taxon herein named *Tapirus webbi* was in the faunal list of the McGehee Farm Site in Hirschfeld and Webb (1968). They listed the McGehee tapir as *Tapiravus* sp., a genus today regarded as composed of small-sized tapirids (Schoch 1984). The original referral of the large McGehee tapir to *Tapiravus* instead of *Tapirus* was probably caused by two factors, a general reluctance of workers at the time to recognize pre-Blancan tapirs as *Tapirus*, and a misleading measurement published by Olsen (1960) for the holotype of "*Tapiravus*" *polkensis* which gave a false impression that the tooth is much larger than it truly is. At about this time, and probably for similar reasons, Webb and Tessman (1968) referred an upper molar from south Florida to *Tapiravus* cf. *polkensis* when in fact it is much too large to represent that species.

By the time Webb et al. (1981) published their review of the Love Site fauna, Schultz et al. (1975) had described *Tapirus johnsoni* and *Tapirus simpsoni* from the late Miocene of Nebraska and Yarnell (1980) had referred the McGehee Farm and Love Site *Tapirus* to *T. simpsoni* in her unpublished thesis. In a short paragraph, Webb et al. (1981:525) cited two reasons for their referral of the Love Site *Tapirus* to *T. simpsoni*, similarity in overall size and degree of molarization of the P1. The McGehee Farm and Love Site tapirids have been regarded as *T. simpsoni* in all subsequent publications (e.g., MacFadden & Hulbert 1990; Colbert &

Schoch 1998; Hulbert et al. 2001). But no detailed analysis of the Love Site and McGehee Farm *Tapirus* was ever done until the current study. While agreeing with Yarnell (1980) that the Love Site and McGehee Farm samples of *Tapirus* are conspecific, a novel result of this study is that they are distinct from *T. simpsoni* of Nebraska.

#### COMPARISONS BETWEEN *TAPIRUS WEBBI* AND OTHER SPECIES OF *TAPIRUS*

##### NORTH AMERICAN FOSSIL SPECIES

*Tapirus webbi* is easily distinguished from all North American fossil species of the genus except *Tapirus simpsoni*. *T. webbi* differs from contemporaneous *Tapirus johnsoni* of Nebraska in having larger overall size (Tables 1, 4), longer and thicker nasals, relatively shorter upper and lower diastemata, a mental foramen located directly ventral to p2 (more anteriorly located in *T. johnsoni*), relatively narrower cheek teeth (Table 5) which are higher crowned and have better separated transverse lophs, and larger parastyles on P3-M3. *T. johnsoni* has a small flange on the dorsal margin of the maxilla, a feature not found in *T. webbi*.

*Tapirus webbi* is distinguished from *Tapirus haysii*, *Tapirus veroensis*, and the new late Blancan species from Florida by having: a much shallower and less extensive mental diverticulum fossa on the dorsal surface of the skull; longer and thicker nasals (Fig. 2); a spicular posterior lacrimal process that does not conceal the dorsal lacrimal foramen; a polygonal (not triangular) interparietal; a sloped (not vertical) posterior surface of the skull dorsal to foramen magnum; a wider maxillary bar between the IOF and lacrimal; a relatively shallower horizontal ramus (especially below the m3); a vertically oriented ascending ramus that does not project anteriorly (Fig. 5); generally narrower cheek teeth (Table 5); posterolabial cingula common on upper cheek teeth; and an articulation between the first and fourth metatarsals (Fig. 12). Detailed comparisons with *Tapirus polkensis* will be done upon description of the extensive Gray Fossil Site, Tennessee sample, but *T. webbi* is much larger (Tables 6-7) and differs in its narrower cheek teeth (Table 5) and having articulation between the first and fourth metatarsals. *T. webbi* has significantly smaller and narrower cheek teeth and a relatively longer diastema than *Tapirus merriami* (Jefferson 1989). Other comparisons between the two are limited by the fragmentary nature of known specimens of the western species.

*Tapirus simpsoni* from Nebraska is known primarily from the holotype palate, UNSM 45106, as well

as an isolated p2 and DP1 (Schultz et al. 1975). Similarities with *Tapirus webbi* include relative upper diastema length, similar relative length and shape of the posterior process of the premaxilla, wide maxillary bar between lacrimal and IOF, location of IOF relative to tooth row, presence of posterolabial cingula and strong parastyles on P3-M3, relatively strong lingual cusp and transverse loph on P1, and general size. The two differ in that the transverse lophs of the P1 and P2 of *T. webbi* are more weakly developed, especially the P2 protoloph. Also, the P1 of *T. simpsoni* is wider than it is long, a state not observed in 20 specimens of *T. webbi* (Table 4). Excluding the M3, upper cheek teeth of *T. simpsoni* have a greater width relative to length than those of *T. webbi* (Table 5). The narrow proportions of the latter's upper teeth are generally similar to those of *Tapirus priscus*, *Tapirus indicus*, and *Tapirus pinchaque*. In contrast, those of *T. simpsoni* are proportionally more similar to those of *Tapirus johnsoni*, *Tapirus polkensis*, *Tapirus haysii*, *Tapirus veroensis*, *Tapirus arvernensis*, and *Tapirus augustus* (Table 5). The upper teeth of *Tapirus bairdii* and *Tapirus terrestris* generally have intermediate relative widths. Lower teeth, not listed in Table 5, show the same basic pattern except the differences are more subtle, and *T. augustus* switches from the broad-toothed group to the narrow-toothed group.

#### *TAPIRUS PRISCUS* KAUP 1833

The typical late Miocene tapir of Europe, *Tapirus priscus* was reviewed by Guérin and Eisenmann (1994). It is of the same general size as *Tapirus webbi* (and *Tapirus simpsoni*). Unfortunately, the dorsal region of the skull of *T. priscus* is undescribed and the quantitative analysis of Guérin and Eisenmann (1994) did not describe potentially significant characters of the skull (such as extent of posterior process of premaxilla) or the mandible (such as location of mental foramen and orientation of ascending ramus). Another potential problem with the results of Guérin and Eisenmann (1994) is that their reported coefficients of variation for tooth measurements of *T. priscus* are much larger than those of *T. webbi* or *Tapirus veroensis* (Table 4) or those reported by Simpson (1945) for *Tapirus terrestris*, which may indicate that their sample contains more than one species, or this could simply be a matter of small sample sizes. Thus it is difficult to critically compare *T. priscus* with *T. webbi*. As noted above, both have relatively narrow cheek teeth. Other similarities are a relatively short muzzle, relatively narrow mandible below the m3,

and long limb bones. Mandibular depth is significantly greater in *T. priscus*. Guérin and Eisenmann (1994) gave an OR of 52-56.5 mm for mandibular depth below the p2 for *T. priscus*, almost 20% deeper than that of *T. webbi* (Table 1). According to Guérin and Eisenmann (1994), *T. priscus* is characterized by an unusually large mandibular condyle height (157 mm in the one reported specimen). Condylar height is 128 mm in the only measurable specimen in the *T. webbi* sample (UF 26191), about the same as in *Tapirus bairdii*.

#### EXTANT *TAPIRUS*

The four extant species of *Tapirus* are easily distinguished from *Tapirus webbi*. Only *Tapirus indicus* also has articulation between the fourth metatarsal and the remnant of the first metatarsal (Radinsky 1963). *Tapirus bairdii* and *T. indicus* both have a deep, extensive fossa on the dorsal surface of the nasal and frontal to house the meatal diverticulum. *T. webbi* is like *Tapirus pinchaque* and *Tapirus terrestris* in having a much shallower, more limited meatal diverticular fossa. The dorsal margin of the maxilla of *T. webbi* is not upturned to form a dorsal flange as in *T. bairdii*, and *T. webbi* has a much longer posterior process of the premaxilla that terminates in an acute point. *T. webbi* has a shorter muzzle and narrower upper cheek teeth than *T. bairdii* and the nasals are not ossified with the mesethmoid. Other features that distinguish *T. webbi* from *T. indicus* are the latter's greatly inflated frontals, shorter nasals, premaxillary-maxillary suture located in middle of alveolus of canine, narrower P1, stronger parastyles, and anteriorly projected ascending ramus of the mandible. In addition to resembling *T. pinchaque* and *T. terrestris* in the development of the depression on the nasal and frontal for the meatal diverticulum, *T. webbi* shares with these two species a spicular, slender posterior lacrimal process. It differs from both *T. pinchaque* and *T. terrestris* by having a much larger interparietal, longer posterior process of premaxilla, labial cingulum common on posterior half of P2-M3, and larger size. The P1 and P2 of *T. pinchaque* are on average narrower than those of *T. webbi*. *T. webbi* lacks the distinctive, high sagittal crest of *T. terrestris* and has a thicker, longer nasal.

#### OTHER LATE MIOCENE TAPIRIDS FROM FLORIDA

In contrast to the relatively complete and numerous samples of *Tapirus* from the Archer Fauna, early Hh sites in Florida that are younger than the Archer Fauna either lack tapirids or produce small numbers of limb elements, isolated teeth, and cranial fragments. Most



such specimens cannot be identified to a particular species, but based simply on size a minimum of two species are represented. Two Hh2 localities from Manatee County in southwestern Florida, the Manatee County Dam and SR 64 sites (Fig. 1), each produced a single

upper molar that represents an indeterminate medium-to large-sized *Tapirus*. Excavations at the new discovered Tyner Farm Site in western Alachua County (Fig. 1; Hulbert et al. 2002) only produced a partial metapodial and a tarsal element of a large, specifically undiagnostic

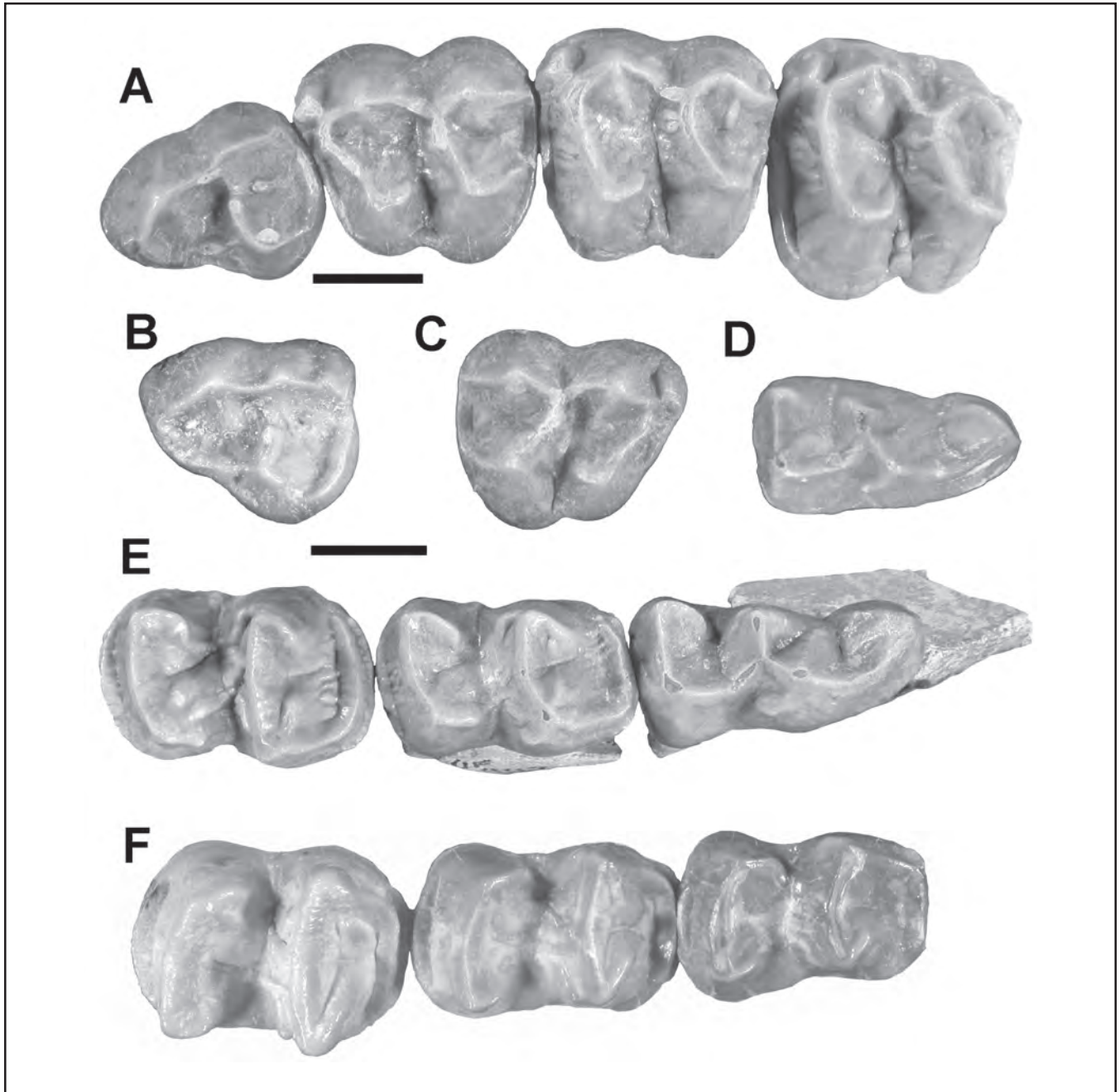


Figure 9. Occlusal views of juvenile dentitions of *Tapirus webbi* n. sp., from the late Miocene of Florida. A-C and E from the McGehee Farm Site, others from the Love Site. A, UF 11117 (paratype), left DP1-DP4. B, UF 211276, left DP1. C, UF 177829, right DP2. D, UF 27071, right dp2. E, UF 11117 (paratype), right dp2-dp4. F, UF 26188, left dp3-m1. Scale bars = 1 cm; upper scale bar for A only, lower bar for B-F.



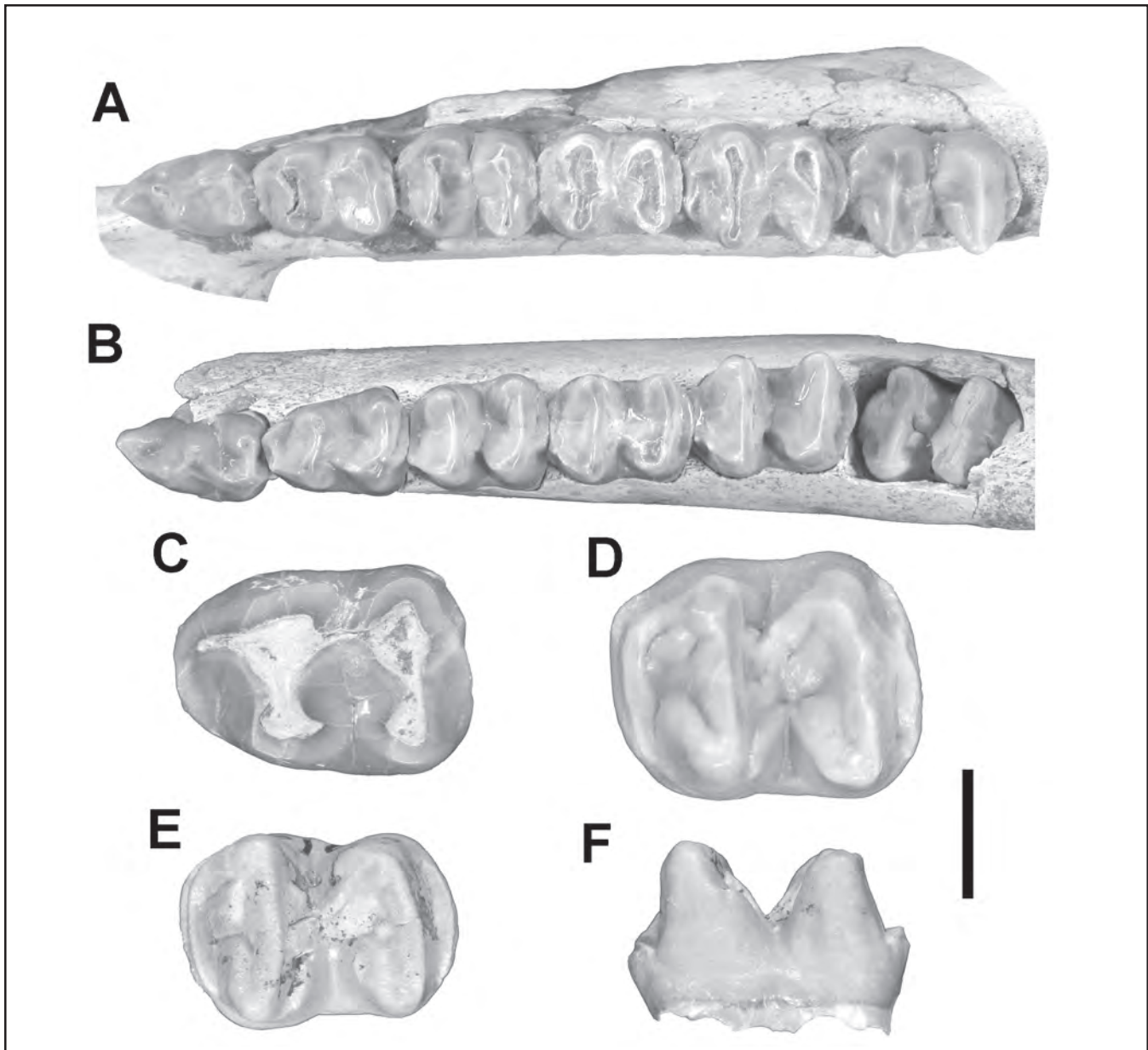


Figure 10. Occlusal (A-E) and medial (F) views of lower cheek teeth of *Tapirus webbi* n. sp., from the late Miocene of Florida. C-D from the McGehee Farm Site, all others from the Love Site. A, UF 26191, right p2-m3. B, UF 28014, left p2-m3 (m3 just beginning to erupt from crypt). C, UF 11005 (holotype), right p2. D, UF 27007, right p4. E-F, UF 26216, unworn right m1. All images oriented so anterior is to the left. Scale bar = 2 cm for A-B, = 1 cm for C-F.

tapirid; in contrast, equids and the rhino *Aphelops* were very abundant. The Withlacoochee River has produced the most Hh2 tapirid specimens from Florida.

The Manatee County Dam molar (UF 11919; Fig. 13A) is barely worn and has the relative proportions of an M1 or M2 (L = 24.0; AW = 28.0; PW = 24.3 mm). Its AW/L ratio of 117 is greater than almost all M1s and M2s of *Tapirus webbi* (Table 5), and instead more similar

to those of the broad-toothed group of *Tapirus*, such as *Tapirus simpsoni*, *Tapirus veroensis*, and *Tapirus haysii*. UF 11919 has a relatively modest parastyle and a faint but distinct labial cingulum bordering the posterior half of the metacone.

The Withlacoochee River 4A locality (Fig. 1; Becker 1985) produced eight specimens of *Tapirus*, including a partial occipital region (UF 177742) and two

Table 6. Summary statistics on measurements of major postcranial elements of *Tapirus webbi* n. sp. from the late Miocene of Florida. Combined samples from the McGehee Farm and Love sites. Abbreviations for measurements generally follow von den Driesch (1976): GL, greatest length; B, breadth (= width); D, depth, SD, smallest breadth of diaphysis; DD, smallest depth of diaphysis; a, articular; l, lateral; p, proximal; and d, distal. Abbreviations specific to one element are: for humerus, GLC, GL from head; BT, breadth of distal trochlea; for radio-ulna, GLU, GL of ulna, LO, length of olecranon process, BPC, greatest articular breadth of ulna; for femur, GLC, GL from head, DC, depth of head. Other abbreviations: MC, metacarpal; MT, metatarsal.

|            |          |       |       |      |       |      |       |      |      |
|------------|----------|-------|-------|------|-------|------|-------|------|------|
| Humerus    |          | GLC   | GLl   | Bp   | Dp    | SD   | Bd    | BT   |      |
|            | <i>x</i> | 263.0 | 261.0 | 90.2 | 118.6 | 31.5 | 76.1  | 62.2 |      |
|            | <i>s</i> | 10.61 | 10.42 | 2.96 | 4.21  | 3.43 | 2.94  | 2.09 |      |
|            | MIN      | 255.5 | 244.0 | 88.1 | 114.5 | 21.8 | 70.5  | 58.7 |      |
|            | MAX      | 270.5 | 272.0 | 95.2 | 125.0 | 35.7 | 81.7  | 66.5 |      |
|            | <i>n</i> | 2     | 5     | 5    | 6     | 16   | 15    | 12   |      |
| Radio-ulna |          | GL    | Ll    | Bap  | SD    | Bad  | GLU   | LO   | BPC  |
|            | <i>x</i> | 251.3 | 224.6 | 60.0 | 32.1  | 53.1 | 327.0 | 88.7 | 50.8 |
|            | <i>s</i> | 6.19  | 2.85  | 2.29 | 1.70  | 2.48 | 5.66  | 4.17 | 3.06 |
|            | MIN      | 243.0 | 221.0 | 54.5 | 29.4  | 47.7 | 323.0 | 82.8 | 47.2 |
|            | MAX      | 259.0 | 228.0 | 64.5 | 35.1  | 57.6 | 331.0 | 93.9 | 54.2 |
|            | <i>n</i> | 6     | 6     | 25   | 12    | 12   | 2     | 5    | 5    |
| MC 2       |          | GL    | Bp    | SD   | DD    | Bd   | Dd    |      |      |
|            | <i>x</i> | 114.7 | 27.0  | 21.2 | 11.6  | 21.6 | 27.3  |      |      |
|            | <i>s</i> | 3.27  | 1.60  | 0.81 | 0.47  | 0.79 | 0.60  |      |      |
|            | MIN      | 107.0 | 24.8  | 19.6 | 10.8  | 20.7 | 26.4  |      |      |
|            | MAX      | 119.2 | 29.9  | 22.5 | 12.4  | 23.2 | 28.3  |      |      |
|            | <i>n</i> | 13    | 10    | 12   | 12    | 12   | 12    |      |      |
| MC 3       |          | GL    | Bp    | SD   | DD    | Bd   | Dd    |      |      |
|            | <i>x</i> | 134.6 | 32.5  | 25.9 | 13.5  | 32.5 | 24.4  |      |      |
|            | <i>s</i> | 3.15  | 0.71  | 1.30 | 0.70  | 1.01 | 0.62  |      |      |
|            | MIN      | 127.9 | 31.4  | 24.0 | 12.4  | 30.9 | 23.4  |      |      |
|            | MAX      | 137.4 | 33.6  | 28.6 | 14.7  | 33.8 | 25.4  |      |      |
|            | <i>n</i> | 8     | 11    | 14   | 14    | 8    | 8     |      |      |
| MC 4       |          | GL    | Bp    | SD   | DD    | Bd   | Dd    |      |      |
|            | <i>x</i> | 112.0 | 23.4  | 21.4 | 13.4  | 22.5 | 26.3  |      |      |
|            | <i>s</i> | 4.84  | 1.50  | 0.98 | 1.06  | 0.97 | 1.93  |      |      |
|            | MIN      | 105.4 | 21.6  | 20.5 | 11.9  | 20.9 | 24.2  |      |      |
|            | MAX      | 116.3 | 25.3  | 23.2 | 14.4  | 23.4 | 28.4  |      |      |
|            | <i>n</i> | 4     | 8     | 6    | 6     | 5    | 5     |      |      |
| MC 5       |          | GL    | Bp    | SD   | DD    | Bd   | Dd    |      |      |
|            | <i>x</i> | 89.7  | 13.4  | 17.3 | 9.9   | 17.8 | 22.5  |      |      |
|            | <i>s</i> | 4.24  | 1.29  | 1.14 | 0.96  | 0.90 | 1.46  |      |      |
|            | MIN      | 83.6  | 11.5  | 15.5 | 8.6   | 15.9 | 20.8  |      |      |
|            | MAX      | 99.4  | 15.4  | 19.1 | 12.1  | 18.7 | 25.3  |      |      |
|            | <i>N</i> | 11    | 11    | 12   | 12    | 11   | 11    |      |      |

Table 6. (Cont.)

|       |          |       |       |       |      |      |      |       |       |
|-------|----------|-------|-------|-------|------|------|------|-------|-------|
|       |          | GL    | GLC   | Bp    | DC   | SD   | Bda  | Ddl   | Ddm   |
|       | <i>x</i> | 358.0 | 339.3 | 113.2 | 48.8 | 39.2 | 86.3 | 101.7 | 112.0 |
|       | <i>s</i> | —     | 1.77  | 8.34  | 1.94 | 3.82 | 1.47 | 2.53  | 2.89  |
| Femur | MIN      | —     | 338.0 | 102.2 | 45.8 | 35.0 | 84.2 | 98.0  | 108.2 |
|       | MAX      | —     | 340.5 | 121.3 | 51.3 | 42.5 | 87.5 | 104.4 | 114.7 |
|       | n        | 1     | 2     | 4     | 7    | 3    | 4    | 5     | 4     |
|       |          | GL    | LI    | Bp    | SD   | Bd   | Dd   |       |       |
|       | <i>x</i> | 288.0 | 260.3 | 87.9  | 30.9 | 54.3 | 48.3 |       |       |
|       | <i>s</i> | 1.41  | 9.00  | 4.83  | 2.07 | 2.18 | 2.18 |       |       |
| Tibia | MIN      | 287.0 | 250.0 | 82.0  | 26.4 | 51.1 | 45.2 |       |       |
|       | MAX      | 289.0 | 266.5 | 95.7  | 32.8 | 58.1 | 52.7 |       |       |
|       | n        | 2     | 3     | 7     | 13   | 20   | 21   |       |       |
|       |          | GL    | Bp    | SD    | DD   | Bd   | Dd   |       |       |
|       | <i>x</i> | 118.3 | 20.1  | 21.0  | 14.5 | 21.8 | 28.4 |       |       |
|       | <i>s</i> | 3.61  | 1.33  | 0.86  | 0.75 | 1.25 | 1.24 |       |       |
| MT 2  | MIN      | 112.1 | 16.9  | 19.5  | 13.4 | 20.1 | 27.0 |       |       |
|       | MAX      | 124.7 | 21.2  | 22.3  | 15.4 | 23.3 | 30.4 |       |       |
|       | n        | 10    | 12    | 12    | 12   | 11   | 10   |       |       |
|       |          | GL    | Bp    | SD    | DD   | Bd   | Dd   |       |       |
|       | <i>x</i> | 132.5 | 32.8  | 24.1  | 15.3 | 31.3 | 24.5 |       |       |
|       | <i>s</i> | 4.23  | 1.11  | 1.14  | 0.94 | 1.24 | 0.86 |       |       |
| MT 3  | MIN      | 121.7 | 31.0  | 22.3  | 13.4 | 29.1 | 22.9 |       |       |
|       | MAX      | 142.7 | 34.8  | 26.2  | 17.0 | 34.7 | 26.4 |       |       |
|       | n        | 19    | 19    | 22    | 20   | 20   | 18   |       |       |
|       |          | GL    | Bp    | SD    | DD   | Bd   | Dd   |       |       |
|       | <i>x</i> | 118.7 | 22.2  | 20.4  | 17.1 | 21.3 | 28.4 |       |       |
|       | <i>s</i> | 4.52  | 1.11  | 1.62  | 0.91 | 0.98 | 1.95 |       |       |
| MT 4  | MIN      | 112.1 | 20.2  | 17.0  | 15.7 | 19.5 | 25.5 |       |       |
|       | MAX      | 127.9 | 24.1  | 23.5  | 19.0 | 22.8 | 31.9 |       |       |
|       | n        | 10    | 15    | 11    | 12   | 10   | 10   |       |       |

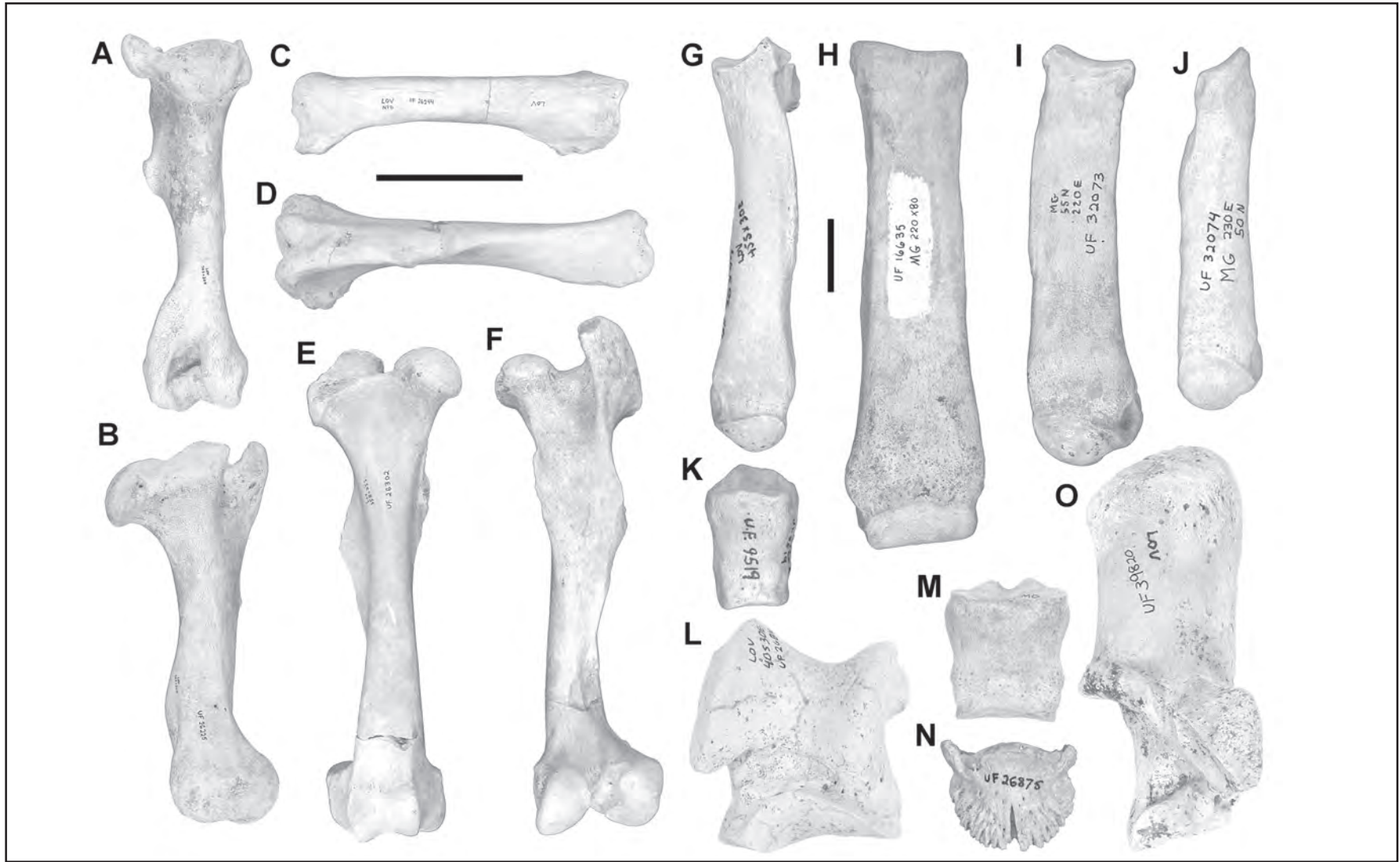


Figure 11. Postcranial skeletal elements of *Tapirus webbi* n. sp., from the late Miocene of Florida. H-K and M from the McGehee Farm Site, all others from the Love Site. A, posterior, and B, medial views of UF 26225, left humerus. C, anterior view of UF 26244, right radius. D, anterior view of UF 26319, right tibia. E, anterior, and F, posterior views of UF 26302, right femur. G, anterior view of UF 26544, right metatarsal 4. H, anterior view of UF 16635, right metatarsal 3. I, anterior view of UF 32073, left metacarpal 4. J, anterior view of UF 32074, left metacarpal 5. K, anterior view of UF 9519, proximal phalanx of digit 2 or 4. L, anterior view of UF 26811, right astragalus. M, anterior view of UF 28008, proximal phalanx of digit 3. N, dorsal view of UF 26875, ungual phalanx of digit 3. O, medial view of UF 39820, right calcaneum. Long scale bar = 10 cm for A-F; short scale bar = 2 cm for G-O.



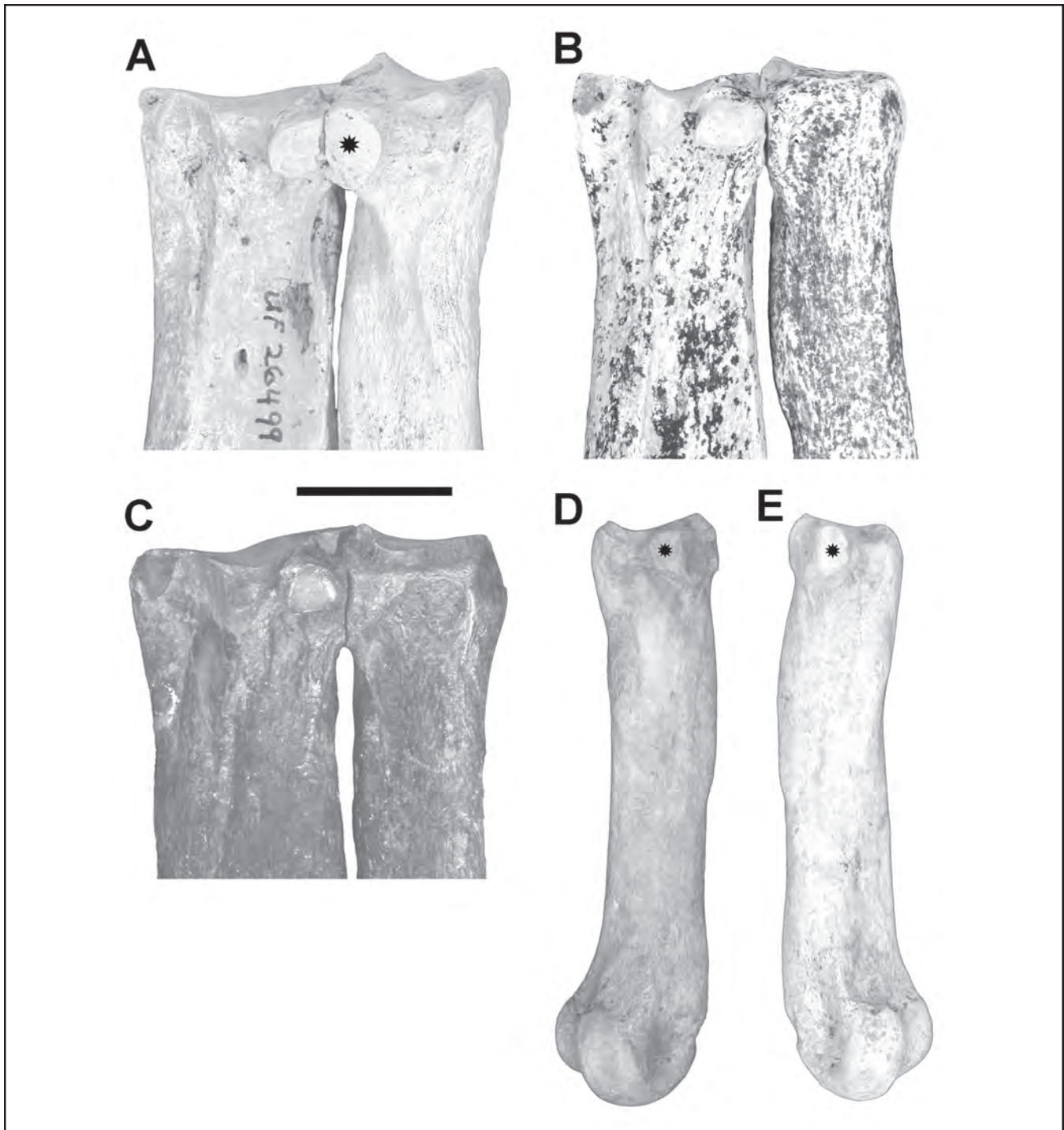


Figure 12. Posterior views of metatarsals 3 and 4 of *Tapirus* from Florida. A and D-E, *Tapirus webbi* n. sp., late Miocene. B, *Tapirus* sp., late Pliocene, Haile 7C, Alachua County. C, *T. haysii*, early Pleistocene, Leisey Shell Pit 1A, Hillsborough County. A, proximal ends of right metatarsal 3 (UF 26499) and metatarsal 4 (UF 26544) shown as if articulated. Both bear large posterior facets for articulation with the metatarsal 1 (Radinsky 1963); the facet on UF 26544 is indicated by a star. B, proximal ends of left metatarsals 3 and 4 (UF 206876), shown reversed. C, proximal ends of left metatarsal 3 (UF 83578) and metatarsal 4 (UF 84442), shown reversed. In B and C, the metatarsal 3 has a posterior facet for the metatarsal 1, but the metatarsal 4 lacks a facet, bearing instead a rugose ridge in the location of the facet in *T. webbi*. D, UF 177820, left metatarsal 4. E, UF 26533, right metatarsal 4. Facets for metatarsal 1 indicated by stars in D and E. Scale bar = 2 cm for A-C, = 3 cm for D-E.

partial dentaries (UF 13884 and 14232). The Withlacoochee River 4A specimens derive from a species smaller than *Tapirus webbi* or *Tapirus simpsoni*, one more similar in size to *Tapirus terrestris* or smaller individuals of *Tapirus veroensis*. UF 177742 has a triangular interparietal about 24 mm wide and 28 mm long that is fused with the occipital (Fig. 3C), weak lambdoidal crests that project mostly posteriorly, only slightly laterally, and the posterior surface of the occipital below the dorsal table is strongly sloped in an anterodorsal-posteroventral orientation. The latter is similar to *T. webbi*, but the shape of the interparietal and development of the lambdoidal crests are not. In some respects

the morphology of the teeth (Fig. 13B-C) is more similar to *Tapirus johnsoni* than *T. webbi*, with lower unworn crown heights, smaller parastyles, and broader teeth (P2 PW/L ratio = 119). But like *T. webbi*, and unlike *T. johnsoni*, the unworn height of the hypolophid is equal to that of the protolophid on the p3 to m3 and dp4, and the mental foramen is located ventral to the p2. Upper teeth have a posterolabial cingulum. Such a mosaic of primitive and derived cranial and dental characters suggests an early member of the group of species that includes *Tapirus veroensis*, *Tapirus haysii*, and *Tapirus bairdii*.

A distinctly smaller tapirid was recovered from the



Figure 13. Late early Hemphillian (Hh2) *Tapirus* from Florida. A, occlusal view of UF 11919, right M1 or M2 of *Tapirus* sp. from the Manatee County Dam Site. B-C, occlusal views of teeth of *Tapirus* sp. from Withlacoochee River Site 4A. B, UF 13885, left P2. C, UF 14232, left p3. D-I, *Tapirus polkensis*. D, UF 177748, left P3, Withlacoochee River Site 5E. E-H, Withlacoochee River, exact location unknown. E, anterior view of UF 177809, right metatarsal 4. F, anterior view of UF 177801, right metacarpal 2. G, anterior view of UF 177803, left metacarpal 5. H, anterior view of UF 177805, proximal phalanx of digit 3. I, anterior view of UF 177746, medial phalanx of digit 3 from the Withlacoochee River Site 5E. Scale bar = 2 cm.

Table 7. Measurements (in mm) of metapodials of *Tapirus polkensis* (Olsen) from the late Miocene and early Pliocene of Florida. Abbreviations for measurements as in Table 6. WITH, Withlacoochee River sites, late early Hemphillian; PALM, Palmetto Fauna, Bone Valley Region, latest Hemphillian; MC, metacarpal; MT, metatarsal.

|           |      |      | GL   | Bp   | SD   | DD   | Bd   | Dd   |
|-----------|------|------|------|------|------|------|------|------|
| UF 177801 | WITH | MC 2 | 85.0 | 16.5 | 12.7 | 7.6  | 13.5 | 17.6 |
| UF 177802 | WITH | MC 4 | 79.7 | 14.4 | 12.6 | 7.6  | 12.6 | 16.9 |
| UF 95737  | PALM | MC 4 | —    | 15.5 | 13.5 | —    | —    | —    |
| UF 177804 | WITH | MC 5 | 61.4 | 8.4  | 11.2 | 5.8  | 10.7 | 14.6 |
| UF 177803 | WITH | MC 5 | 60.3 | 7.9  | 10.9 | 6.2  | 12.1 | 15.4 |
| UF 101962 | PALM | MC 5 | 61.9 | 8.3  | 12.4 | 6.8  | 10.9 | —    |
| UF 220450 | PALM | MT 3 | —    | 24.4 | 17.6 | 10.5 | —    | —    |
| UF 177809 | WITH | MT 4 | 87.4 | 13.9 | 12.9 | 8.2  | 13.4 | 18.7 |
| UF 68006  | PALM | MT 4 | —    | 13.7 | —    | —    | —    | —    |

Hh2 Withlacoochee River 5E locality as well as from unspecified regions on the riverbed (Fig. 13D-I). The sample includes a P3 (UF 177748), five metapodials (UF 177801-177804, 177809), carpal elements, and phalanges. UF 177748 is unworn, rectangular in outline, with a strong, tall protoloph, metaloph, and ectoloph, and a well developed anterior cingulum (Fig. 13D). It lacks a posterolabial cingulum. The dimensions of UF 177748 (L 16.1 mm, AW 18.5, and PW 18.2) are smaller than in any extant species of *Tapirus* and about 20% smaller than the smallest known P3 of *Tapirus veroensis*. The metapodials are very small and slender (Table 7; Fig. 13E-G). The fourth metatarsal (UF 177809) does not bear a facet for the first metatarsal at its proximal end.

Similar very small tapirid metapodials (Table 7) and teeth are known from the latest Hemphillian (Hh4) Palmetto Fauna of south-central Florida (Fig. 1), and these are referred to *Tapirus polkensis* (Olsen) 1960. The geologic age of Olsen's species has long remained problematic in the literature, as the phosphate mining operations of the Bone Valley Region excavate and mix middle and late Miocene, early Pliocene, and Pleistocene sediments and fossils (Webb & Hulbert 1986; Webb et al. in press), and because the holotype lacks stratigraphic provenance. Eight referred Bone Valley specimens of *T. polkensis* (UF 14445, 133911, 177740, 177814, and 220447-220450) from Polk County, Florida, were collected in situ from early Pliocene strata in direct association with Hh4 mammals such as *Agriotherium schneideri*, *Dinohippus mexicanus*, *Teleoceras hicksi*, *Eocoileus gentryorum*, and *Rhynchotherium edense* (Webb et al. in press). Other referred specimens of *T. polkensis* in the UF collection derive from phosphate mines, or specific regions within mines, that produced

almost exclusively early Pliocene, Hh4 terrestrial vertebrates, such as the Palmetto, Gardiner, and Ft. Green mines (Fig. 1; Webb et al. in press). In contrast, Bone Valley mines that over the past three decades have produced hundreds of Miocene land vertebrate fossils (ranging in age from early Barstovian to early Hemphillian) have not produced specimens of *T. polkensis*, or any tapirid for that matter. The most logical conclusion is that *T. polkensis* is a member of the Hh4 Palmetto Fauna, and that is not present in any of the older Bone Valley faunas. However, the Withlacoochee River specimens indicate that its chronologic range does extend back to the Hh2 in Florida. Specimens from Nebraska that were referred to *T. polkensis* by Schultz et al. (1975) and Schoch (1984) and purported to be middle Miocene (Barstovian) almost certainly either represent a different taxon of similar size, or are actually Hemphillian in age.

#### CONCLUSIONS

A relatively large, long-limbed tapir lived in north-central Florida during the late Miocene. A particularly abundant sample of teeth, jaw sections with teeth, and postcranial elements is known from the late Clarendonian Love Site; it is one of the richest known, single quarry samples for a Miocene tapirid. The same species is present at the slightly younger McGehee Farm and Mixson's Bone Bed localities, including some fragmented crania. Its cranial morphology is quite different from those of other species of *Tapirus* known as fossils from North America. Among its more notable features are its long, thick, triangular-shaped nasal bones on which the fossa for the meatal diverticulum is very shallow and limited to the posterolateral corner; a large, polygo-



nal interparietal; a narrow lacrimal with a spicular posterior process; and a relatively shallow dentary in which the anterior border of the ascending ramus does not project anteriorly. This Florida tapir shares some features of the dentition and rostrum with *Tapirus simpsoni* of Nebraska, and previous workers assigned it to that taxon. But *T. simpsoni* differs from the Florida species in having significantly broader cheek teeth and better developed lophos on the P1 and P2. The Florida populations are regarded as specifically distinct from *T. simpsoni* and here designated *Tapirus webbi* n. sp.

A minimum of two species of *Tapirus* are found in Hh2 faunas in Florida. One is a moderate-sized species, currently lacked specific designation, that features a curious mix of primitive and derived features. The best sample of this taxon is from the Withlacoochee River 4A locality, but even this sample is fragmentary and limited. A much smaller species of *Tapirus* was collected in similar-aged deposits in the bed of the Withlacoochee River, and is referred to *Tapirus polkensis* based on similarity of size and slenderness of the metapodials. Most previous estimates of the age of *T. polkensis* (usually referred to the genus *Tapiravus*) were middle Miocene, but specimens collected in situ by UF personnel in the Bone Valley Formation during the past three decades demonstrate that it lived much later in the Neogene and is more properly referred to the genus *Tapirus*. This has been further confirmed by the discovery of a large quarry sample of *T. polkensis* at the Hh Gray Fossil Site in Tennessee (Wallace & Wang 2004; Wallace & Hulbert 2005).

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