THE GIANT TAPIR, *TAPIRUS HAYSII*, FROM LEISEY SHELL PIT 1A AND OTHER FLORIDA IRVINGTONIAN LOCALITIES

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ABSTRACT

Twelve new records of the giant North American tapir *Tapirus haysii* are reported from Alachua, Levy, Citrus, Polk, and Hillsborough counties, Florida. Biochronologic analysis of associated vertebrates indicates *T. haysii* was limited to the late early-middle Irvingtonian (ca. 1.5-0.6 Ma) in Florida. The sample of *T. haysii* from the Leisey Shell Pit 1A site is the most complete yet recovered, and second only to the Port Kennedy Cave population in numbers of measurable teeth. All known cranial features of *T. haysii* resemble those of *T. veroensis*, including a low, double-ridged sagittal crest, ontogenetically delayed fusion of the interparietal with adjacent cranial elements, massive mandibular ramus, and relatively short diastema. Phylogenetic analysis of New World *Tapirus* produces two equally parsimonious cladograms. In both, *T. haysii* and *T. veroensis* form one monophyletic clade, and the extant Neotropical species *T. pinchaque*, *T. terrestris*, and *T. bairdii* another. They differ with respect to the position of *T. simpsoni*, a late Miocene North American species.

RESUMEN

Se reportan 12 nuevos registros del tapir gigante Norte americano *Tapirus haysii* provenientes de los condados de Alachua, Levy, Citrus, Polk y Hillborough, Florida. El análisis biocronológico de vértebras asociadas, indica que la ocurrencia de *T. haysii* en Florida se limita al Irvingtoniano temprano y medio (aproximadamente 1.5 - 0.6 Ma atrás). La muestra de *T. haysii* recuperada del depósito de conchuelas de Leisey 1A es la más completa registrada hasta ahora y segunda en número de dientes medibles, con respecto a la población de la cueva de Puerto Kennedy. Todas las características craneales conocidas para *T. haysii* se asemejan a aquellas de *T. veroensis*, incluyendo la presencia de una cresta sagital baja de doble borde; el retraso ontogénico en la fusión del interparietal con los elementos craneales adyacentes; una gran rama mandibular y un diastema relativamente corto. El análisis filogenético de las especies del género *Tapirus* del nuevo mundo producen dos cladogramas igualmente parsimoniosos. En ambos cladogramas, *T. haysii* y *T. veroensis* conforman un clado monofilético, mientras que las especies neotropicales actualmente existentes *T. pinchaque*, *T. terrestris* y *T. bairdii* conforman otro clado. Ambos cladogramas difieren con respecto a la posición de *T. simpsoni*, especie norteamericana del Mioceno tardío.

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INTRODUCTION

Two Pleistocene species of *Tapirus* are currently recognized in eastern and central North America: *T. veroensis*, a well known species similar in size or slightly larger on average than modern New World *Tapirus*; and *T. haysii*, a poorly known, larger species. As used here, *T. veroensis* includes *T. excelsus* Simpson 1945 (Lundelius and Slaughter 1976), and *T. haysii* includes *T. copei* Simpson 1945 (Ray and Sanders 1984). Both species have been recorded from Florida (Sellards 1918; Ray 1957, 1964; Ray and Sanders 1984), although many of the earlier reports of *T. haysii* probably instead represent *T. veroensis* (e.g. Saber-tooth Cave and Melbourne; Simpson 1945; Ray and Sanders 1984). Ray and Sanders (1984:296) listed only four specimens from Florida that unequivocally represented *T. haysii*; none was recovered with an associated fauna. Prophetically they noted, "Undoubtedly more specimens of large Pleistocene tapirs [*T. haysii*] from Florida are already in collections, or will come to light as new faunas, especially of pre-Wisconsin age, are found. The richness of the record in Florida and its southerly latitude make it the most likely source of the material needed for significant improvement of understanding not only of *T. haysii* but of fossil tapirs generally."

Referred specimens of *T. haysii* are represented in the collections of fossil vertebrates of the Florida Museum of Natural History and the American Museum of Natural History from 12 Florida localities in addition to those listed in Ray and Sanders (1984). Most were collected since 1983. These specimens are important for several reasons. First, unlike all previous records from Florida, and most of those from other regions as well (Ray and Sanders 1984:295-297), many were found in direct association with diverse suites of other vertebrates. Various geochronologic methods can be used to date these sites and thereby provide for the first time a biochronologic range for *T. haysii* in Florida. Second, taken together, the Florida sample of *T. haysii* now constitutes a sufficiently large, geographically (and probably chronologically) restricted sample with which to make valid quantitative comparisons with modern species of *Tapirus*, with samples of *T. veroensis*, and with the only previously known population of *T. haysii*, that of the Port Kennedy Cave site from Pennsylvania (Simpson 1945). Over half of the Florida material derives from a single site, Leisey Shell Pit 1A, which thus forms the second largest sample of *T. haysii* known, exceeded only by the Port Kennedy population in terms of numbers of measurable teeth. Third, unlike the Port Kennedy sample, the material from Leisey 1A includes several nearly complete, undistorted maxillae and mandibles, well preserved occipital regions of three crania, and a large sample of postcranial elements. In part, the Leisey 1A sample fulfills the wishes of previous authors (e.g. Simpson 1945:66; Ray and Sanders 1984:297) for cranial material of *T. haysii*, without which its phylogenetic affinities and specific status were uncertain. Unfortunately, some of the phylogenetically most critical regions of the skull, including the nasals and frontals, are not present in the Leisey 1A sample. Nevertheless, many previously unknown or poorly known cranial features are represented in the new material.

The primary purpose of this study is to describe all records of *Tapirus haysii* from Florida, concentrating on the largest and most complete sample, that of Leisey Shell Pit 1A. Description of cranial material receives the most attention, both because it was previously unknown, and because dental and postcranial elements are very conservative in tapirs, and thus of secondary importance in elucidating phylogenetic information (Simpson 1945; Hershkovitz 1954). The biochronologic distribution of species of *Tapirus* in Florida is discussed, and a tentative phylogeny of New World *Tapirus* using cladistic methodology is proposed.

ACKNOWLEDGEMENTS

I thank the many persons who excavated Leisey 1A in 1984, and Frank A. Garcia, Ronald J. Schrader, William Smith, and Leroy Doll who donated tapir specimens they collected in 1983. Their combined efforts resulted in the fine sample of *T. haysii* described in this study. The excellent UF collection of fossil *Tapirus* has also benefitted from the donations of Eric Fernandez, L. Martin, G. Heslep, L. Roberts, Kent Ainslie, and Pierce Brodkorb. Clayton E. Ray provided valuable advise, casts of comparative material, and permission to study USNM fossils. M. Carlton and L. Gordon allowed access to the collection of Recent *Tapirus* skeletal material at the USNM, and loaned comparative specimens. Access to the F:AM collection was provided by Richard H. Tedford. As always, Gary S. Morgan helped numerous times in dealing with the UF collection. Critical reviews of the manuscript by Clayton E. Ray, Ernest Lundelius, and S. David Webb helped improve the study. This is University of Florida Contribution to Paleobiology No. 345.

ABBREVIATIONS

AMNH - Department of Vertebrate Paleontology, American Museum of Natural History, New York.
ANSP - Academy of Natural Sciences, Philadelphia.
F:AM - Frick Collection, housed with AMNH collection.
UF - Florida Museum of Natural History, University of Florida, Gainesville.
UF/FGS - Florida Geological Survey collection of fossil vertebrates, housed with UF collection.
USNM - National Museum of Natural History, Smithsonian Institution, Washington, D.C.
I/i - upper/lower incisor.
C/c - upper/lower canine.
P/p - upper/lower premolar (e.g. P4 is an upper fourth premolar).
M/m - upper/lower molar (e.g. m2 is a lower second molar).
D/d - upper/lower deciduous tooth (e.g. dp2 is a deciduous lower second premolar).
MC/MT - metacarpal/metatarsal.
x - sample mean.
s - sample standard deviation.
n - sample size.
CV - sample coefficient of variation.
OR - observed range of a sample.
MIN - observed minimum value of a sample.

MAX - observed maximum value of a sample.
assoc. - associated.
Ma - Mega-anna, millions of years before present.
myr - millions of years (in duration).
L - length.
AW - anterior width.
PW - posterior width.
BASALLTH - basilar length of skull.
PALLTH - palate length.
SAGCREST - height from basioccipital to top of skull.
I3P1DLTH - diastema length between I3 and P1 alveoli.
CP1DLTH - diastema length between C and P1 alveoli.
CANLTH - upper canine alveolar length.
CANWTH - upper canine alveolar width.
MUZWDTH - maximum upper muzzle width measured across I3s.
CONDWDTH - breadth of occipital condyles.
P1M3LTH - length of upper cheektooth row.
P1P4LTH - length of upper premolar series.
M1M3LTH - length of upper molar series.
GRTLTH - greatest length of mandible.
i3p2DLTH - diastema length between i3 and p2 alveoli.
cp2DLTH - diastema length between c and p2 alveoli.
SYMPHWDTH - symphysial width across the lower canines.
SYMPHLTH - length of the mandibular symphysis.
p2MDPTH - mandibular depth measured anterior to the p2.
m3MDPTH - mandibular depth measured posterior to the m3.
canLTH - lower canine alveolar length.
canWTH - lower canine alveolar width.
p2m3LTH - length of lower cheektooth series.
p2p4LTH - length of lower premolar series.
m1m3LTH - length of lower molar series.

MATERIALS AND METHODS

The vast majority of fossil specimens described herein are housed at the Florida Museum of Natural History, either in the UF or UF/FGS collection. The USNM has a comparatively small collection of Leisey 1A material, including three specimens of *Tapirus* that were examined and measured. The F:AM collection contains material from one major Irvingtonian site in Florida, McLeod Limerock Mine, Pocket A. The limited sample of *Tapirus* from McLeod was examined and measured. *Tapirus* specimens retained by private collectors were not included in this study unless casts were deposited in the UF collection. The localities that produced the specimens under study are all of Irvingtonian age; detailed descriptions, locality information, and a relative chronology of these sites are presented in Webb (1974) and Morgan and Hulbert (this volume). The Apollo Beach mandible recovered from dredged material provisionally regarded by Ray (1964) as Rancholabrean is much more likely to be Irvingtonian. Unbeknownst to Ray, strata of Irvingtonian age (Bermont Formation) are apparently widespread is southern Hillsborough County, and taxa restricted to the Irvingtonian have been found at Apollo Beach (e.g. *Pachyarmatherium leiseyi*).

Comparative material examined included specimens of all four extant species of *Tapirus* (*T. bairdii*, 21 skulls, USNM and UF; *T. terrestris*, 20 skulls, USNM and UF; *T. pinchaque*, 3 skulls, USNM; *T. indicus*, 4 skulls, USNM), a large sample of *T. veroensis* from the Rancholabrean of Florida (including holotype skull UF/FGS 277; numerous palates and maxillae; and mandibles), and referred material of two late Miocene species, *T. johnsoni* and *T. simpsoni* (F:AM and UF; Yarnell 1980). Museum acronyms used in conjunction with Recent species refer to specimens in mammalogy collections; those with fossil species refer to specimens in vertebrate paleontology collections.

Up to 12 cranial and 12 mandibular characters (described in Abbreviation section above) were measured. Values greater than 200 mm were taken with anthropometers to the nearest 0.5 mm; those less than 200 mm were taken to the nearest 0.01 mm (but later rounded off to nearest 0.1 mm) with either dial or digital calipers. Only adult individuals were measured for cranial and mandibular variables, as judged by the eruption of the P4/p4. The standard three dental measurements for tapir cheekteeth (Simpson 1945), length, anterior width, and posterior width, were taken with calipers (to nearest 0.01 mm), except for the DP1, P1, dp2,and p2 for which only length and posterior width were taken. Maximum tooth length was measured, usually across the ectoloph for uppers and along the midline for lowers, except when lessened by interdental wear. Maximum width was measured at about the enamel-dentine boundary, across the protoloph and metaloph on upper cheekteeth, and the protolophid and hypolophid on lowers. Postcranial elements were measured with a subset of Eisenmann's standard characters used in the study of equids (e.g. Eisenmann 1986). These generally included greatest length, diaphysial (mid-shaft) transverse width and A-P diameter, and width and A-P diameter of the proximal and distal articular surfaces. These data were entered onto a microcomputer and statistically analyzed using the Quattro spreadsheet program. Based on examination of the comparative specimens listed above and a review of the literature (especially Sellards 1918; Simpson 1945; Colbert and Hooijer 1953; Hershkovitz 1954; Lundelius and Slaughter 1976; and Ray and Sanders 1984), 26 cranial and dental characters were selected for use in a phylogenetic analysis using the PAUP computer program, version 2.4 (Swofford 1985). The BRANCH AND BOUND option of PAUP was used to produce the most parsimonious cladogram(s) possible based on the provided dataset.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen 1848
Family TAPIRIDAE Burnett 1830
Genus *TAPIRUS* Brünnich 1771
Tapirus haysii Leidy 1859

Selected Synopsis of Usage:

Tapirus haysii Leidy 1852a:106 (nomem nudum); Leidy 1852b:148 (nomen nudum); Leidy 1855:200 (nomen nudum); Leidy 1859:106 (first valid description); Sellards 1918:59; Simpson 1945:65-66 (regarded as nomen dubium); Ray and Sanders 1984:288-298 (type locality and topotypes described, name regarded as valid).

Tapirus copei Simpson 1945:66-69; Ray 1964:61-66; Strain 1966:48-50; Hager 1974:13; Lundelius and Slaughter 1976:227, 237-239; Ray and Sanders 1984:287, 293-296 (regarded as junior synonym of *T. haysii*).

Type Specimen.-- ANSP 11504, R p4 (Leidy 1859, pl. 17, figs. 7 and 8; Ray and Sanders 1984, fig. 2D).

Type Locality.-- Benners Estate, Pamlico County, North Carolina (see Ray and Sanders 1984:288-293 for an extensive discussion of the location and geology of this site).

Distribution.– Late Pliocene (late Blancan) through middle Pleistocene (Irvingtonian). Ray and Sanders (1984:293-297, fig. 3) demonstrated a near continuous range for *T. haysii* across the southern half of the United States east of the Rocky Mountains, with northernmost records in north-central Nebraska and southeastern Pennsylvania. All records of demonstrative age from Florida are early to middle Irvingtonian, ca. 1.5-0.6 Ma. Western specimens referred to *T. merriami* by Jefferson (1989) are tentatively retained in that species pending critical comparison with *T. hayi*.

Referred Florida Specimens.– Haile 16A, Alachua County. UF 91243 R MC III; 91244 L distal MC III; 91245 L MC V; 91246 L distal tibia; 46923 R MT IV; 91247, 91248 2 R astragali; 91250 2 proximal phalanges, lateral digits.

Haile 21A, Alachua County. UF 62601 L mandible with dp2-m1 (cast only); 62602 L mandible with m3.

McLeod Limerock Mine, Pocket A, Levy County. F:AM 37410 L maxilla with DP3-DP4; F:AM 37411 R mandible with dp2-dp3.

Crystal River Power Plant, Citrus County. UF 17336 proximal phalanx, digit III.

Pool Branch, Polk County. UF 11416 L M3.

Chicora Mine, Polk County. UF 65575 L scapula.

Phosphoria Mine, Polk County. UF 40060 R M2.

Tiger Bay Mine, Polk County. UF 22590 L P3.

Apollo Beach, Hillsborough County. UF 8225 assoc. R mandible with i1-i2, p2-m3 and L mandible with i1, p4-m2.

Leisey Shell Pit, Hillsborough County. **Leisey 1A**: UF 89539 assoc. L maxilla with P2-M3 and R & L mandibles with i1-m3 (cast only); 82783 assoc. R & L maxillae with DP1-DP4; 84190 assoc. R & L maxillae with P1-M3; 82782 R maxilla with P4-M3; 87231 R maxilla with P1-P3, DP4, M1-M2; 60873 R maxilla with P3-P4; 60874 L maxilla with P2-P3, DP4, M1; 60872 L maxilla with M1-M3; 65974 L maxilla with P2-P3; 65999 R edentulous maxillary fragment; 86113 assoc. premaxillae with R I1-I3 and L I1, I3; 86363 assoc. premaxillae with R I1-I3 and L I3; 80446 posterior half of skull; 83305 occipital region and R parietal; 83835 occipital region and L squamosal; 85315 L supraoccipital; 80973 assoc. mandibles missing only R i3 and c; 83580 assoc. mandibles with R & L p2-m3; 87230 assoc. mandibles with R dp2-m1 and L dp2-dp3, m1; 87947 L mandibular fragment with dp4; 65971 mandibular symphysis with R i1, c, p2 and L c; 81103 R DP1; 82784 L DP4; 86193 R P1; 80240 L P2; 87948 R M1; 89533 R M3; 65972, 86777, 86851, 87956, 88117 5 partial upper molars; 82876 L C; 83307, 86890, 81105 3 L I1s; 81104 L I2; 88778 L I3; 65973, 80838 2 R p2s; 87941 R p3; 86940, 86945 2 L p3s; 87935 L m1; 86941, 87937 2 R m2s; 63899, 87942 2 R m3s; 86790, 87468, 87936, 87944 4 partial lower cheekteeth; 86741 R c; 83993 L c; 87951 R i1; 80528, 80972, 87946 3 L i1s; 86690, 87949 2 R i2s; 87954 L i2; 88250 R i3; 65978, 84362 2 atlases; 65979, 83173 2 axes; 67538 R scapula;

65980, 67539 2 L scapulae; 87229 R distal humerus; 87228/87945 R radioulna; 81068 L radioulna; 83721 R magnum; 87955 R scaphoid; 65996 L scaphoid; 125413 R lunar; 81089 L lunar; 87467 R cuneiform; 80447, 87943 2 R unciforms; 81381 L unciform; 85317, 87938 2 R pisiforms; 80576, 81915 2 L pisiforms; 67536, 87958, 89535 3 R MC IIs; 83389, 87959 2 L MC IIs; 87950 R MC III; 81771, 89534 2 L MC IIIs; 65990, 89537 2 R MC IV; 83390, 83658, 89538 3 L MC IVs; 84082, 87952, 88777 3 R MC Vs; 82428, 84916 2 L MC Vs; 65975, 80449, 83441 3 L femora; 67537 patella; 65977 R tibia; 65976, 80653, 83579 3 L tibiae; 86866 R fibula; 81633 L fibula; 65986 R calcaneum; 65983-65985, 81235 4 L calcanea; 65982, 86883, 87705, 87960 4 R astragali; 63901, 65981, 67325, 81917, 82403, 87953 6 L astragali; 65997 R navicular; 65998, 85316, 86913 3 L naviculars; 80990 R cuboid; 65992 R ectocuneiform; 65988, 65989 2 R MT IIs; 81311, 82374 2 L MT IIs; 65987 R MT II; 81703, 83578 2 L MT IIIs; 86865 R MT IV; 63900, 84442, 89536 3 L MT IVs; 65993, 65994, 80604, 86338, 89532 5 proximal phalanges, digit III; 82375, 83816 2 distal phalanges, digit III; 84081, 84169, 87939, 87940, 89528, 89529 6 proximal phalanges, lateral digits; 65996, 81918, 83672, 86852, 88249, 89530, 89531 7 medial phalanges, lateral digits; 82121, 82463, 83996 3 distal phalanges, lateral digits. **Leisey 1B**: UF 95648 R mandible with m3; 60864 L femur. **Leisey 1**: UF 115945 R P2; 115946 R maxilla with M1-M2; 115947 R mandible with m3; 115948 L mandible with m2-m3; 115949 L m2. **Leisey 2.**: UF 115950 R P3. **Leisey 3A**: UF 115943 R DP4. **Leisey 3B**: UF 115944 L P3. **Leisey 3**: UF 130017 atlas; 142233 L MT IV; 142234 R astragalus.

Revised Diagnosis.– Significantly larger than *T. johnsoni*, *T. simpsoni*, *T. veroensis*, *T. bairdii*, *T. terrestris*, or *T. pinchaque*, with only minor overlap (if any) in cranial and dental dimensions. On average, larger than but with considerable overlap in OR of cranial and dental dimensions of *T. indicus*. Smaller than *T. augustus* and, on average, *T. merriami*. Lower toothrow length (p2-m3) 153 to 167 mm. Development of sagittal crest as in *T. johnsoni*, *T. veroensis*, and *T. pinchaque*; low, double-ridged in subadults; not like either the sagittal table of *T. bairdii* nor the high crest of *T. terrestris*. Large, subtriangular interparietal remains unfused relatively late in ontogeny, until at least the full eruption of M3. Lambdoidal crests strongly developed, flair outward. Posterodorsal process of premaxilla terminates in an acute point. Upper premolars relatively "molarized," with well developed protolophs on P2 and P3, and a variably developed transverse loph on the P1.

Description.– The following description of cranial features of *T. haysii* from Leisey 1A follows the same sequence as the comprehensive summary presented by Ray and Sanders (1984:303-308) that compared *T. veroensis* with the four extant species of *Tapirus*.

Both available premaxillae separated from their respective maxillae along the sutures. On the right side of the more complete specimen, UF 86113, it is evident that the posterior process of the premaxilla ends in an acute point, although the posteriormost portion is broken off. In dorsal view, the premaxillary-maxillary suture veers slightly laterally, which would have allowed minor exposure of the maxilla medial to the premaxilla. This arrangement is most similar to that observed in the majority of specimens of *T. veroensis* and *T. terrestris*. In *T. indicus* the amount of exposed maxilla is greater; in *T. pinchaque* (and some *T. terrestris* and *T. veroensis*) very little or none of the maxilla is exposed; and in *T. bairdii* the premaxilla terminates more bluntly. The greatest length of the premaxilla is about 105 mm (this assumes about 5 mm broken off UF 86113). In *T. veroensis*, premaxillary length is 89 to 95 mm (n = 4).

The dorsal margins on all available maxillae are broken. The most complete specimen in this regard is the juvenile UF 82783. Portions of the maxilla dorsal to the infraorbital foramen are preserved, and show the beginnings of the smoothly rounded dorsomedial border evident on maxillae of all other *Tapirus* except *T. bairdii*. *T. bairdii* has a strong dorsally directed flange on the maxilla in this region. Since this flange forms very early in ontogeny in *T. bairdii* (Ray and Sanders 1984), the young age of UF 82783 does not contribute to its absence. Although conclusive evidence is lacking, *T. haysii* probably lacked the ossified anterior mesethmoid cartilage of *T. bairdii*, as it is associated with the development of the dorsal maxillary flange. No portions of the posterodorsally ascending process of the maxilla, the lacrimals, nasals, or frontals are preserved in the available Leisey 1A sample, or any other sample of this species.

The development of the sagittal crest in *T. haysii* is shown in two specimens, UF 80446 and 83305, both of which include the occipital region and at least one complete parietal (Fig. 1A). In both the cranial sutures between the parietals, interparietal, frontals, and supraoccipital had not fused, implying that the age at death for both individuals was at most young adult. USNM 14219, a female *T. bairdii* with an erupted but only slightly worn M3, retains similarly open cranial sutures, as does the holotype of *T. veroensis*, UF/FGS 277. UF 83305 was found in close proximity with a number of other specimens, which together probably represent a single individual. These include the palate UF 84190, premaxillae (UF 86113), atlas (UF 84362), axis (UF 83173), and mandibles (UF 83580). The M3 of UF 81490 is slightly worn and represents the same wear stage as the M3 of USNM 14219. UF 83305 therefore very likely represents the young-adult stage of development of the sagittal crest in *T. haysii*. The sagittal crest on the anterior portion of the parietal begins the wide divergence that would have been carried further on the frontals. The low, double-ridged, narrow crest is formed solely on the parietals. Both UF 80446 and 83305 have very similar sagittal crests to those of young adults of *T. johnsoni* (Yarnell 1980), *T. veroensis* (Lundelius and Slaughter 1976), and *T. pinchaque* (Hershkovitz 1954; Ray and Sanders 1984). At

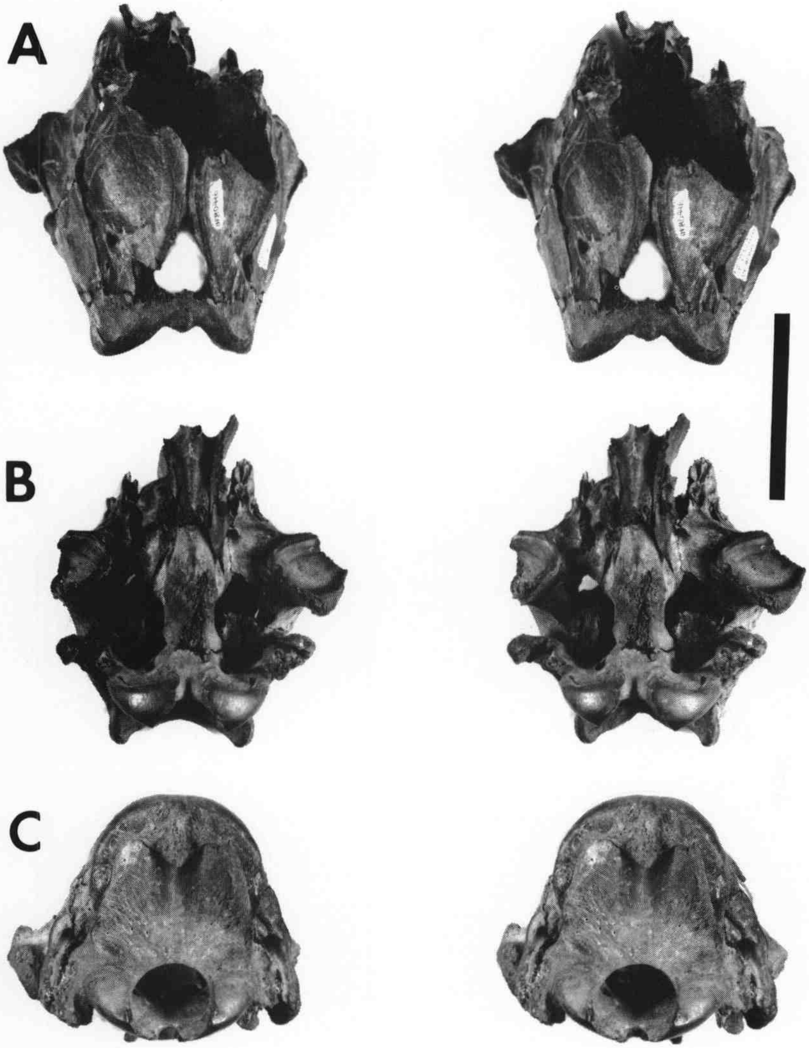

Figure 1. Dorsal (A), ventral (B), and posterior (C) views of UF 80446, partial skull of *Tapirus haysii* from Leisey Shell Pit 1A, Hillsborough County, Florida. Length of scale bar = 10 cm.

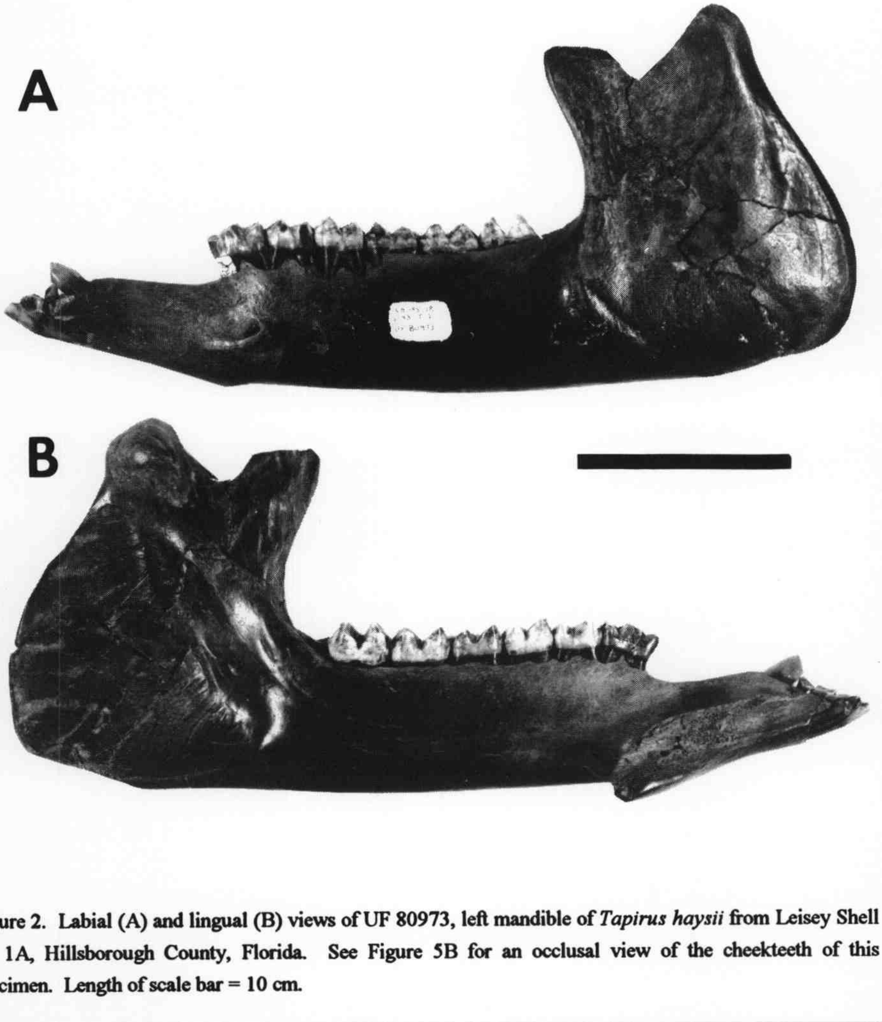

Figure 2. Labial (A) and lingual (B) views of UF 80973, left mandible of *Tapirus haysii* from Leisey Shell Pit 1A, Hillsborough County, Florida. See Figure 5B for an occlusal view of the cheekteeth of this specimen. Length of scale bar = 10 cm.

its narrowest point, the crest on UF 80446 is about 12 mm across, that of UF 83305 about 10 mm. The latter is probably the older individual of the two. This type of sagittal crest (with minor differences) is found on all *Tapirus* except *T. bairdii* and *T. terrestris*. *T. terrestris* develops a very pronounced sagittal ridge, which is evident even in juvenile individuals (Hershkovitz 1954). *T. bairdii* retains a broad, low sagittal table throughout ontogeny, a modification of the juvenile condition in other species. Following Simpson (1945:56), most authors have stated that *T. indicus* has a sagittal table similar to *T. bairdii*. This is true only in juveniles, but adults develop a double crest across the parietals as in *T. veroensis* (e.g. USNM

155410; Colbert and Hooijer 1953). The dorsal surface of the supraoccipital is flat and smooth, not expanded and rugose as in *T. indicus* and *T. augustus*.

UF 80446 and 83305 both retained large, unfused interparietal bones. Although not preserved, their shape and size can be discerned from the vacancy left in the cranium (Fig. 1A). The interparietal is approximately the shape of an isosceles triangle, about 36 mm long and 26 mm wide on UF 80446, 25 mm long and 29 mm wide on UF 83305. On a third, and apparently older, individual (UF 83835) the interparietal had fused with the supraoccipital and the suture between them is not visible. These specimens suggest that *T. haysii*, like *T. veroensis*, retained an independent interparietal into early adulthood, but that it fused with the surrounding cranial elements in older adults.

The lambdoidal crests are strongly developed, more so than *T. veroensis*, and project both laterally and posteriorly (Fig. 1A, 1C). In this they resemble most individuals of *T. veroensis*, *T. pinchaque*, and *T. indicus*, and differ from *T. bairdii* and *T. terrestris* in which there is much less of a lateral component (Simpson 1945). The strong development of these crests is related to the increased size of the species (Colbert and Hooijer 1953).

The anterodorsal process of the maxilla that projects medial to the premaxilla would have been narrowly visible in lateral view. It thus resembles most individuals of *T. veroensis* and *T. terrestris* in this region. The ventral premaxillary-maxillary suture in lateral view descends anteroventrally to just anterior to the canine, as in all other New World *Tapirus*. In *T. indicus* and *T. augustus*, the suture descends towards the middle of the canine (Ray and Sanders 1984).

The postglenoid and mastoid processes converge very slightly, but the external auditory meatus is open ventrally on the left side of UF 80446 (Fig. 1B). This is the only specimen where both processes are well preserved. Their convergence is less than in *T. veroensis* (e.g. UF/FGS 277), and is most similar to *T. indicus* among living tapirs in this regard.

Quantitative comparisons of cranial, mandibular, and dental characters of *T. haysii* with other species are presented in Tables 1-3. Greatest length of the mandible is the best indicator of body size known by several individuals in *T. haysii* (n = 4, including one individual from Port Kennedy). For this linear character, *T. haysii* is about 13% greater than *T. bairdii* or *T. veroensis*, and 20% greater than *T. pinchaque* or *T. terrestris*. Among living tapirs only *T. indicus* displays considerable overlap with *T. haysii* in size related dimensions (Tables 1-2). Simpson (1945:59) erred when he stated that the teeth of *T. indicus* were smaller than those of *T. veroensis*. The "giant" *T. haysii* is dwarfed by the enormous Asiatic Pleistocene *T. augustus*, which has a mandibular length 30% greater than that of *T. haysii* (445-450 mm, Colbert and Hooijer 1953). Relative muzzle width of *T. haysii* and *T. veroensis* appear to fall within the "normal" range for *Tapirus* when adjusted for size, but diastema length is on average lower (Fig. 2; Table 2). *T. bairdii* has a relatively long muzzle and small teeth. Relative to

Table 1. Univariate statistics for cranial measurements of *Tapirus*.

	BASAL LTH	PAL LTH	SAG CREST	P1M3 LTH	P1P4 LTH	M1M3 LTH	I3P1D LTH	CP1D LTH	CAN LTH	CAN WTH	MUZ WDTH	COND WDTH
						Tapirus bairdii						
n	18	21	20	18	20	19	21	21	20	20	21	18
x	379.39	223.43	120.34	138.17	74.94	65.59	74.84	53.89	11.38	9.87	50.49	83.26
s	11.45	8.27	5.25	5.27	3.30	2.56	5.00	4.50	1.63	1.18	2.96	4.18
MIN	361.0	207.5	110.0	126.0	67.2	61.1	65.8	43.5	7.2	7.6	44.6	77.1
MAX	409.00	239.0	132.7	148.4	80.9	70.8	84.0	60.7	14.6	11.9	55.1	91.9
CV	3.02	3.70	4.36	3.82	4.40	3.90	6.68	8.35	14.30	11.94	5.87	5.02
						Tapirus terrestris						
n	16	18	16	18	18	18	18	17	18	18	16	16
x	350.59	190.77	122.78	134.75	71.83	65.37	63.31	47.92	8.74	7.20	42.97	71.40
s	15.83	8.72	5.99	4.93	3.42	2.48	4.27	4.35	2.46	1.96	3.37	3.88
MIN	328.0	172.5	115.5	125.3	66.0	61.0	56.3	40.7	0.0	0.0	37.0	64.7
MAX	384.0	211.0	132.2	147.4	80.8	71.4	73.1	57.4	11.0	8.8	50.0	79.3
CV	4.52	4.57	4.88	3.65	4.77	3.80	6.75	9.07	28.14	27.22	7.85	5.44
						Tapirus pinchaque						
n	3	3	3	2	3	2	3	3	3	3	3	3
x	347.50	200.33	97.12	141.01	74.12	67.67	67.18	48.21	10.28	8.35	43.55	76.27
s	7.47	3.51	5.06	0.83	3.85	1.00	7.89	6.38	0.35	0.58	4.08	2.55
MIN	342.0	197.0	91.3	140.4	69.8	67.0	58.2	40.9	9.9	7.7	40.6	74.5
MAX	356.0	204.0	100.7	141.6	77.3	68.4	72.8	52.8	10.5	8.7	48.2	79.2
CV	2.15	1.75	5.21	0.59	5.20	1.47	11.74	13.23	3.37	6.96	9.37	3.34

Table 1 continued.

	BASAL LTH	PAL LTH	SAG CREST	P1M3 LTH	P1P4 LTH	M1M3 LTH	I3P1D LTH	CP1D LTH	CAN LTH	CAN WTH	MUZ WDTH	COND WDTH
Tapirus indicus												
n	3	3	3	3	3	3	3	3	3	3	3	3
x	403.33	222.00	115.58	163.97	89.28	78.05	71.35	49.85	10.30	8.78	50.32	89.23
s	4.37	6.08	8.07	11.06	5.11	6.52	8.23	8.43	1.80	1.07	0.69	4.02
MIN	398.5	218.0	106.5	151.8	84.5	70.6	62.0	40.1	8.4	7.7	49.5	86.9
MAX	407.0	229.0	122.0	173.3	94.7	82.4	77.5	55.1	12.0	9.8	50.9	93.9
CV	1.08	2.74	6.98	6.75	5.73	8.35	11.54	16.91	17.51	12.24	1.37	4.50
Tapirus veroensis												
n	2	4	2	5	9	8	5	6	4	4	3	2
x	349.50	184.72	106.03	145.77	77.97	71.08	59.53	44.04	7.80	7.85	46.36	77.66
s	17.68	6.32	1.23	8.22	4.24	4.20	5.86	5.42	0.93	0.42	0.94	3.08
MIN	337.0	179.9	105.2	139.5	71.0	65.5	50.9	35.0	6.8	7.3	45.7	75.5
MAX	362.0	194.0	106.9	159.0	84.2	77.9	65.6	50.1	9.0	8.2	47.4	79.8
CV	5.06	3.42	1.16	5.64	5.44	5.90	9.85	12.30	11.98	5.31	2.02	3.97
Tapirus haysii												
n	0	0	3	1	1	4	0	0	2	2	2	3
x	—	—	115.23	166.58	87.69	79.83	—	—	13.86	13.29	50.25	83.50
s	—	—	3.20	—	—	1.63	—	—	0.13	1.07	2.19	1.03
MIN	—	—	112.0	166.6	87.7	77.5	—	—	13.8	12.5	48.7	82.5
MAX	—	—	118.4	166.6	87.7	81.3	—	—	14.0	14.1	51.8	84.5
CV	—	—	2.78	—	—	2.04	—	—	0.92	8.09	4.36	1.23

Table 2. Univariate statistics for mandibular measurements of *Tapirus*.

	GRT lth	i3p2D lth	cp2D lth	p2m3 lth	p2p4 lth	m1m3 lth	SYMPH wdth	SYMPH lth	p2M dpth	m3M dpth	can lth	can wth
							Tapirus bairdii					
n	20	21	21	17	18	19	21	21	21	20	21	21
x	304.23	81.44	65.30	128.33	61.93	66.86	50.95	92.45	47.59	55.25	16.78	14.33
s	9.80	4.74	4.72	4.86	2.63	2.35	3.43	5.06	2.20	3.14	1.61	1.48
MIN	289.0	71.7	53.9	119.7	58.3	61.7	47.6	80.1	41.7	51.3	13.4	11.6
MAX	323.0	92.6	73.1	138.5	67.9	70.9	61.4	100.9	51.3	64.6	19.6	17.1
CV	3.22	5.82	7.23	3.79	4.25	3.51	6.73	5.47	4.63	5.68	9.59	10.35
							Tapirus terrestris					
n	14	14	15	14	14	15	13	13	15	15	15	15
x	283.64	68.32	54.73	126.60	59.87	67.38	44.06	89.77	44.75	52.21	14.85	11.71
s	13.66	4.73	4.64	5.51	2.97	2.77	4.34	5.84	4.94	3.56	2.01	1.10
MIN	266.5	62.5	48.2	118.5	55.9	63.0	36.6	80.8	37.6	46.9	11.4	10.2
MAX	315.0	80.2	65.9	141.1	67.1	74.8	53.8	98.2	54.6	57.4	17.3	13.3
CV	4.82	6.92	8.49	4.35	4.96	4.11	9.86	6.50	11.03	6.82	13.57	9.37
							Tapirus pinchaque					
n	3	3	3	1	2	1	3	3	3	2	3	3
x	287.83	72.12	56.83	132.85	63.48	68.70	45.22	83.54	43.15	50.06	15.75	12.77
s	7.77	4.97	6.08	—	1.60	—	2.96	5.32	1.59	0.65	1.25	0.31
MIN	281.5	66.5	49.9	132.9	62.4	68.7	42.5	77.4	41.4	49.6	14.5	12.5
MAX	296.5	75.8	61.4	132.9	64.6	68.7	48.4	87.2	44.4	50.5	17.0	13.1
CV	2.70	6.89	10.69	—	2.52	—	6.54	6.37	3.68	1.30	7.94	2.46

Table 2 continued.

	GRT lth	i3p2D lth	cp2D lth	p2m3 lth	p2p4 lth	m1m3 lth	SYMPH wdth	SYMPH lth	p2M dpth	m3M dpth	can lth	can wth
						Tapirus indicus						
n	3	3	3	3	3	3	3	3	3	2	3	3
x	336.83	77.48	59.26	151.86	73.58	79.05	52.97	102.38	54.14	60.22	17.68	13.44
s	3.88	4.56	5.58	12.63	4.05	7.58	2.47	2.51	2.46	2.98	0.90	1.32
MIN	332.5	72.6	53.3	137.9	69.5	70.4	50.8	99.6	51.6	58.1	17.0	12.6
MAX	340.0	81.6	64.3	162.5	77.6	84.5	55.7	104.5	56.5	62.3	18.7	15.0
CV	1.15	5.89	9.42	8.32	5.50	9.58	4.66	2.45	4.54	4.96	5.06	9.80
						Tapirus veroensis						
n	1	3	3	2	2	5	3	2	2	3	3	3
x	308.00	59.58	46.76	134.38	65.97	72.11	44.53	81.02	45.96	61.15	11.83	11.00
s	—	5.48	3.09	0.37	0.10	2.66	3.47	1.97	5.46	3.52	0.54	0.99
MIN	308.0	56.3	44.9	134.1	65.9	69.4	41.1	79.6	42.1	58.5	11.4	10.0
MAX	308.0	65.9	50.3	134.7	66.0	75.2	48.0	82.4	49.8	65.1	12.4	12.0
CV	—	9.20	6.61	0.28	0.15	3.69	7.79	2.44	11.88	5.75	4.56	8.96
						Tapirus haysii						
n	4	5	4	5	5	6	3	4	6	5	4	4
x	343.63	74.31	61.20	158.14	73.87	82.81	52.89	93.22	53.78	71.63	13.59	12.60
s	13.54	3.68	5.40	6.13	2.72	4.83	1.60	8.92	4.48	4.15	0.68	0.49
MIN	326.0	70.5	55.7	153.4	71.7	76.7	51.1	82.8	45.6	67.3	12.8	12.3
MAX	359.0	79.9	68.4	166.1	78.5	89.6	54.2	102.4	58.2	78.2	14.2	13.3
CV	3.94	4.95	8.83	3.88	3.68	5.83	3.02	9.57	8.32	5.79	5.01	3.93

modern *Tapirus*, both *T. haysii* and *T. veroensis* have smaller lower canines and deeper mandibles below the m3 (Table 2; Fig. 2).

Measured characters of the cheekteeth show only minor differences between the referred Florida and Port Kennedy populations of *T. haysii* (Table 3). Only four of 37 parameters (P2AW, P4L, M1L, and p4L) are significantly different based on univariate *t*-tests ($0.05 \geq p \geq 0.01$). The Florida *T. haysii* population is significantly larger on average than that of *T. veroensis* for 36 of the same 37 parameters, although there is overlap in almost all variates (Table 3). The *T. veroensis* sample was derived from numerous localities, of which only a few (e.g. Vero, Arredondo, Hornsby Springs, Rock Springs) were collected in situ with an associated Rancholabrean fauna. The majority instead came from the beds of rivers, including the Ichetucknee, Sante Fe, Aucilla, Wacissa, Waccasassa, and Oklawaha. The preponderance of vertebrates produced by these are Rancholabrean, but the presence of early Pleistocene specimens is possible. A similar sample was measured by Lundelius and Slaughter (1976; it included many of the same UF specimens), who also found more substantial overlap in tooth dimensions between *T. veroensis* and *T. haysii* (their *T. copei*) than did Simpson (1945). Their identifications were questioned by Ray and Sanders (1984), who queried why large individuals assigned to *T. veroensis* did not represent *T. haysii*. In the case of UF 8225, the Apollo Beach mandible, Ray and Sanders were undoubtedly correct in assigning this specimen to *T. haysii* (its absence probably accounts for the much larger observed maximum values for *T. veroensis* lower cheekteeth reported by Lundelius and Slaughter [1976, table 3] than those listed here in Table 3). Other large-sized, putative *T. veroensis* individuals are less easily reassigned. In many cases the longest tooth for a particular locus is not the widest, many having widths that fall below the OR of *T. haysii*, and their apparent great length is because they are unworn and have not suffered interdental wear. Thus to reassign species identification to *T. haysii* on the basis of single measurements would cause substantial decreases in the means and observed minima in other characters, and this would in turn lead to greater apparent overlap between the two species. The only morphological criterion of the dentition that has been used to separate the two species other than size is the more highly molarized anterior premolars of *T. haysii* (Simpson 1945; Ray and Sanders 1984). A quantitative measure of this is the ratio P2AW/P2PW, which is greater (on average) in *T. haysii* than *T. veroensis*. If the larger individuals referred to *T. veroensis* by Lundelius and Slaughter (1976) and this study are actually Rancholabrean *T. haysii*, then large P2s (those with lengths greater than 20.6 mm, the MIN for *T. haysii*) should have relatively high AW/PW ratios. The five P2s with lengths greater than 20.6 mm assigned to *T. veroensis* in fact have low AW/PW ratios (87-90, $x = 89$) which are not different from those of smaller P2s. Without morphological evidence, it seems best to retain these individuals in *T. veroensis* until unquestionable Rancholabrean *T. haysii* is recovered from Florida.

Table 3. Univariate statistics for measurements on cheekteeth of fossil species of *Tapirus*. The Florida sample of *T. haysii* is a composite from a number of early Irvingtonian localities, although about three-fourths are from a single site, Leisey Shell Pit 1A. Likewise the *T. veroensis* sample is a composite from numerous Rancholabrean localities from throughout Florida. The Port Kennedy sample of *T. haysii* is taken from Simpson (1945). Results of *t*-tests between the two samples of *T. haysii*, and between the two Florida samples are reported to the right of the statistics for *T. veroensis* and the Port Kennedy *T. haysii*. Simpson (1945) did not report the standard deviation for upper ckeektooth measurements; *t*-tests were done assuming equal variances between the two samples of *T. haysii* for these teeth. "NS" indicates that the means are not significantly different from one another ($p \geq 0.05$); "*", a significant difference with $0.05 > p \geq 0.01$; "**", a significant difference with $0.01 > p \geq 0.001$; and "***", a significant difference with $p < 0.001$.

		n	*x*	*s*	MIN	MAX	*CV*
			TAPIRUS HAYSII (FLORIDA)				
P1	L	4	21.73	1.55	20.3	23.3	7.13
	PW	4	20.21	1.46	18.9	22.0	7.21
P2	L	7	22.26	1.33	20.6	24.3	6.00
	AW	8	24.10	1.26	22.0	25.4	5.22
	PW	8	26.47	1.51	23.8	28.0	5.69
P3	L	8	22.84	1.20	21.6	24.5	5.25
	AW	8	27.19	1.20	25.7	29.0	4.40
	PW	9	26.94	1.37	25.4	29.3	5.07
P4	L	5	23.39	0.96	22.6	25.0	4.12
	AW	5	29.27	1.73	28.0	31.9	5.90
	PW	5	28.46	1.68	27.2	30.8	5.89
M1	L	10	24.94	0.76	23.9	25.9	3.06
	AW	9	29.14	1.20	26.9	30.7	4.11
	PW	10	26.19	1.26	24.5	28.5	4.83
M2	L	9	27.79	0.91	26.3	29.2	3.26
	AW	9	32.67	1.42	30.9	34.5	4.34
	PW	8	28.98	1.16	27.4	30.5	4.01
M3	L	5	27.94	0.58	27.1	28.5	2.08
	AW	5	32.60	0.81	31.5	33.6	2.49
	PW	5	26.83	1.36	25.1	28.9	5.06
p2	L	6	27.22	1.27	25.6	28.8	4.68
	PW	7	17.71	1.33	15.4	19.2	7.53
p3	L	9	23.71	0.93	22.5	25.2	3.92
	AW	9	17.42	0.44	16.8	17.9	2.51
	PW	9	19.35	1.09	18.1	21.5	5.63

Table 3 continued.

		n	*x*	*s*	MIN	MAX	*CV*	*t*	df	sig
	L	5	23.59	0.89	22.5	25.0	3.76			
p4	AW	5	20.43	0.27	20.0	20.6	1.34			
	PW	5	21.35	0.72	20.2	21.9	3.37			
	L	8	25.71	1.61	23.0	27.6	6.25			
m1	AW	8	21.15	0.99	19.9	22.5	4.70			
	PW	8	19.61	0.78	18.3	20.7	3.99			
	L	9	28.30	0.95	27.0	30.4	3.37			
m2	AW	8	22.17	0.35	21.8	22.7	1.59			
	PW	9	21.20	0.94	19.5	22.7	4.41			
	L	11	30.36	1.60	28.7	33.5	5.28			
m3	AW	10	22.21	0.88	21.2	24.2	3.99			
	PW	11	19.93	1.37	17.3	22.0	6.88			
					TAPIRUS HAYSII (PORT KENNEDY)					
	L	3	23.80		22.4	24.9		-1.702	5	NS
P1	PW	3	20.40		19.6	21.5		-0.167	5	NS
	L	5	22.60		21.9	24.0		-0.435	10	NS
P2	AW	4	25.90		25.5	26.5		-2.279	10	*
	PW	4	27.60		27.4	27.9		-1.198	10	NS
	L	5	23.70		22.7	24.5		-1.240	11	NS
P3	AW	4	28.60		27.0	29.5		-1.876	10	NS
	PW	4	28.10		26.1	29.0		-1.379	11	NS
	L	4	25.30		24.1	26.4		-2.916	7	*
P4	AW	4	30.60		29.9	31.8		-1.134	7	NS
	PW	4	29.30		28.4	30.1		-0.738	7	NS
	L	5	26.10		25.8	26.4		-2.729	13	*
M1	AW	5	30.30		28.9	31.1		-1.709	12	NS
	PW	5	27.30		25.8	27.9		-1.570	13	NS
	L	5	28.10		27.3	29.7		-0.609	12	NS
M2	AW	4	32.60		31.3	34.9		0.085	11	NS
	PW	4	29.70		28.0	31.5		-0.992	10	NS
	L	5	28.20		26.8	29.2		-0.709	8	NS
M3	AW	5	32.30		31.0	34.1		0.585	8	NS
	PW	5	27.80		26.5	29.0		-1.128	8	NS
	L	6	25.90	0.70	24.7	27.0	2.70	2.218	10	NS
p2	PW	6	16.57	0.67	15.5	17.6	4.04	1.890	11	NS

Table 3 continued.

		n	*x*	*s*	MIN	MAX	*CV*	*t*	df	sig
p3	L	9	24.22	0.67	23.0	25.1	2.77	-1.342	16	NS
	AW	9	17.01	0.73	16.1	18.0	4.29	1.446	16	NS
	PW	9	19.19	0.68	17.8	20.2	3.54	0.382	16	NS
p4	L	6	24.60	0.26	24.1	24.9	1.06	-2.688	9	*
	AW	8	20.41	1.13	18.3	21.7	5.54	0.031	11	NS
	PW	8	21.28	1.11	19.5	22.8	5.22	0.125	11	NS
m1	L	6	25.53	1.10	23.4	27.0	4.31	0.232	12	NS
	AW	7	20.83	0.97	19.8	22.9	4.66	0.636	13	NS
	PW	7	19.56	0.58	18.7	20.8	2.97	0.149	13	NS
m2	L	10	28.91	1.06	27.4	30.8	3.67	-1.318	17	NS
	AW	9	21.56	1.09	20.5	24.1	5.06	1.518	15	NS
	PW	10	20.17	1.26	18.3	22.8	6.25	2.005	17	NS
m3	L	6	30.78	0.58	30.1	31.5	1.88	-0.606	15	NS
	AW	6	22.70	0.69	21.7	23.8	3.04	-1.168	14	NS
	PW	5	19.84	0.51	19.2	20.5	2.57	0.141	14	NS
TAPIRUS VEROENSIS (FLORIDA)										
P1	L	17	18.75	1.33	16.4	20.6	7.12	3.920	19	***
	PW	17	16.40	1.75	13.7	18.8	10.67	4.015	19	***
P2	L	15	19.83	1.02	18.4	21.7	5.14	4.719	20	***
	AW	15	21.22	0.91	19.5	23.1	4.27	6.352	21	***
	PW	15	23.59	1.02	21.9	25.8	4.31	5.458	21	***
P3	L	14	20.47	0.94	19.4	22.6	4.60	5.140	20	***
	AW	14	24.88	1.01	22.7	26.5	4.05	4.832	20	***
	PW	14	24.90	1.07	22.8	26.7	4.32	4.007	21	***
P4	L	13	21.37	1.12	19.6	23.0	5.25	3.545	16	**
	AW	13	26.83	1.26	24.1	28.7	4.71	3.325	16	**
	PW	13	26.46	1.04	24.7	28.2	3.93	3.093	16	**
M1	L	14	22.70	1.45	20.4	25.5	6.39	4.432	22	***
	AW	13	26.24	1.32	24.6	28.5	5.04	5.239	20	***
	PW	14	23.91	1.14	22.4	26.1	4.77	4.625	22	***
M2	L	18	25.14	1.21	23.1	27.5	4.83	5.757	25	***
	AW	17	29.07	1.31	26.9	31.2	4.49	6.496	24	***
	PW	18	25.85	1.08	24.2	28.3	4.16	6.673	24	***

Table 3 continued.

		n	*x*	*s*	MIN	MAX	*CV*	*t*	df	sig
M3	L	14	24.84	1.03	22.7	26.3	4.15	6.304	17	***
	AW	14	28.89	1.35	26.7	31.5	4.68	5.720	17	***
	PW	14	24.39	1.00	22.5	26.2	4.10	4.284	17	***
p2	L	9	23.86	0.91	22.7	25.1	3.82	5.968	13	***
	PW	9	14.73	1.34	12.6	16.7	9.10	4.416	14	***
p3	L	8	21.61	1.53	20.4	24.6	7.07	3.471	15	**
	AW	8	15.81	0.91	14.8	16.8	5.75	4.730	15	***
	PW	8	17.98	1.29	15.9	19.8	7.18	2.379	15	*
p4	L	11	22.20	0.94	20.8	23.7	4.25	2.768	14	*
	AW	11	19.18	1.09	17.6	21.0	5.68	2.485	14	*
	PW	11	20.29	1.35	18.0	22.9	6.64	1.642	14	NS
m1	L	15	22.88	1.23	21.0	25.8	5.35	4.735	21	***
	AW	14	18.99	1.17	17.3	20.8	6.16	4.392	20	***
	PW	15	17.69	1.22	15.9	20.6	6.89	4.024	21	***
m2	L	14	25.42	1.09	23.7	27.6	4.27	6.482	21	***
	AW	13	20.54	1.19	18.8	22.3	5.80	3.752	19	**
	PW	13	19.59	1.22	18.2	21.8	6.21	3.339	20	**
m3	L	14	26.63	1.31	24.4	29.8	4.92	6.415	23	***
	AW	14	20.18	0.97	18.5	21.5	4.79	5.233	22	***
	PW	14	18.44	1.12	16.7	20.0	6.10	2.996	23	**

The only qualitative characters commonly attributed to *T. haysii* dentitions that differentiate it from *T. veroensis* are the relatively molarized P1 and P2. As discussed above, the latter can be analyzed by comparing the AW relative to the PW, and also by the development of the protoloph on the P2. On the P1, molarization is judged by relative width, strength of the inner cusp, development of a transverse loph, and presence of an anterolingual cingulum (Simpson 1945; Hershkovitz 1954). In all of these characters, the Leisey 1A sample is intermediate between that observed in the Port Kennedy sample of *T. haysii*, and that in *T. veroensis* or *T. terrestris* (Figs. 3, 4C). As in all samples of *Tapirus*, there is considerable intraspecific variation in these characters, which should temper their widespread use as systematic indicators. For example, Simpson (1945) reported a range for the ratio of P2AW to P2PW of 92 to 95 (n = 4) for *T. haysii*, and 87 to 92 (n = 7) for *T. veroensis*. In the Leisey 1A sample it ranges from 90 to 96 (n = 6), but in four of the six it ranges between 90 and 92, below the OR of the Port

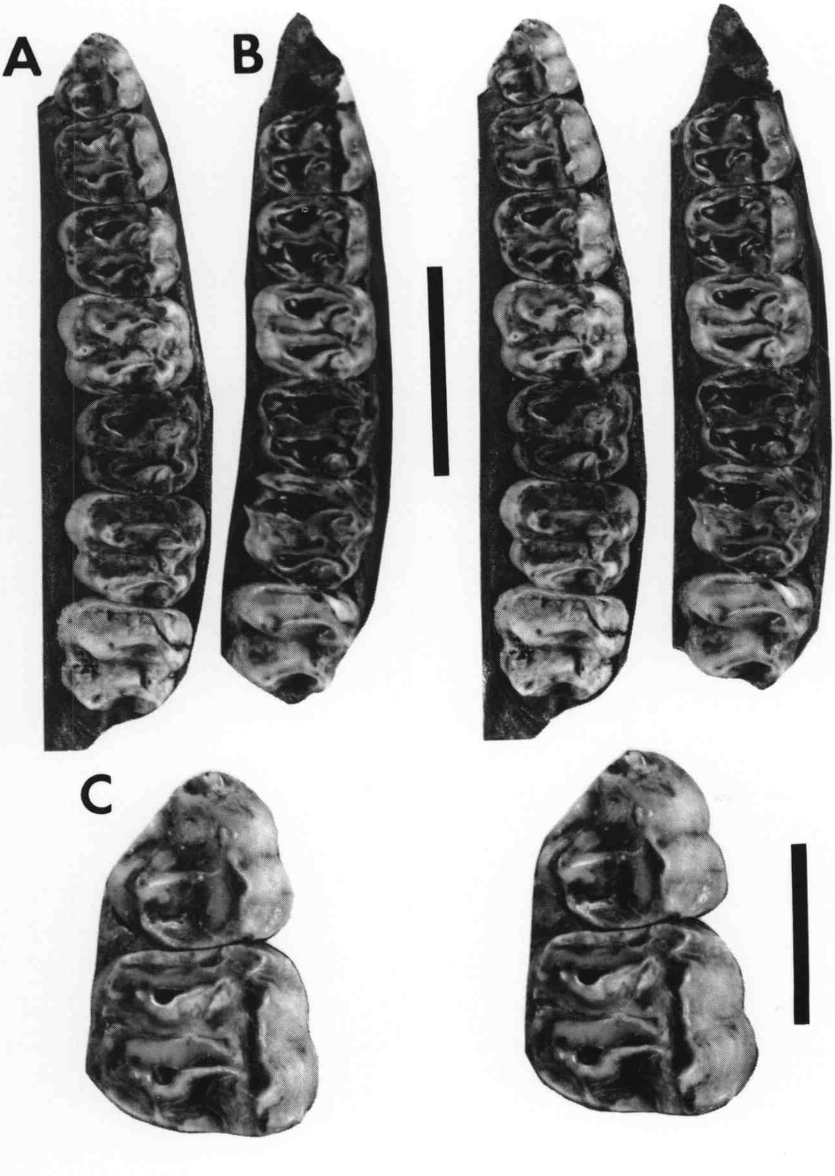

Figure 3. Occlusal views of upper cheekteeth of *Tapirus haysii* from Leisey Shell Pit 1A, Hillsborough County, Florida. (A) UF 84190, left P1-M3; (B) UF 89539, left P2-M3; (C) UF 84190, detail of left P1-P2. Length of scale bar for A and B is 50 mm; for C it is 20 mm.

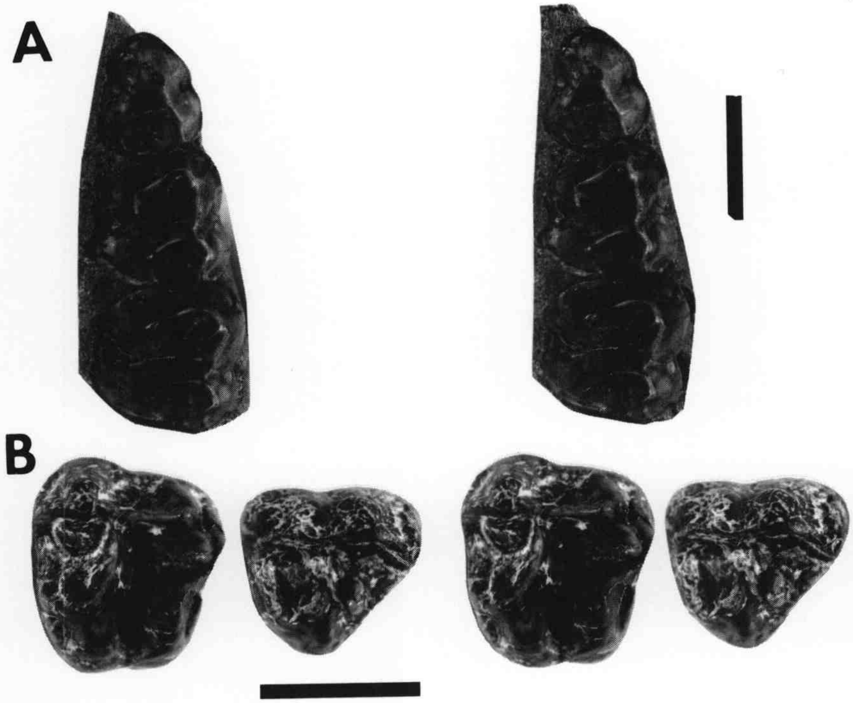

Figure 4. Occlusal views of upper cheekteeth of *Tapirus haysii* from Leisey Shell Pit 1A, Hillsborough County, Florida. (A) UF 82783, left DP1-DP3; (B) UF 87231, right P1-P2. Scale bar is 20 mm.

Kennedy population. This difference results from a significantly shorter P2AW in the Leisey 1A sample, while the P2L and P2PW are not significantly different from the Port Kennedy population (Table 3; Figs. 3, 4B). Similarly, the protoloph of the P2 and the transverse loph of the P1 in the Leisey sample vary between the relatively weakly developed states observed in *T. veroensis*, *T. terrestris* and *T. bairdii*, and the well developed states of Port Kennedy *T. haysii* (Figs. 3-4; Simpson 1945, fig. 10A). While Simpson (1945) and subsequent authors have noted this intergradation caused by intraspecific variation (e.g. Hershkovitz 1954 regarding the P1 of *T. pinchaque*), Simpson especially appears to have underemphasized the extent of the morphological overlap in these characters. The relative "primitiveness" of the modal states of the Leisey *T. haysii* may be due to their greater antiquity (by about 0.5-1.0 myr) than the Port Kennedy population.

The lower cheekteeth in the Leisey 1A sample exhibit a single morphological character not observed in *T. veroensis*, the presence of well developed metastylids on the dp2-dp4 (Fig. 5, 6). In *T. veroensis*, metastylids are very weakly developed or absent on the deciduous premolars (n = 13). Weak metastylids are also the observed character state in the referred Love Site and McGehee Farm populations of *T. simpsoni* (Fig. 6C, 6D, 6F). As the sample of dps from Leisey 1A is quite small and represents only two individuals, the consistency of this character in uncertain. The metastylids are relatively weak on the dp2 and dp3 of F:AM 37411 (McLeod), suggesting that this character too is subject to intraspecific variation. Excluding this character, size, and slightly more molarized P1s and P2s, the dentitions of Florida *T. haysii* are practically indistinguishable from those of *T. veroensis* and Neotropical *Tapirus*.

Postcranial elements of a large tapir were also recovered from Leisey 1A (Table 4). There is no indication from their statistical distribution that more than one species is represented. Relative to cranial dimensions and the proportions of the postcranial elements of other species (especially *T. indicus*), the limbs of *T. haysii* seem relatively gracile. The limbs are characteristicaly tapirid, with no peculiar features. The skeletal element with the highest relative representation at Leisey 1A is the astragalus. The minimum number of individuals (MNI) of *T. haysii* recovered at Leisey 1A is six, based on right astragali. A greater MNI of 9 is obtained from maxillae, if it is assumed that unmatched right and left maxillae represent different individuals. A limited number of postcranial elements of *T. haysii* are known from other localities, most notably Haile 16A, from which no cranial material was recovered. The size of the elements from Haile 16A supports their identification as *T. haysii* (Table 4), as does its Irvingtonian age.

Discussion.– Based on tooth size (which forms the only mutual basis for comparison), there is little doubt that the Florida and Port Kennedy samples of large tapirs represent the same species. The species name *T. haysii* seems the most appropriate for these populations (Ray and Sanders 1984). Although the holotype p4 from North Carolina falls above the OR of the Florida sample for length and AW (it also is longer than any of the Port Kennedy p4s), the size of most of the referred topotypes described by Ray and Sanders (1984) are within the OR of the referred samples for all three measured variates. The differences in P1 and P2 morphology between the Florida and Port Kennedy samples, if not purely an artifact of sampling (the sample sizes are still relatively small, especially for the P1), most likely represent chronoclinal variation. A similar wide degree of intraspecific variation is observed for these characters in other species.

The Leisey Shell Pit and other Florida Irvingtonian records of *Tapirus* confirm the existence of a tapir significantly larger on average than the typical Rancholabrean *T. veroensis*. They do little in the way of demonstrating significant morphological differences between *T. veroensis* and *T. haysii*, as all cranial features now known for *T. haysii* resemble those of *T. veroensis*. Arguably, with its relatively primitive upper premolars, the Leisey sample blurs what little

Table 4. Measurements and univariate statistics of postcranial elements of *Tapirus haysii* from Florida. See Referred Specimens listing for exact localities. Measurements after Eisenmann (1986).

HUMERUS

	UF 87229
MIDSHAFT TRW	31.4
MIDSHAFT A-P L	40.3
DIST ART W	62.4
DIST MEDIAL A-P L	68.0

RADIUS

	UF 81068	UF 87228	*x*	*s*	*CV*
GRT LENGTH	–	235.0	235.0		
MIDSHAFT TRW	28.9	30.1	29.5	0.85	2.88
MIDSHAFT A-P L	24.1	21.3	22.7	1.98	8.72
PROX ART W	58.6	62.9	60.8	3.04	5.01
PROX ART A-P L	–	33.9	33.9		
DIST ART W	66.1	66.4	66.3	0.21	0.32
DIST A-P L	35.7	33.2	34.5	1.77	5.13

METACARPAL II

	UF 83389	UF 87958	UF 87959	UF 89535	*x*	*s*	*CV*
GRT LENGTH	114.1	109.5	109.3	110.0	110.7	2.27	2.05
MIDSHAFT TRW	19.4	21.5	22.5	–	21.1	1.58	7.49
MIDSHAFT A-P L	11.1	11.2	13.5	–	11.9	1.36	11.38
PROX ART W	22.5	23.1	–	25.6	23.7	1.64	6.93
PROX ART A-P L	17.5	20.5	18.8	–	18.9	1.50	7.95
DIST ART W	21.7	21.0	22.1	–	21.6	0.56	2.58
DIST A-P L	24.4	25.0	27.2	–	25.5	1.47	5.77

METACARPAL III

	UF 81771	UF 87950	UF 89534	UF 91243	UF 91244	*x*	*s*	*CV*
GRT LENGTH	132.9	128.9	133.8	125.5	–	130.3	3.83	2.94
MIDSHAFT TRW	28.8	30.5	29.7	31.0	28.9	30.0	0.96	3.21

Table 4 Continued.

METACARPAL III Continued

	UF 81771	UF 87950	UF 89534	UF 91243	UF 91244	*x*	*s*	*CV*
MIDSHAFT A-P L	13.9	14.2	15.4	16.5	15.8	15.0	1.19	7.94
PROX ART W	34.2	34.8	35.7	35.2	–	35.0	0.63	1.81
PROX ART A-P L	27.0	26.5	–	26.7	–	26.7	0.25	0.94
DIST ART W	31.6	32.5	33.2	33.4	31.6	32.7	0.81	2.49
DIST A-P L	25.4	24.9	24.7	24.8	25.6	24.9	0.31	1.25

METACARPAL IV

	UF 65990	UF 83390	UF 89537	UF 89538	*x*	*s*	*CV*
GRT LENGTH	–	–	107.0	107.7	107.3	0.49	0.46
MIDSHAFT TRW	20.9	–	19.9	22.7	21.2	1.42	6.70
MIDSHAFT A-P L	12.8	–	12.4	13.1	12.8	0.35	2.75
PROX ART W	22.1	23.2	22.2	–	22.5	0.61	2.70
PROX ART A-P L	24.4	25.1	–	24.6	24.7	0.36	1.46
DIST ART W	–	–	20.2	–	20.2		
DIST A-P L	–	–	23.0	–	23.0		

METACARPAL V

	UF 84082	UF 84916	UF 87952	UF 88777	UF 91245	*x*	*s*	*CV*
GRT LENGTH	83.7	86.7	88.4	86.5	78.5	86.3	1.95	2.25
MIDSHAFT TRW	15.8	18.3	17.9	18.0	19.2	17.5	1.15	6.55
MIDSHAFT A-P L	10.2	10.1	11.0	10.2	10.6	10.4	0.42	4.04
PROX ART W	12.8	13.5	12.4	13.7	12.6	13.1	0.61	4.62
PROX ART A-P L	25.4	–	21.7	23.3	23.5	23.5	1.86	7.91
DIST ART W	18.4	18.3	19.0	18.3	17.1	18.5	0.34	1.82
DIST A-P L	20.7	20.6	21.1	–	20.3	20.8	0.26	1.27

FEMUR

	UF 60864	UF 80449	UF 65975	UF 83441	*x*	*s*	*CV*
GRT LENGTH	–	342.0	337.0	320.5	333.2	11.25	3.38
MEDIAL LENGTH	330.5	–	316.0	301.0	315.8	14.75	4.67
MIDSHAFT TRW	38.6	34.9	37.9	37.1	37.1	1.60	4.32
MIDSHAFT A-P L	39.9	36.9	39.3	35.6	37.9	2.02	5.33
PROX W	105.2	–	109.8	106.8	107.3	2.34	2.18
A-P DIAM HEAD	46.2	–	46.9	44.8	46.0	1.07	2.33

Table 4 Continued

FEMUR Continued

	UF 60864	UF 80449	UF 65975	UF 83441	*x*	*s*	*CV*
DIST ART W	–	82.3	77.3	78.5	79.4	2.61	3.29
DIST MED A-P L	95.0	105.3	96.0	96.2	98.1	4.81	4.90

TIBIA

	UF 65976	UF 65977	UF 80653	UF 83579	UF 91246	*x*	*s*	*CV*
GRT LENGTH	260.0	259.0	254.0	248.0	–	255.3	5.50	2.15
MIDSHAFT TRW	28.9	29.6	28.7	29.0	30.8	29.1	0.39	1.33
MIDSHAFT A-P L	34.0	33.0	31.4	31.2	34.8	32.4	1.34	4.13
PROX ART W	81.7	84.4	81.4	79.7	–	81.8	1.94	2.38
PROX ART A-P L	–	–	66.0	67.0	–	66.5	0.71	1.06
DIST ART W	43.4	42.8	41.5	41.4	46.3	42.3	0.98	2.33
DIST A-P L	34.9	34.5	37.4	36.3	36.6	35.8	1.33	3.72

ASTRAGALUS

	UF 63901	UF 65981	UF 65982	UF 67325	UF 81917	UF 86883	UF 87953
MEDIAL LENGTH	55.2	54.3	54.6	50.5	49.9	50.6	52.4
LATERAL LENGTH	60.7	62.9	62.1	59.7	60.4	60.2	60.3
MEDIAL L TROCHLEA	44.2	43.2	43.5	41.8	41.6	41.4	43.1
GRT WIDTH	50.1	53.9	57.2	50.9	49.8	53.4	51.1
DIST ART W	44.6	47.7	49.4	45.3	44.9	45.1	44.4
DIST ART A-P L	29.9	–	–	27.4	30.2	29.4	29.2

ASTRAGALUS Continued

	UF 87960	UF 91247	UF 91248	*x*	*s*	*CV*
MEDIAL LENGTH	53.4	51.5	58.8	53.1	2.73	5.14
LATERAL LENGTH	59.8	60.9	–	60.8	1.07	1.75
MEDIAL L TROCHLEA	42.5	42.8	48.0	43.2	1.90	4.40
GRT WIDTH	52.0	55.1	56.5	53.0	2.64	4.99
DIST ART W	45.1	47.6	48.6	46.3	1.85	4.00
DIST ART A-P L	29.8	27.9	29.8	29.2	1.01	3.47

Table 4 Continued

CALCANEUM

	UF 65983	UF 65984	UF 65986	UF 81235	*x*	*s*	*CV*
GRT LENGTH	114.3	–	–	108.9	111.6	3.82	3.42
GRT TRW	53.3	49.2	53.7	51.9	52.0	2.04	3.91
GRT A-P L	46.1	42.6	43.3	45.9	44.5	1.79	4.02

METATARSAL II

	UF 65988	UF 65989	UF 82374	UF 81311	UF 89536	*x*	*s*	*CV*
GRT LENGTH	113.5	109.9	112.3	110.5	114.9	111.5	1.65	1.48
MIDSHAFT TRW	22.2	19.0	20.9	18.9	21.2	20.3	1.59	7.87
MIDSHAFT A-P L	14.5	13.4	14.1	13.5	14.3	13.9	0.52	3.74
PROX ART W	16.4	15.8	17.6	19.0	17.1	17.2	1.41	8.22
PROX ART A-P L	14.8	–	17.9	16.2	18.5	16.3	1.55	9.52
DIST ART W	22.8	19.3	20.7	20.8	21.3	20.9	1.44	6.89
DIST A-P L	25.8	26.0	28.0	26.1	28.4	26.5	1.02	3.87

METATARSAL III

	UF 65987	UF 81703	UF 83578	*x*	*s*	*CV*
GRT LENGTH	130.0	130.0	125.8	128.6	2.42	1.89
MIDSHAFT TRW	28.2	29.3	26.9	28.1	1.20	4.27
MIDSHAFT A-P L	14.9	14.8	14.0	14.6	0.49	3.39
PROX ART W	32.0	30.3	28.9	30.4	1.55	5.11
PROX ART A-P L	25.2	25.1	25.3	25.2	0.10	0.40
DIST ART W	32.2	30.7	31.1	31.3	0.78	2.48
DIST A-P L	25.1	25.2	24.3	24.9	0.49	1.98

METATARSAL IV

	UF 46923	UF 63900	UF 84442	UF 86865	UF 142233	*x*	*s*	*CV*
GRT LENGTH	107.4	111.4	110.1	–	117.6	111.6	4.32	3.87
MIDSHAFT TRW	19.8	18.8	18.4	19.6	22.5	19.8	1.60	8.09
MIDSHAFT A-P L	13.9	14.7	12.7	13.4	15.3	14.0	1.03	7.35
PROX ART W	20.3	19.8	18.9	18.6	20.7	19.7	0.90	4.56
PROX ART A-P L	23.1	–	20.6	22.2	–	22.0	1.27	5.76
DIST ART W	20.8	20.1	20.3	–	21.3	20.6	0.54	2.61
DIST A-P L	27.6	27.6	26.3	–	30.5	28.0	1.78	6.34

Figure 5. Occlusal views of lower cheekteeth of *Tapirus haysii* from Leisey Shell Pit 1A, Hillsborough County, Florida. (A) UF 83580, left p2-m3; (B) UF 80973, left p2-m3. Scale bar is 20 mm.

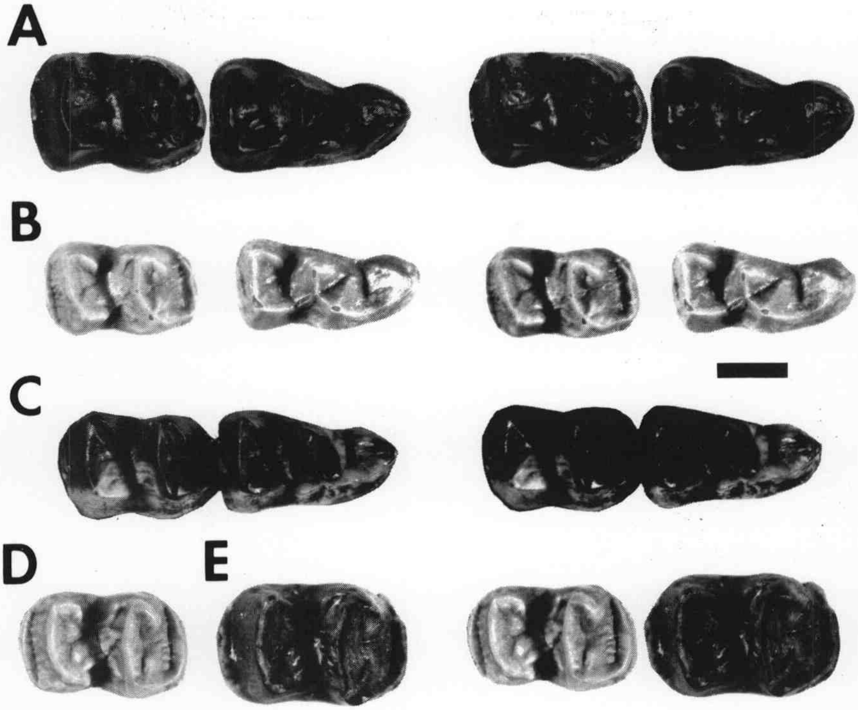

Figure 6. Occlusal views of lower deciduous cheekteeth of *Tapirus* from Florida. (A) UF 87230, right dp2-dp3 of *T. hayi*, Leisey Shell Pit 1A (early Irvingtonian); (B) UF 11117, right dp2-dp3 of *T. simpsoni*, McGehee Farm Site, Aachua County (early Hemphillian); (C) UF 47928, right dp2-dp3 of *T. veroensis*, Aucilla River 1A, Jefferson-Taylor county line (late Rancholabrean); (D) UF 11117, right dp4. (E) UF 87230, right dp4. Scale bar is 10 mm.

morphological distinction was thought to exist between the two species. If the two different size populations cannot be shown to have been sympatric, and if the absence of significant morphological differences continues, then the hypothesis that *T. haysii* and *T. veroensis* represent a single chronoclinal lineage is difficult to falsify, as was perceived by Ray (1964:65). Late Pleistocene (Rancholabrean) records of large tapirs in eastern North America (e.g. in Kurtén and Anderson 1980) have not proven to be *T. haysii*, and instead represent larger than average-sized individuals of *T. veroensis*. Some late Pleistocene records of unequivocally *T. haysii*-sized individuals are known from the southwestern United States, e.g. the Lehner Mammoth Site (Lance 1959; Ray and Sanders 1984), but these have been referred to the western species *T. merriami* by Jefferson (1989). There remains much to be learned about the enigmatic giant North American tapir.

BIOCHRONOLOGY OF FLORIDA TAPIRS

Since the publication of the first definite records of *T. haysii* from Florida (Simpson 1945; Ray 1964), much has been learned about the pre-Rancholabrean Pleistocene history of the state (Webb 1974; Morgan and Hulbert this volume). Of the 12 new records of *T. haysii* reported in this study, the following eight were collected in direct association with a suite of mammalian taxa that in combination are now recognized as diagnostic of either the late early or middle Irvingtonian in Florida: Leisey 1A, Leisey 3A, Leisey 3B, Haile 16A, Haile 21A, McLeod Limerock Mine, Crystal River Power Plant, and Pool Branch. These mammals include *Sigmodon libitinus*, *Canis edwardii*, *Smilodon gracilis*, *Mammuthus hayi*, and *Pachyarmatherium leiseyi* (Webb et al. 1989; Morgan and Hulbert this volume). They typically lack Blancan holdovers such as *Chasmaporthetes*, *Sigmodon medius*, and *Capromeryx arizonensis*, as well as taxa characteristic of the late Irvingtonian such as *Didelphis* and *Smilodon populator*. All but one of the new records of *T. haysii*, plus all previous records of the species from Florida, are late early Irvingtonian (early Pleistocene). The youngest record of *T. haysii* from Florida is McLeod, middle Irvingtonian, ca. 0.6 Ma (Morgan and Hulbert this volume). This distribution confirms and amplifies previous suggestions that *T. haysii* is especially characteristic of (or limited to?) the Blancan and Irvingtonian (Hibbard and Dalquest 1966; Ray and Sanders 1984).

Present evidence suggests that *T. haysii* was not present in Florida during the late Blancan or earliest Irvingtonian (ca. 2.5 to 1.6 Ma). Faunas of that interval either lack *Tapirus* altogether (e.g. Macasphalt [= APAC] Shell Pit, St. Petersburg Times Site; Morgan and Ridgway 1987), or contain a relatively small, presently undescribed species of *Tapirus* (e.g. Inglis 1A, De Soto Shell Pit, Haile 7C, Haile 15A). As *T. haysii* is known from the late Blancan of Texas and Colorado (Strain 1966; Hager 1974; Ray and Sanders 1984) and *T. merriami* the Blancan of California (Jefferson 1989), it seems most likely that three species of *Tapirus* were present but not sympatric in North America at that time.

The late Irvingtonian in Florida is presently represented by a single fauna, Coleman 2A. Two specimens, a distal tibia (UF 125414) and an MC II (UF 125415), record *Tapirus* at Coleman. They represent *Tapirus veroensis* and not *T. haysii* on the basis of size. This is the first report of a tapir from the Coleman 2A l.f., and the oldest record of *T. veroensis* in Florida.

The number of known Rancholabrean local faunas in Florida is quite large, probably numbering over a hundred. *Tapirus* is a common constituent of the Florida late Pleistocene megafauna. All tapir specimens directly associated with

Rancholabrean mammals in Florida are *T. veroensis*. The biochronologic range of *T. veroensis* within the Rancholabrean in Florida is difficult to establish because many faunas have not been or cannot be more precisely dated. Early Rancholabrean records of *T. veroensis* include Williston (Holman 1959:18) and Bradenton 51st Street (UF 2361, 3275, 4762). *T. veroensis* persisted into the latest Pleistocene in Florida, based on records associated with Paleoindian artifacts (Aucilla River).

PHYLOGENY OF NEW WORLD *TAPIRUS*

The earliest records of *Tapirus* in North America are late middle Miocene (early Clarendonian, ca. 11 Ma) from the Ash Hollow Formation of Nebraska (Schultz et al. 1975; Yarnell 1980). The genus first appeared in the Oligocene of Europe (Radinsky 1965; Guerin and Eisenmann 1982), so its first occurrence in North America reflects an immigration event, presumably from Asia. Schultz et al. (1975) described two Miocene species from Nebraska, ?*Tapirus johnsoni* (Clarendonian) and ?*Tapirus simpsoni* (early Hemphillian), but only provisionally assigned them to the extant genus. On the basis of more complete cranial material, Yarnell (1980) demonstrated that both could be referred to *Tapirus*, and extended the range of *T. simpsoni* to the late Clarendonian (Love Site). The only early Pliocene sample of *Tapirus* is derived from the Palmetto Fauna of central Florida, and has yet to be studied. *Tapirus* is first recorded in South America during the Uquian (late Pliocene), when it was a member of the first major exchange of terrestrial vertebrates between North and South America following the formation of the Panamanian Isthmus (Marshall et al. 1984). *Tapirus* n. sp. (Florida), *T. merriami* (California), and *T. haysii* (Texas, Colorado) are known from similar-aged late Blancan faunas in North America (Strain 1966; Hager 1974; Jefferson 1989; Hulbert in prep.).

The phylogenetic relationships among extant Neotropical *Tapirus* and fossil North American species have long remained enigmatic (Simpson 1945; Hershkovitz 1954). In order to elucidate these relationships, 26 cranial and dental characters were selected for cladistic analysis (Table 5). Most of these characters have been widely used in the literature to describe fossil and Recent *Tapirus*. Character states for each of the seven species under study (*T. johnsoni*, *T. simpsoni*, *T. haysii*, *T. veroensis*, *T. pinchaque*, *T. bairdii*, and *T. terrestris*) were determined by observation of pertinent skeletal material from the USNM, F:AM, and UF collections. *T. johnsoni*, the oldest species, was used as the outgroup to determine character state polarities. PAUP analysis of the data (Table 6) produces two equally parsimonious cladograms (Fig. 7). Even excluding characters with single autapomorphies, each cladogram has a high overall consistency index of 0.75.

Table 5. Characters and character states used in the phylogenetic analysis of New World *Tapirus*.

1. Height of sagittal crest; 0 = low, 1 = high.
2. Adult width of sagittal crest; 0 = narrow, 1 = broad.
3. Dorsal surface of frontals; 0 = relatively broad, 1 = relatively narrow.
4. Frontal inflation; 0 = none or slight, 1 = moderate to very inflated.
5. Interparietal; 0 = fused relatively early in ontogeny, 1 = fused late in ontogeny.
6. Anteromedial process of frontal; 0 = extends between nasals, 1 = does not extend between nasals.
7. Nasal length; 0 = long, 1 = short.
8. Depth of spiral groove on nasal; 0 = shallow, 1 = deep.
9. Spiral groove on nasal; 0 = extensive, close to midline of skull, 1 = not extensive or close to midline.
10. Depth of ascending groove for nasal diverticulum; 0 = shallow, 1 = deep.
11. Lambdoidal crests; 0 = flair both posteriorly and laterally, 1 = directed posteriorly with little or no outward flair.
12. Dorsal contour of skull; 0 = relatively straight, 1 = nasals notably stept down from frontals.
13. Posterior process of premaxilla; 0 = long, terminates in acute point; 1 = short, bluntly terminated.
14. Anteromedial process of maxilla; 0 = very slender, little or no lateral exposure, 1 = slender, moderate lateral exposure, 2 = broad, well exposed laterally.
15. Premaxillary-maxillary suture; 0 = descends anterior to canine in lateral view, 1 = descends to middle of canine.
16. Dorsal maxillary flange; 0 = absent, 1 = present.
17. Relative width of paroccipital process; 0 = narrow and slender, 1 = broad and massive.
18. Anterior lacrimal process(es); 0 = absent or weak, 1 = well developed.
19. Lacrimal depression; 0 = absent, 1 = present.
20. Relative diastema length; 0 = short, 1 = moderate, 2 = long.
21. P1 shape; 0 = short, broad, 1 = elongate.
22. Metastylids on dp2-dp4; 0 = weak, often absent on dp3 and dp4, 1 = well developed on all three deciduous premolars.
23. P2 molarization; 0 = poor (low AW/PW ratio), 1 = moderate, 2 = well molarized.
24. Relative mandibular ramus depth; 0 = slender, 1 = massive.
25. Crown height of cheekteeth; 0 = short-crowned teeth, 1 = higher crowned teeth.
26. Cheektooth width; 0 = teeth relatively narrow, 1 = teeth broad.

Both cladograms in Figure 7 hypothesize that *T. haysii* and *T. veroensis* share a closer common ancestor than either does with any of the Neotropical species. Similarly, the three extant species form a monophyletic group united by five synapomorphies (node 4, Fig. 7). *T. terrestris* and *T. bairdii* are closest sister taxa. The difference between the two cladograms is in the position of the late Miocene species *T. simpsoni*. In one, *T. simpsoni* is the sister taxon to the five Pleistocene and Recent species (Fig. 7A). The latter group (node 2, Fig. 7A) is hypothesized to share two derived character states in the dentition, wider cheekteeth and a more molarized P2 (the latter is found in the primitive state in *T. pinchaque*; this is regarded as a reversal in Fig. 7A). Figure 7A more closely corresponds with the

Table 6. Character states for seven New World species of *Tapirus*. Character numbers (1-26) and codes for states refer to those listed in Table 5. A "?" denotes an unknown or missing value for a character state.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13
T. johnsoni	0	0	0	0	?	0	0	0	0	0	0	0	0
T. simpsoni	0	0	?	?	0	0	0	?	1	?	0	0	0
T. haysii	0	0	?	?	1	?	?	?	?	?	0	?	0
T. veroensis	0	0	0	1	1	0	?	0	0	0	0	0	0
T. pinchaque	0	0	0	1	0	1	0	0	1	1	0	0	0
T. terrestris	1	0	1	0	0	0	1	0	1	1	1	1	0
T. bairdii	0	1	1	0	0	0	0	1	1	1	1	1	1

Character	14	15	16	17	18	19	20	21	22	23	24	25	26
T. johnsoni	?	?	?	0	0	0	0	0	0	0	0	0	0
T. simpsoni	1	0	0	1	?	?	0	0	0	0	0	1	0
T. haysii	1	0	0	1	?	?	0	0	1	2	1	1	1
T. veroensis	1	0	0	0	0	1	0	0	0	1	1	1	1
T. pinchaque	0	0	0	0	1	0	1	1	?	0	0	1	1
T. terrestris	0	0	0	0	1	0	1	0	0	1	0	1	1
T. bairdii	2	0	1	0	0	0	2	0	0	1	0	1	1

known fossil record of the group, and with their biogeographic relationships. It suggests that the closest ancestor (node 2) shared by North and South American *Tapirus* was of early Pliocene age, unfortunately a time when the fossil record is very poor.

The alternate phylogenetic hypothesis (Fig. 7B) has *T. simpsoni* as the sister taxon to the three Neotropical species only, and *T. veroensis* + *T. haysii* is the sister group of these four species. Only a single known apomorphy unites *T. simpsoni* and the extant species at node 3, a reduction in the development of the nasal diverticulum scroll. This arrangement requires no reversal to attain a primitive P2 in *T. pinchaque*, but rather parallel development of a molarized P2 in the groups *T. terrestris* + *T. bairdii* and *T. haysii* + *T. veroensis*. This arrangement implies the existence of an as yet unknown common ancestor of *T. veroensis* and *T. haysii* in the late Miocene and early Pliocene.

Which of the two competing hypotheses more closely reflects the true phylogenetic history of the group is difficult to determine at present, but each can be tested with a more complete fossil record, or the inclusion of more taxa in the analysis. The states of two important cranial characters, the development of an

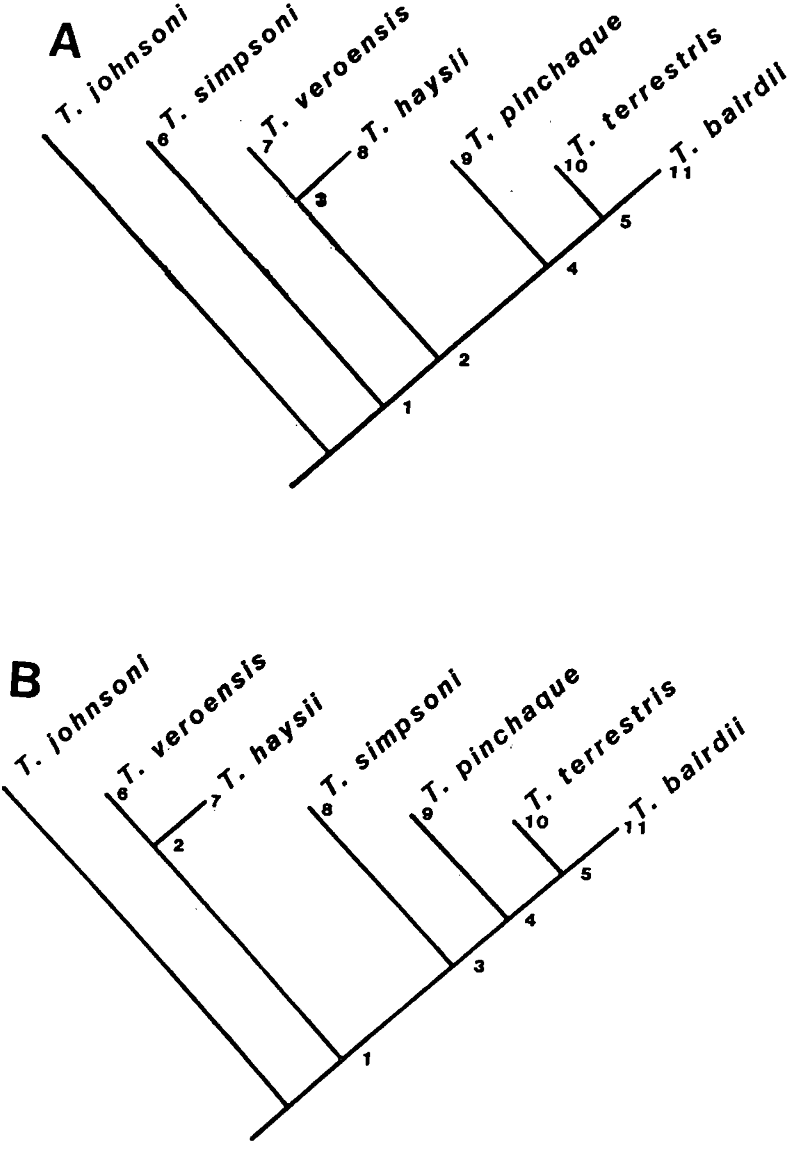

Figure 7. Two equally most parsimonious cladograms produced by the PAUP program for seven New World species of *Tapirus*. *T. johnsoni* was used as an outgroup in the analysis. Numbers refer to nodes mentioned in text.

anterior lacrimal process and the depth of the ascending diverticular channel, are presently unknown in *T. simpsoni*. If either were shown to be synapomorphic with the derived state observed in the Neotropical tapirs, then the cladogram in Fig. 7B would become more parsimonious than the other. This analysis is obviously very tentative, as it includes neither any South American fossil species (which are very poorly known), nor Asiatic species. It assumes that *T. indicus* is more closely related to other Asiatic and European species, and that the few similarities it shares with Neotropical *Tapirus* represent homoplasy. Only a comprehensive study of all fossil and Recent *Tapirus* could substantiate that assumption and possibly eliminate one (or both) of the two alternative phylogenies proposed here.

CONCLUSIONS

Three Plio-Pleistocene tapirs are known from Florida. A large species, referred to *Tapirus haysii* Leidy, is known from at least 14 late early to middle Irvingtonian (ca. 1.5-0.6 Ma) localities. The sample from Leisey Shell Pit 1A is the largest and most complete of these, and includes the first described cranial elements of the species. It demonstrates that *T. haysii* shares many cranial character states with the late Pleistocene *T. veroensis*, although a majority of these are interpreted to be plesiomorphic for New World *Tapirus*. The P1 and P2 of the Leisey sample are, on average, less "molarized" than those of the best known population of *T. haysii*, from the Port Kennedy site, Pennsylvania. The difference is interpreted as the result of chronoclinal variation, and the two samples are otherwise quite similar. All previous records of *T. haysii* from the Rancholabrean of Florida are either instances of misinterpretation of the age of the specimen (e.g. Ray 1964), or are relatively large individuals of *T. veroensis*. *T. haysii* and *T. veroensis* are very closely related, and a hypothesis that they represent a single, polytypic species is not easily falsified, as their chronologic and geographic distributions never seem to intersect (at least with identifiable specimens). *T. haysii* has at least two apomorphies that imply they are distinct species, well developed metastylids on deciduous premolars, and more "molarized" anterior upper premolars. There is, however, intraspecific variation in both of these, and only small sample sizes are known for the former.

The late Pliocene species of *Tapirus* from Florida is slightly smaller than average-sized individuals of *T. veroensis*, but falls within the observed ranges of the latter for dental dimensions. It is thus much smaller than the giant *Tapirus haysii*, and apparently represents a new species. It occurs only in faunas that are older than those producing *Tapirus haysii* (Inglis 1A, Haile 7C, Haile 15A; late Blancan-very early Irvingtonian), so there is no evidence the two were sympatric. The absence of *T. haysii* from the earliest Irvingtonian and late Blancan in Florida is interesting, as it is known from similar-aged sites in Texas and Colorado. *T.*

veroensis ranges from the late Irvingtonian (Coleman 2A) to the latest Rancholabrean.

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