

Tapirs from the Pleistocene of Venezuela

ELIZETE C. HOLANDA and ASCANIO D. RINCÓN



Holanda, E.C. and Rincón, A.D. 2012. Tapirs from the Pleistocene of Venezuela. *Acta Palaeontologica Polonica* 57 (3): 463–472.

The living tapir *Tapirus terrestris* is widely distributed in Venezuela, occurring mainly south of the Orinoco, while being absent from arid, high Andean and insular areas. Here, we describe new material of fossil tapirs from two Pleistocene localities of Venezuela: Zumbador Cave and El Breal de Orocuai. Based on its size and morphology, the material from Zumbador Cave (skull, mandible and postcrania) is assigned to the extant *T. terrestris*, and represents the most northwestern fossil record of this species in South America. By contrast, the remains from the tar seep of El Breal de Orocuai are more gracile, and differ from *T. terrestris* and other fossil and living species from South America in the presence of a metastylid on the lower cheek teeth. We tentatively assign the latter remains to *Tapirus* sp., based on juvenile and isolated dentary material. However, the possibility that these specimens may represent a new species or an immigrant from North America cannot be completely excluded.

Key words: Mammalia, Perissodactyla, *Tapirus*, Pleistocene, El Breal de Orocuai, Zumbador Cave, Venezuela.

Elizete C. Holanda [elizete.holanda@gmail.com], Programa de Pós-Graduação em Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brasil and Setor de Paleontologia, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Av. Dr. Salvador França, 1427, Jd. Botânico, CEP 90690-000, Porto Alegre, Rio Grande do Sul, Brazil;

Ascanio D. Rincón [ascaniodaniel@gmail.com], Instituto Venezolano de Investigaciones Científicas, Lab. Biología de Organismos Centro de Ecología, Km 11 de la Carretera Panamericana, Apartado Postal 20632, Caracas 1020A, Venezuela.

Received 7 January 2011, accepted 12 July 2011, available online 25 July 2011.

Introduction

The family Tapiridae contains a single extant genus, *Tapirus*, with one species living in southeastern Asia and a further three in America (Brooks et al. 1997). The origins of the family are likely to be found in the Holarctic, and more specifically in the Eocene of North America (Eberle 2005). The earliest records of *Tapirus* in North America date from the Late Miocene (Late Clarendonian) (Hulbert 2005). Although it has been suggested that tapirs entered South America in the Late Miocene (Campbell et al. 2010), other evidence suggests that the genus appeared in South America at about 2.6–1.0 Ma with the Ensenadan immigrants, after the formation of the Isthmus of Panama and during the faunal events of the Great American Biotic Interchange (GABI) (Woodburne et al. 2006; GABI 2 sensu Woodburne 2010).

Remains of *Tapirus* have been recorded from Pleistocene deposits of Brazil, Bolivia, Peru, Argentina and Uruguay (Rusconi 1928; Cattoi 1951; Ubilla 1983; Marshall et al. 1984; Holanda and Cozzuol 2006), including three species from the Ensenadan (Early to Middle Pleistocene, according to Cione and Tonni 2005): *T. tarijensis* (Tarija, Bolivia), *T. rioplatensis* (Buenos Aires Province, Argentina) and *T. oliverasi* (Department of Montevideo, Uruguay) (Ameghino 1902; Cattoi 1957; Ubilla 1983). However, the validity of the last species is dubious (Holanda et al. 2011).

Only three fossil species have so far been described from the Late Pleistocene: *T. cristatellus* from Minas Gerais and Bahia states, Brazil (Winge 1906; Cartelle 1999; Holanda et al. 2007); *T. mesopotamicus* from Entre Rios Province, Argentina (Ferrero and Noriega 2007); and *T. rondoniense* from southwestern Amazonia (Holanda et al. 2011). Molecular analyses suggest the two living South American species, *T. terrestris* and *T. pinchaque*, to be sister taxa, having separated at about 3 Ma (Ashley et al. 1996). In addition, morphology-based phylogenetic analyses including both fossil and living taxa indicate a dichotomy between the Late Miocene–Early Pleistocene North American species (*T. veronensis*, *T. haysii*, and *T. polkensis*) and their South American counterparts (*T. terrestris*, *T. pinchaque*, and *T. mesopotamicus*), with *T. bairdii* being more closely related to the first group (Ferrero and Noriega 2007; Hulbert 2010).

The extant neotropical species of the genus *Tapirus* have been associated with humid, forested environments, including lowland forest, primary and secondary forest, Amazonian floodplains, and montane cloud forest (Brooks et al. 1997). They are browsers and frugivores, playing a critical role in the structuring of tropical forests by dispersing seeds (Fragoso and Huffman 2000), and, together with their fossil counterparts, are considered indicators of ancient forested environments (DeSantis and MacFadden 2007). In Venezuela, *T. terrestris* is widely distributed, occurring mainly

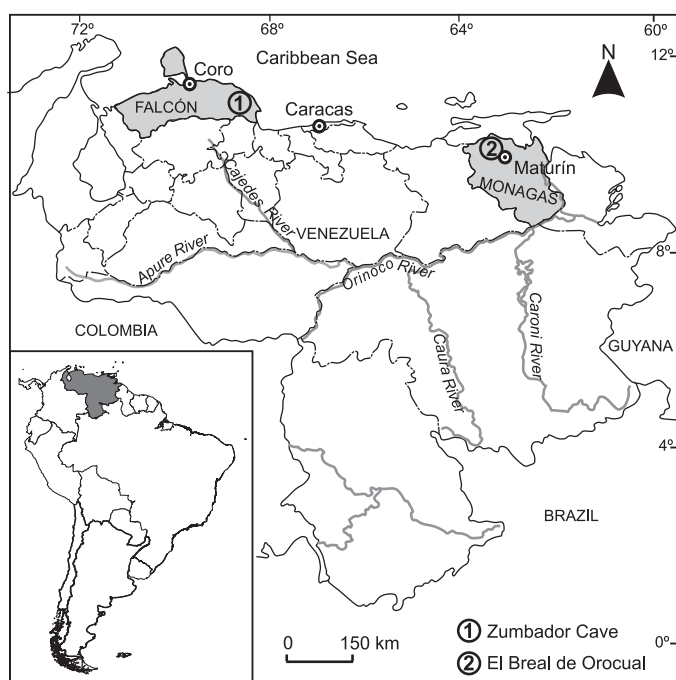


Fig. 1. Map of the localities in Venezuela from which fossil tapirs have been reported.

south of the Orinoco. The species is usually found in rainforests and savannahs, though a few occurrences have also been reported from montane forests located north of the Orinoco (Perijá, Mérida, Coastal, and Oriental Mountain ranges); by contrast, *T. terrestris* is completely absent from arid, high Andean and insular areas (Torres and Gutiérrez 2001).

Here, we describe new fossil material of tapirs collected from two localities from the Pleistocene of Venezuela, Zumbador Cave and El Breal de Orocuai (Fig. 1), and compare the recovered specimens to extant and fossil American species of *Tapirus*.

Geological setting

Zumbador Cave is located in the eastern part of Falcón State ($10^{\circ}51'26''$ N, $68^{\circ}36'41''$ W), where it is developed in the limestone of the Middle Miocene Capadare Formation (Cerro Misión). Water transported fossil bones into the karstic system, creating a fossil-rich cave deposit (Rincón 2003). Based on its fossil contents, the latter is likely to be Late Pleistocene in age, with palaeoenvironmental indicators suggesting a savannah-type landscape with patches of dispersed trees (Rincón 2003).

El Breal de Orocuai is located in Monagas State ($9^{\circ}50'48''$ N, $63^{\circ}19'46.05''$ W), near Maturin City, and represents an inactive natural tar seep from which 24 mammalian taxa have been reported (Rincón et al. 2009). The tar seep forms part of the Mesa Formation, which comprises fluvial-deltaic strata considered to have been deposited during the Early to Middle Pleistocene (González de Juana et al. 1980). How-

ever, new evidence based on faunal assemblage data has also raised the possibility of a Plio-Pleistocene age for this formation (Rincón et al. 2009, 2011).

Material and methods

The material is stored as part of the palaeovertebrate collection of the Instituto Venezolano de Investigaciones Científicas. The specimens studied here were compared to several extant and fossil specimens from a range of collections (see Appendix 1). The cranial and postcranial nomenclature follows Ray and Sanders (1984) and Radinsky (1965), while the dental terminology follows Butler (1952). The measurements employed here follow Simpson (1945) and Hue (1907). Whenever possible, morphometric analyses were performed using version 2.09 of the Palaeontological Statistics—PAST software (Hammer et al. 2001). Principal component analysis (PCA) was used as an exploratory tool to illustrate key differences between groups using multiple variables, such as width and length of the upper and lower cheek teeth, as well as eight measures of the humerus. All measurements were log₁₀ transformed prior to analysis. Bivariate analyses or simple descriptive statistics were used for fragmentary specimens not preserving all of the measured variables (e.g., M1 of OR1369). All of the selected postcranial specimens possessed completely fused epiphyses, suggesting skeletally mature individuals.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CICYTTP, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Argentina; F:AM, Frick fossil mammal collection, AMNH; IVIC-P, palaeontology collection, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MLP, Museo de La Plata, La Plata, Argentina; MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; OR, El Breal de Orocuai collection, housed at the Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela; UF, Florida Museum of Natural History, Gainesville, USA; UF/FGS, Florida Geological Survey Collection, now housed at the Florida Museum of Natural History; UNIR, Universidade Federal de Rondônia, Porto Velho, Brazil.

Measurement abbreviations.—Humerus: CDD, craniocaudal diameter of the distal portion; CDP, craniocaudal diameter of the proximal portion; L, maximum length; MDB, mediolateral diameter of the body; MDD, mediolateral diameter of the distal portion; MDH, mediolateral diameter of the humeral head; MDP, mediolateral diameter of the proximal portion; TMD, mediolateral diameter of the humeral trochlea. Teeth: L, maximum length; W, maximum width.

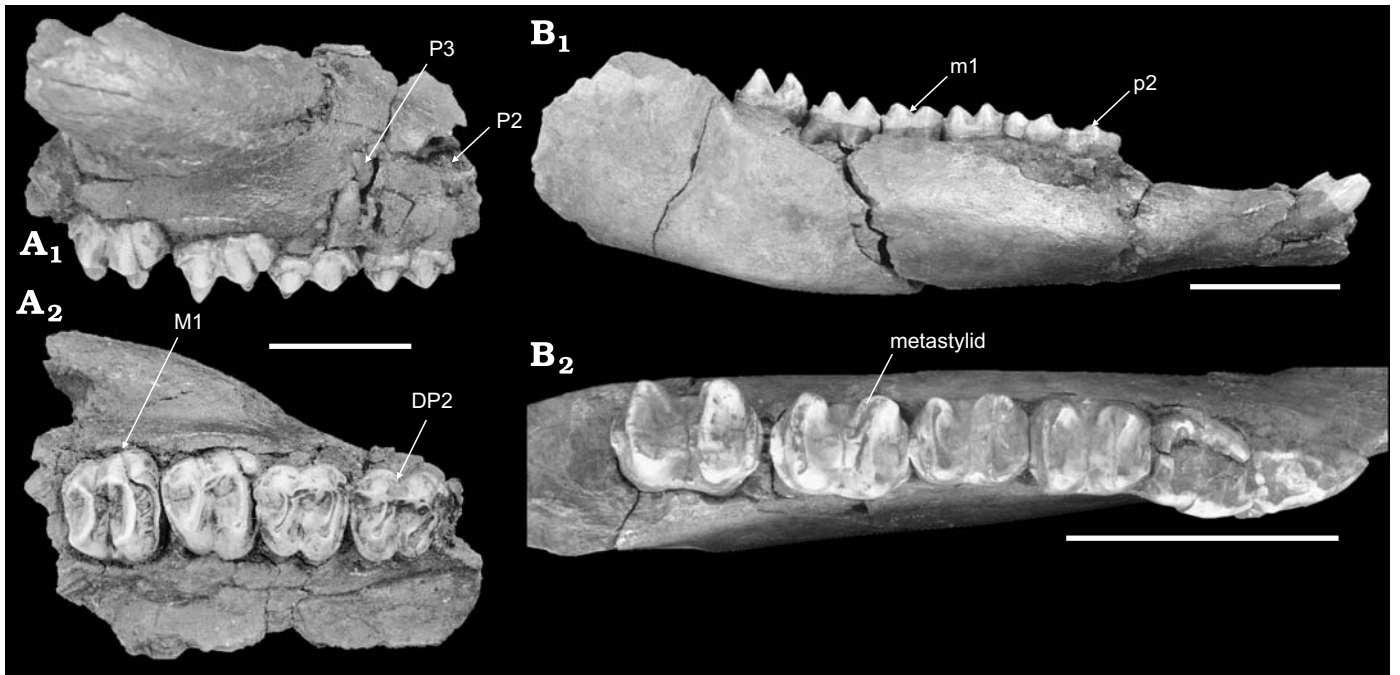


Fig. 2. *Tapirus* sp., El Breal de Orocuai, Plio-Pleistocene. **A.** ORI1369, right maxilla in lateral (A_1) and occlusal (A_2) views. **B.** ORI1367, mandible in labial (B_1) and occlusal (B_2) views. Scale bars 30 mm.

Other abbreviations.—N, size of sample; OR, observed range; PC, principal component.

Systematic palaeontology

Class Mammalia

Order Perissodactyla Owen, 1848

Infraorder Ceratomorpha Wood, 1937

Family Tapiridae Burnett, 1830

Genus *Tapirus* Brisson, 1762

Type species: *Hippopotamus terrestris* Linnaeus, 1758; Pernambuco, Brazil, Oligocene–Recent.

Tapirus sp.

Fig. 2A, B.

Material.—Incomplete right maxilla, ORI1369; incomplete mandible, ORI1367 from El Breal de Orocuai, Monagas State (Fig. 1), Plio-Pleistocene.

Description.—Maxilla: ORI1369 is a juvenile bearing DP2–4 in wear, as well as a fully erupted M1. In lateral view, P2 and P3 are preserved in crypt (Fig. 2A, B). Rincón et al. (2009) erroneously considered the deciduous teeth to be the P4–M3 of an adult individual.

DP2 is trapezoidal in shape and bears a small parastyle. The reduced protocone is located next to the hypocone, and is connected to the paracone by the base of the ectoloph. The protoloph is oriented obliquely relative to the ectoloph, and less transverse than the metaloph. DP3 is slightly trapezoidal and marked by a poorly developed parastyle. Its protoloph

and metaloph are oriented transversely, with the former being wider than the latter. DP4 is more molariform than DP3 and shows less wear. As in DP3, the protoloph is wider than the metaloph, with both being oriented transversely. The DP4 parastyle is more developed than on DP2–3. All of the preserved deciduous teeth bear relatively poorly developed mesial and distal cingula. By contrast, labiodistal cingula are present and well developed on the cheek teeth. M1 presents no wear, and bears a well developed parastyle, as well as a mesial cingulum. The suture between the maxilla and the jugal is partially fused.

Mandible: ORI1367 represents a partial mandible preserving the alveoli for i1–3, as well as the canines and the right dentary bearing p2–m3 in situ (Fig. 2B). The mandibular symphysis is solidly fused and the bone is relatively slender. On the preserved cheek teeth, the lophids show little wear and lack accessory cusps. The p2 and p3 are bent distolabially and mesolabially, respectively, and show wear. On p3–m3, cingulids are present and well developed mesially and distally, but absent labially and lingually. A small, but distinct, metastylid is present on the distolingual side of the metaconid on p3, m1, and m3. A better developed metastylid is present on m2 (Fig. 2B₂).

Measurements.—ORI1369: DP2L = 19.8; DP2W = 19.82; DP3L = 19.21; DP3W = 20.3; DP4L = 20; DP4W = 23; M1L = 22; M1W = 23.8. ORI1367: see Table 1.

Remarks.—The mental foramen in ORI1367 is located directly ventral to the p2, as in most species of *Tapirus*. While ORI1369 and ORI1367 resemble *T. terrestris* in size, the specimens are very slender. The presence of a well-developed metastylid on m2, as well as a small but distinct metastylid on p3, m1 and m3

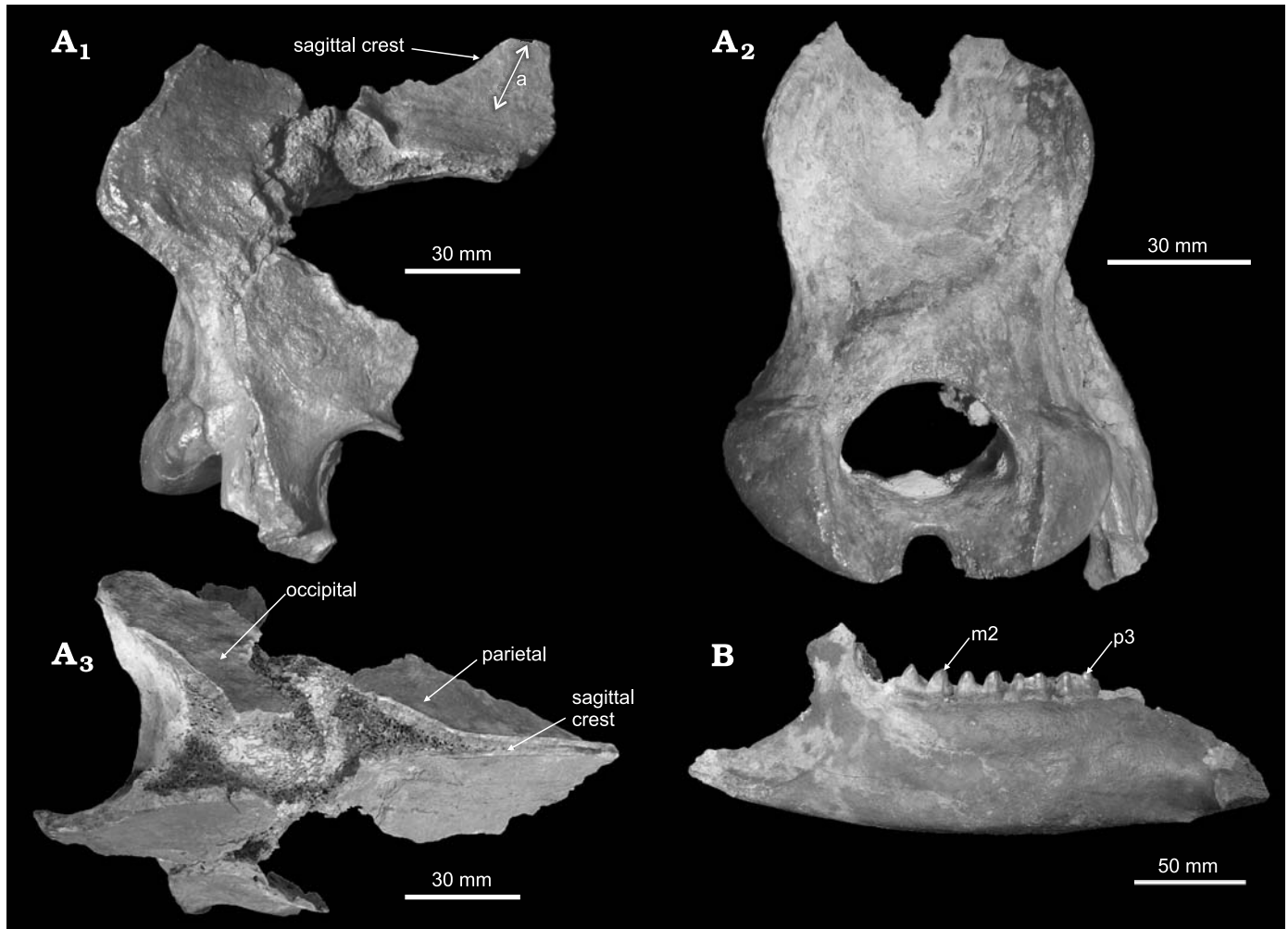


Fig. 3. *Tapirus terrestris* (Linnaeus, 1758), Zumbador Cave, Pleistocene. A. IVIC-P-2080, incomplete skull in lateral (A₁), posterior (A₂), and dorsal (A₃) views. B. IVIC-P-2081, left dentary in lingual view; a, height of the sagittal crest.

Table 1. Measurements (in mm) of the lower cheek teeth of OR 1367 and *Tapirus* from South America. Maximum width is distal width for p2–4, and mesial width for m1–3. Data for “*Tapirus oliverasi*” and *Tapirus cristatellus* are from Ubilla (1983) and Winge (1906), respectively. When N>1, the first line represents the mean, the second line the overall range, and the third line the total number of specimens.

		p2	p3	p4	m1	m2	m3
OR 1367	length	22	19.40	20.60	21	25.1	26.3
	maximum width	13.10	17.70	17.84	16.46	17.8	18.3
<i>Tapirus tarijensis</i>	length	27.6	25.7	26	24.2	29.3	31.3
	maximum width	17	20.2	22.1	20.2	21.4	22.7
<i>Tapirus rioplatensis</i>	length	–	30	27.1	30	–	–
	maximum width	–	21	21	23.2	–	–
“ <i>Tapirus oliverasi</i> ”	length	–	–	–	26.6	29.5	30.3
	maximum width	–	–	–	21.4	22.8	23.3
<i>Tapirus cristatellus</i>	length	–	–	–	–	25.19	26.6
	maximum width	–	–	–	–	19	20
<i>Tapirus terrestris</i>	length	21.38 19.4–24.24 (36)	19.95 17.95–22.56 (36)	20.32 18.2–22 (36)	20.04 17–21.7 (22)	23.01 21–26.38 (22)	24.25 22.35–27.76 (22)
	maximum width	13.35 11.8–15.35 (36)	15.63 13–17.5 (36)	17.62 14.9–20.4 (36)	16.48 14.9–17.82 (22)	18.1 17–19.8 (22)	18.72 17.3–20.6 (22)

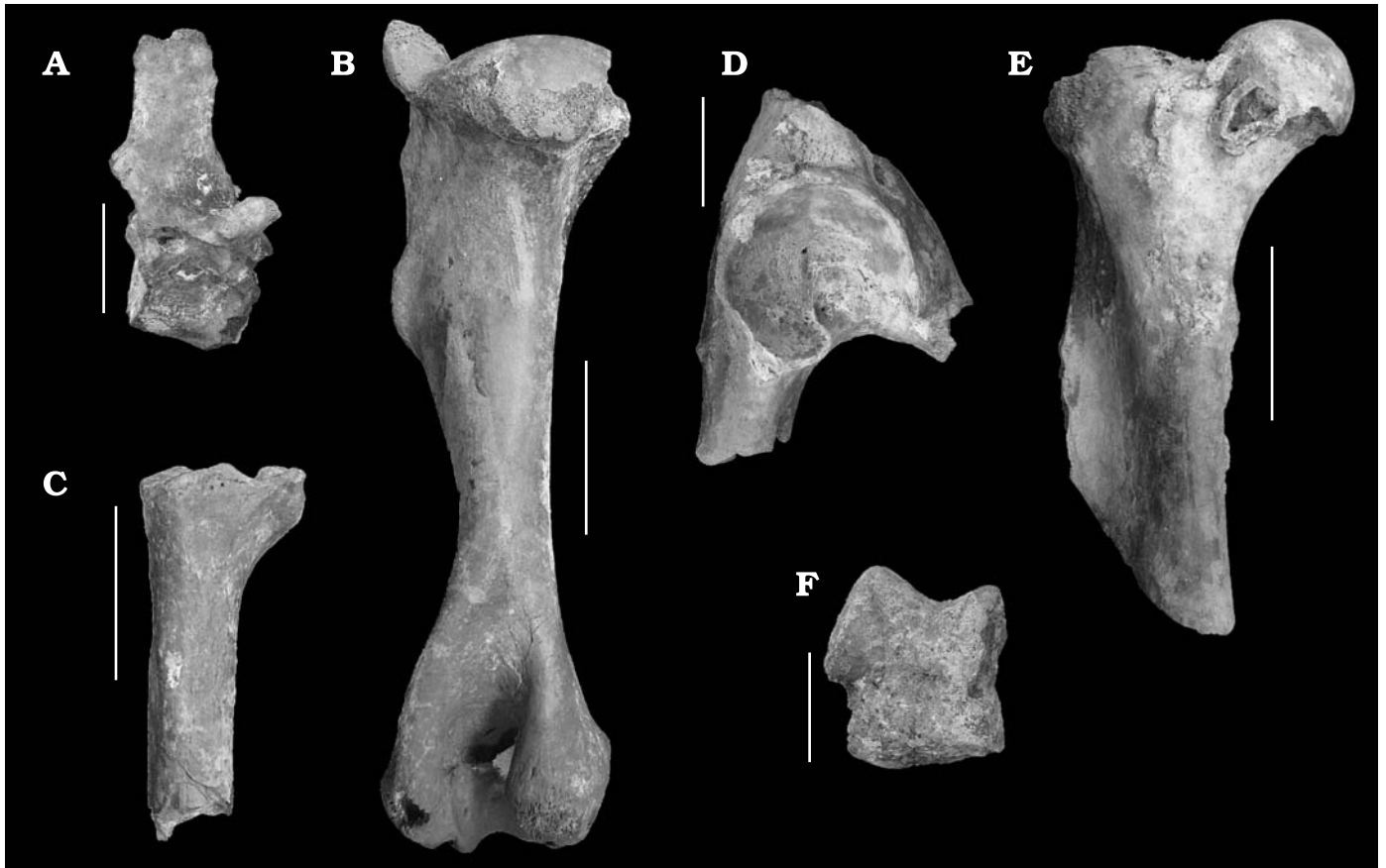


Fig. 4. *Tapirus terrestris* (Linnaeus, 1758), Zumbador Cave, Pleistocene. **A.** IVIC-P-2083, thoracic vertebra in right lateral view. **B.** IVIC-P-2088, left humerus in posterior view. **C.** IVIC-P-2077, left radius in anterior view. **D.** IVIC-P-2086, incomplete right pelvis in lateral view. **E.** IVIC-P-2076, left femur in anterior view. **F.** IVIC-P-2084, right astragalus in dorsal view. Scale bars 30 mm.

in OR1367 differs from the condition in other extinct and extant South American species, in which it is usually absent. Among the North American species, a relatively well-developed metastylid frequently occurs on p4 and m1–2 in *T. johnsoni* (e.g., F:AM 37302) and on the deciduous teeth of *T. polkensis* (Hulbert et al. 2009), while being poorly developed or absent in *T. webbi*, *T. veroensis*, and *T. haysii*. However, while *T. polkensis* differs from other species of *Tapirus*, as well as OR1369 and OR1367, by its overall smaller size, *T. johnsoni* is distinguished by relatively short cheek tooth crowns bearing a moderately developed parastyle.

Tapirus terrestris (Linnaeus, 1758)

Figs. 3, 4.

Material.—Incomplete skull, IVIC-P-2080; incomplete left dentary, IVIC-P-2081; incomplete thoracic vertebrae, IVIC-P-2082, IVIC-P-2083; incomplete left radius, IVIC-P-2077; left humerus, IVIC-P-2088; incomplete left femur, IVIC-P-2076, IVIC-P-2079, IVIC-P-2087; right astragalus, IVIC-P-2084; incomplete right pelvis, IVIC-P-2086; Zumbador Cave, Cerro Misión, Falcón State (Fig. 1), Pleistocene.

Description.—Skull: IVIC-P-2080 is a subadult, with unfused sutures (Fig. 3A₁, A₃). Only the posterior portions of the parietals are preserved, and form a narrow and high

sagittal crest. The occipital is marked by strongly developed and posterolaterally projecting lambdoidal crests. The interparietal region is partially fused. A partial left post-tympanic process and the dorsal margin of external acoustic meatus are all that is preserved of the temporal.

Mandible: IVIC-P-2081 is a left dentary of a young adult bearing p4–m2 and an unerupted m3 (Fig. 3B), while missing the coronoid process and the symphyseal region. The body of the dentary is robust and thick. The m1 is slightly worn and marked by perpendicularly arranged lophids, with the protolophid being as wide as the hypolophid. Accessory cuspids and metastylids are absent. The m2 shows little wear and is distinguished by a protolophid exceeding the hypolophid in width.

Postcrania: IVIC-P-2083 is a fractured thoracic vertebra, with a tall and posteriorly inclined spinous process (Fig. 4A). The transverse processes are anteroposteriorly elongated, while the mammillary processes are elongate and directed dorsally. IVIC-P-2088 represents an almost complete left humerus (Fig. 4B). The proximal part of the head is flatter and wider than its distal part, strongly convex, and sloping distally. The greater tubercle is smoothly curved proximally, greatly increases in thickness antero-posteriorly, and extends to a position above the head of the

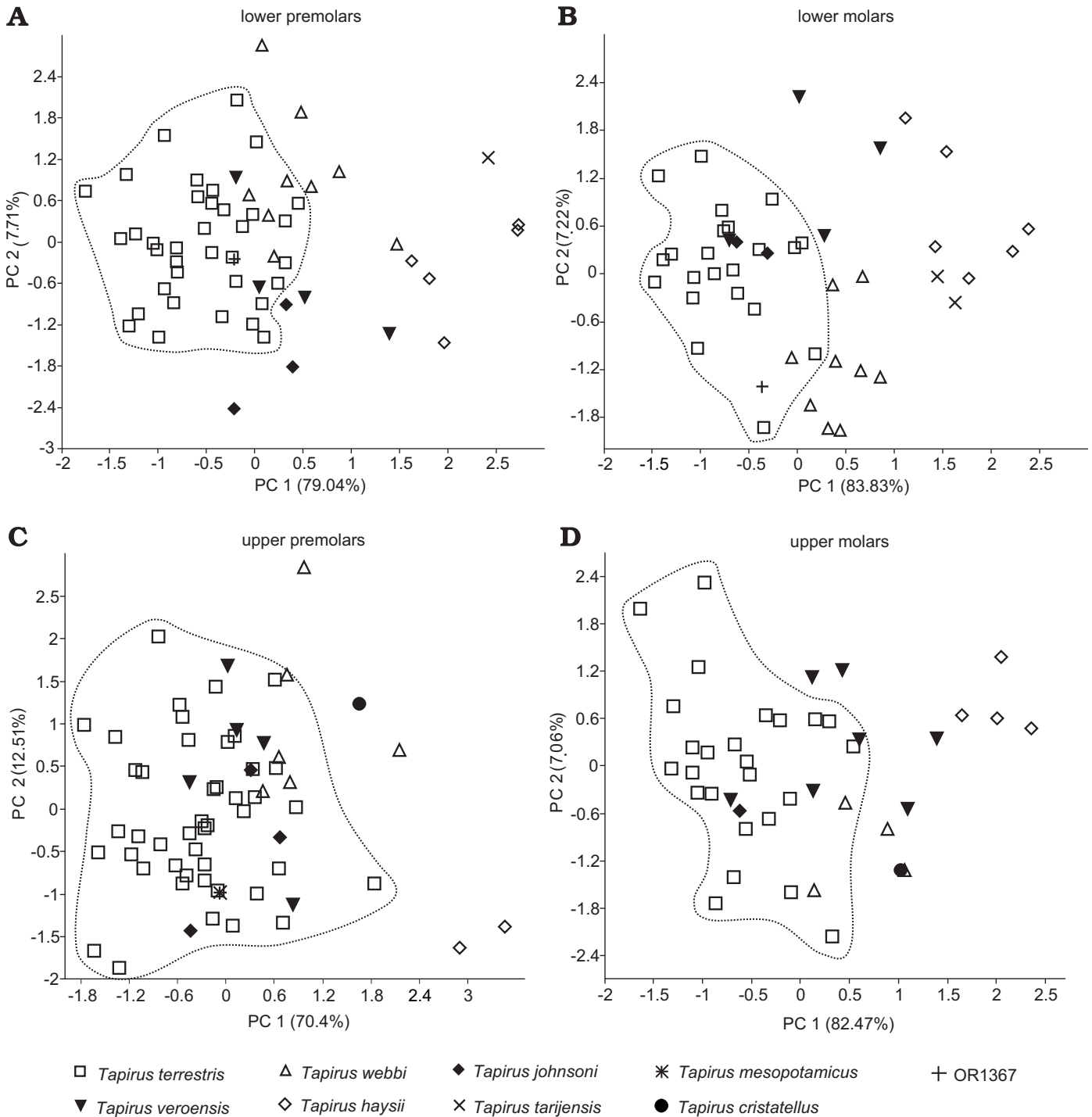


Fig. 5. Scatter plots of the first two principal component scores arising from the PCAs of the premolar and molar measurements. Abbreviations: PC, principal components; % percentage of variation explained.

humerus. The deltopectoral crest of the humerus begins at the greater tubercle and extends distally to the deltoid tuberosity, with the latter being very prominent and somewhat rounded. The distal end of the humerus is slightly rounded. IVIC-P-2077 (Fig. 4C) represents the proximal end of a left radius, lacking any sign of fusion to the ulna. The radial head is rectangular and wide. The radial tuberosity is developed as a small rugosity.

IVIC-P-2086 corresponds to the iliac part of a right pelvis, in addition to a complete acetabulum (Fig. 4D). The latter is about 50 mm in diameter and marked by a distinct fossa extending to its ventral margin, with the latter most likely representing a site of attachment for ligaments. Three fragments of the left femur are preserved. The proximal end (IVIC-P-2076) is transversely wider than it is thick anteroposteriorly. The greater trochanter is broken (Fig. 4E), as are

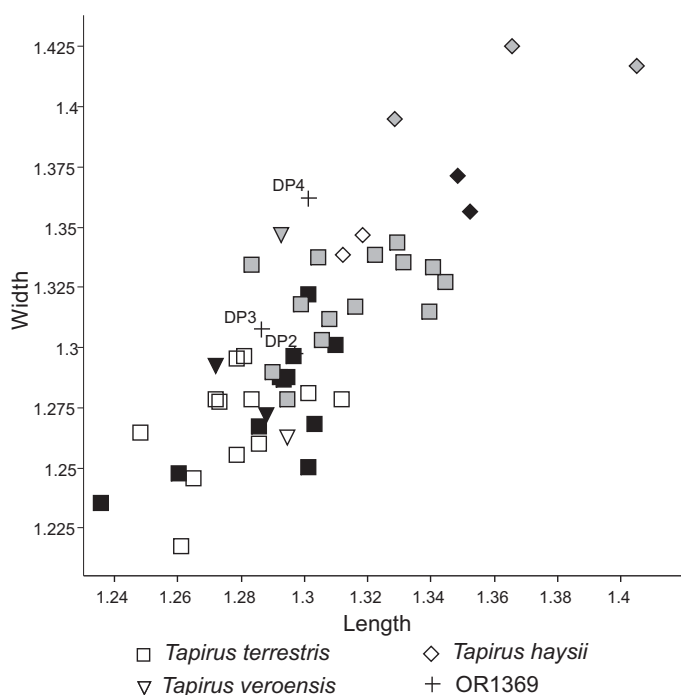


Fig. 6. Scatter plot of the widths and lengths of DP2 (open symbols), DP3 (black symbols), and DP4 (grey symbols).

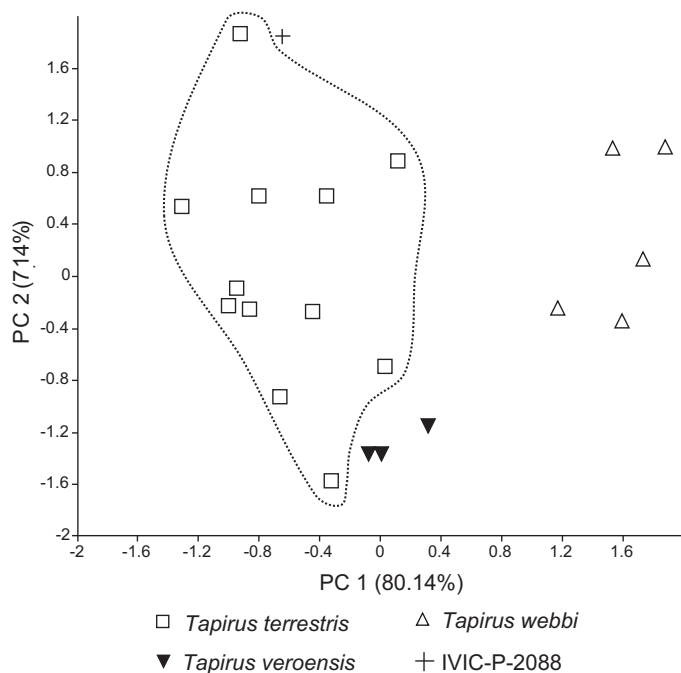


Fig. 7. Scatter plot of the first two principal component scores arising from the PCA of the humerus measurements. Abbreviations: PC, principal components; % percentage of variation explained.

the distal portions of the lesser and third trochanters. The body of the femur (IVIC-P-2079) is rather cylindrical in cross section, becoming wider and somewhat flattened distally. The distal end of the humerus (IVIC-P-2087) is transversely wider than it is thick anteroposteriorly, and slightly

triangular in shape. The supracondylar fossa is very deep and rough, and lanceolate in outline. IVIC-P-2084 is a heavily eroded right astragalus (Fig. 4F). It is slightly square in outline, with the proximal trochlea being inclined at an angle of about 15 degrees with respect to the body. The lateral condyle is higher and projects more proximally than the medial one, and ends abruptly without reaching the plantar surface. The distal articular surface is slightly rectangular and consists of two asymmetrical facets: the navicular facet is rectangular, transversely wider, and thicker dorsoplantarly; by contrast, the cuboid facet is about half the width of the navicular facet, slightly squared, and convex.

Measurements.—IVIC-P-2088: L = 263; MDP = 76.3; CDP = 77; MDH = 55.6; MDB = 29; MDD = 73.4; CDD = 64.4; DTt = 41.1. IVIC-P-2077: MDP = 50; CDD = 26.8.

Remarks.—The cranial anatomy of IVIC-P-2080 resembles that of *T. terrestris*. Despite being a juvenile, as indicated by the unfused sutures, the specimen displays a fully formed, high and narrow sagittal crest (Fig. 3A₂). By contrast, *T. bairdii* has a sagittal table and never forms a true sagittal crest (e.g., MLP 1451), while in *T. veroensis* (UF/FGS277), *T. haysii* (UF80466), and *T. pinchaque* (Holbrook 2002) the sagittal crest is low. The crest of the South American fossil tapirs *T. mesopotamicus*, *T. cristatellus*, and *T. rondoniensis* is intermediate in size, being much higher than in *T. pinchaque*, but lower than that of *T. terrestris*.

Unlike in any of the North American species, the lambdoidal crests of IVIC-P-2080 are strongly developed and project posterolaterally as in *T. terrestris* (Fig. 3B, C).

The postcranial morphology of *Tapirus* is rather conservative, and hence of little diagnostic value (Simpson 1945). Wherever possible, the present specimens were compared to other species with preserved postcrania, but, apart from their size, there were few differences. The humerus from Zumbador Cave (IVIC-PV-2088) and that of *T. terrestris* are virtually identical, and differ from *T. webbi* and *T. veroensis* in a more cranially directed greater tubercle. In addition, the supracondylar crest of *T. webbi* (e.g., UF26225) is very prominent and directed more laterally than in other species. At the present time, we are unable to establish whether these characters can truly distinguish different species, or test their intra- and interspecific variability.

Geographic and stratigraphic range.—South America, Oligocene–Recent.

Morphometric analysis

The lower teeth of OR1367 are similar in size to those of *T. terrestris* (Table 1), with the teeth of the North American species being significantly larger than those of both *T. terrestris* and *T. pinchaque*. The only two exceptions are *T. polkensis*, the smallest known North American species (Hulbert et al. 2009), and *T. veroensis*, whose size range usually overlaps with that of *T. terrestris* (Simpson 1945). Our analysis of den-

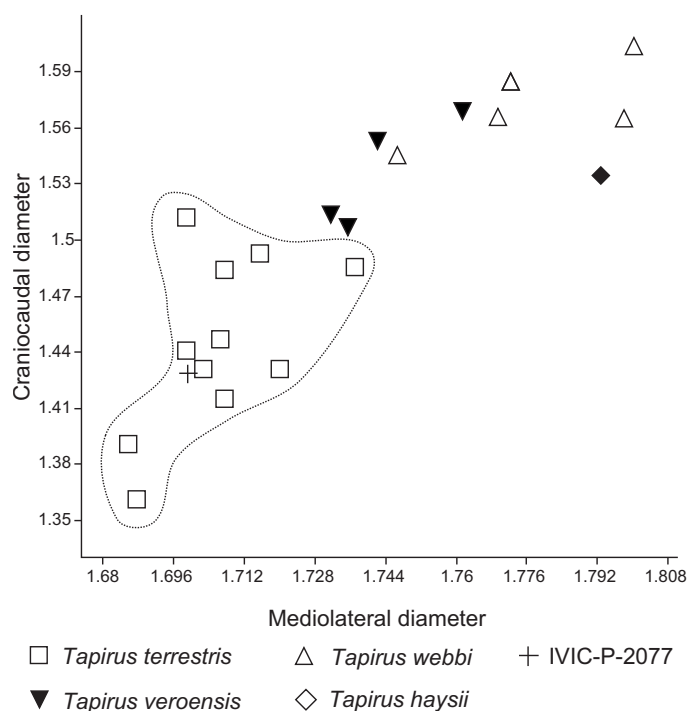


Fig. 8. Scatter plot of the craniocaudal and mediolateral diameters of the proximal portions of the measured humeri.

tal measurements revealed that some South American fossil species, including *T. rioplatensis*, “*T. oliverasi*”, and *T. tarijensis*, are larger than *T. terrestris*, while *T. cristatellus* and OR1367 are within the size range of the latter (Table 1).

These size differences were most pronounced in the lower tooth PCAs (Fig. 5B), where the first principal component (PC1) distinguished larger species of *Tapirus* (*T. haysii* and *T. tarijensis*) from *T. terrestris* and OR1367 (Fig. 5A, B). Although there was a slight distinction between *T. terrestris* and *T. veroensis* + *T. webbi* + *T. johnsoni*, there was also some overlap along PC1. The latter was a multivariate expression of size, with its eigenvector mostly influenced by the widths of p2 and p3, both the length and width of m1, and the length of m2 (Table 2). The second principal component (PC 2) distinguished *T. webbi* from *T. johnsoni* based on the premolars (Fig. 5A) and *T. webbi* from *T. haysii* + *T. veroensis* + *T. johnsoni* based on the molars (Fig. 5B). PC2 reflected shape, with its eigenvector mostly determined by the width of p2, the length of p3, the width of m1, and both the length and width of m2 (Table 2).

Unlike those of the lower teeth, the sizes of the upper premolars broadly overlapped along the first principal component, distinguishing only the large-sized *T. haysii* from all of the other species (Fig. 5C). Based on the data from the upper molars, PC1 distinguished *T. cristatellus* from *T. terrestris* (Fig. 5D, Table 2). OR1367 and *T. mesopotamicus* fell within the range of *T. terrestris*, no matter whether the upper or lower teeth were considered (Fig. 5). The deciduous upper teeth showed differences in width and length between *T. haysii* and *T. terrestris*; however, the dimensions

Table 2. Factor loadings of the Principal Components analyses. High loadings are in bold. Abbreviations: CDD, craniocaudal diameter of distal portion; CDP, craniocaudal diameter of proximal portion; L, length; MDB, mediolateral diameter of the body; MDD, mediolateral diameter of distal portion; MDH, mediolateral diameter of humeral head; MDP, mediolateral diameter of proximal portion; TMD, mediolateral diameter of humeral trochlea; W, maximum width.

	PC 1	PC 2
Lower teeth		
p2L	0.3998	0.3173
p2W	0.4837	-0.4992
p3L	0.3609	0.5434
p3W	0.4777	-0.1602
p4L	0.3187	0.4343
p4W	0.3822	-0.3749
m1L	0.4580	-0.3447
m1W	0.4629	0.5785
m2L	0.4370	-0.4740
m2W	0.3671	0.4084
m3L	0.3930	-0.3175
m3W	0.3095	0.2330
Upper teeth		
P1L	0.4585	0.0005
P1W	0.4374	-0.7547
P2L	0.4229	0.4806
P2W	0.3429	-0.0575
P3L	0.2815	0.3220
P3W	0.2730	0.0671
P4L	0.2853	0.2601
P4W	0.2587	-0.1426
M1L	0.4539	-0.5332
M1W	0.3984	0.2407
M2L	0.4208	-0.3608
M2W	0.4050	0.4766
M3L	0.3958	-0.2096
M3W	0.3709	0.5065
Humerus		
L	0.1327	0.1823
MDP	0.4178	0.5386
CDP	0.4464	-0.2811
MDH	0.3483	0.2406
MDB	0.4415	-0.6145
MDD	0.2444	0.3962
CDD	0.3896	-0.0694
TMD	0.2844	-0.0209

of *T. veroensis* overlapped with those of *T. terrestris*, as well as those of OR1369 (Fig. 6).

The postcranial material from Venezuela fell within the size range of *T. terrestris*. Variation along the first principal component of the PCA of the humeral measurements supported the separation of *T. webbi* and *T. terrestris* (Fig. 7), and furthermore revealed an overlap of the latter with *T.*

veroensis + IVIC-P-2088. The craniocaudal and medio-lateral diameters of the proximal portion, as well as the mediolateral diameter of the body were the major loadings of PC 1 (Table 2). By contrast, PC 2 separated *T. webbi* + IVIC-P-2088 from *T. veroensis*, with the mediolateral diameter of the proximal portion and of the body being the most important factors (Table 2). Finally, the craniocaudal and mediolateral diameters of the proximal end of the radius separated *T. terrestris* + IVIC-P-2077 from *T. webbi* and *T. haysii*, with the ranges of *T. veroensis* and *T. terrestris* slightly overlapping (Fig. 8).

Discussion and conclusions

Some of the fossil species of *Tapirus* from South America, such as *T. rioplatensis* and *T. tarijensis*, were described based on isolated mandibular or postcranial elements. In the original studies, the authors provided few or no morphological characters which could help to distinguish these species from *T. terrestris*, apart from their relatively large size. Other species, such as *T. cristatellus* and *T. mesopotamicus*, have associated cranial material and are therefore more consistently defined.

Our morphometric analysis showed that, in addition to the morphological differences found mostly in the cranial characters, *T. haysii* and *T. webbi* are larger than *T. terrestris* in both their dental and postcranial dimensions. As far as can be judged from the available dental material, "*T. oliverasi*", *T. rioplatensis*, and *T. tarijensis* are also larger than *T. terrestris*. By contrast, *T. veroensis* and *T. johnsoni* slightly overlap with *T. terrestris* in terms of the size of their teeth and postcrania, though in terms of the dental data *T. johnsoni* seems more distinct from *T. terrestris* than *T. veroensis*.

Based on its size and morphology, we here assign the material from Zumbador Cave to the extant species *T. terrestris*, thereby making it the most northwestern fossil occurrence of this species in South America.

The remains from El Breal de Orocuál tar seep are more gracile, and the presence of a metastylid on the lower cheek teeth in particular differs from the condition observed in *T. terrestris* and other living and fossil species occurring in South America. However, this character varies both inter- and intraspecifically among the North American species, and cannot be considered of high taxonomic value at the species level. Overall, given the problems associated with referring a juvenile specimen or isolated mandibular remains to any particular species of tapir, we prefer to assign the present material to *Tapirus* sp. However, the possibility that these specimens might represent a new species or an immigrant from North America, as proposed by Rincón et al. (2009), cannot be completely excluded. If a Pliocene–Pleistocene age is confirmed for the El Breal de Orocuál tar seep, this will be the earliest record of tapirs from intertropical South America.

Acknowledgements

The authors wish to thank Jorge I. Noriega (CICYTTP), David Flores and Alejandro G. Kramarz (MACN), Márcia Martins (MCN), Mariano Merino (MLP), João A. de Oliveira (MN), Mario de Vivo (MZUSP), and Richard C. Hulbert (UF), for access to comparative material under their care, as well as the Florida Museum of Natural History for a travel grant awarded to one of the authors (ECH). We also thank Alessandra D. Boos (Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil) for language revision, and Richard C. Hulbert and Martín Ubilla (Universidad de La República, Montevideo, Uruguay) for their critical revisions that helped to improve this manuscript. This study was partially funded by a CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) fellowship to ECH, as well as the Exploration and Production Unit of Petróleos de Venezuela S.A. (PDVSA), División Oriente, PDVSA La Estancia, and the Instituto Venezolano de Investigaciones Científicas.

References

- Ameghino, C.F. 1902. Notas sobre algunos mamíferos fósiles nuevos o poco conocidos del Valle de Tarija. *Anales del Museo de Historia Natural de Buenos Aires* 3: 225–261.
- Ashley, M.V., Norman, J.E., and Stross, L. 1996. Phylogenetic Analysis of the Perissodactylan Family Tapiridae using mitochondrial cytochrome c oxidase (COII) sequences. *Journal of Mammalian Evolution* 3: 315–325.
- Brooks, D.M., Bodmer, R.E., and Matola, S. (compilers) 1997. *Tapirs-Status Survey and Conservation Action Plan*. viii + 164 pp. IUCN/SSC Tapir Specialist Group. IUCN, Gland.
- Butler, P.M. 1952. The milk-molars of Perissodactyla, with remarks on molar occlusion. *Proceedings of the Zoological Society of London* 121: 777–817.
- Campbell, K.E., Jr., Prothero, D.R., Romero-Pittman, L., Hertel, F., and Rivera, N. 2010. Amazonian magnetostratigraphy: Dating the first pulse of the Great American Faunal Interchange. *Journal of South American Earth Sciences* 29: 619–626.
- Cartelle, C. 1999. Pleistocene Mammals of the Cerrado and Caatinga of Brazil. In: J.F. Eisenberg and K.H. Redford (eds.), *Mammals of the Neotropics—The Central Neotropics*, 3, 27–46. The University of Chicago Press, Chicago.
- Cattoi, N. 1951. El status de *Tapirus dupuyi* (C. Amegh.). *Comunicaciones del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales* 2: 103–112.
- Cattoi, N. 1957. Una especie extinguida de *Tapirus* Brisson (*T. rioplatensis* nov. sp.). *Ameghiniana* 1: 15–21.
- Cione, A.L. and Tonni, E.P. 2005. Bioestratigrafía basada em mamíferos del Cenozoico Superior de la Provincia de Buenos Aires, Argentina. In: R.E. Barrio, R.O. Etcheverry, M.F. Caballé, and E. Llambias (eds.), *Geología y recursos minerales de la Provincia de Buenos Aires*, 183–200. Quick Press, La Plata.
- DeSantis, L.R.G. and MacFadden, B. 2007. Identifying forested environments in Deep Time using fossil tapirs: evidence from evolutionary morphology and stable isotopes. *Courier Forschungsinstitut Senckenberg* 258: 147–157.
- Eberle, J.J. 2005. A new "tapir" from Ellesmere Island, Arctic Canada – Implications for northern high latitude palaeobiogeography and tapir palaeobiology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 227: 311–322.
- Ferrero, B. and Noriega, J.I. 2007. A new upper Pleistocene tapir from Argentina: remarks on the phylogenetics and diversification of neotropical Tapiridae. *Journal of Vertebrate Paleontology* 27: 504–511.
- Fragoso, J.M. and Huffman, J.M. 2000. Seed-dispersal and seedling recruit-

- ment patterns by the last Neotropical megafaunal element in Amazonia, the tapir. *Journal of Tropical Ecology* 16: 369–385.
- González de Juana, C., Iturralde de Arozena, J.M., and Picard Cadillat, X. 1980. *Geología de Venezuela y de sus Cuencas Petrolíferas, Volumes 1 and 2*. 1021 pp. Ediciones Foninves, Caracas.
- Hammer, O., Harper, D.A.T., and Ryan, P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4: 1–9.
- Holanda, E.C. and Cozzuol, M.A. 2006. New records of *Tapirus* from the late Pleistocene of southwestern Amazonia, Brazil. *Revista Brasileira de Paleontologia* 9: 193–200.
- Holanda, E.C., Ferigolo, J., and Cartelle, C. 2007. Novas considerações sobre a espécie *Tapirus cristatellus* Winge (Mammalia, Perissodactyla), Pleistoceno superior, Estado da Bahia, Brasil. *Ameghiniana* 44 (4): 23R.
- Holanda, E.C., Ferigolo, J., and Ribeiro, A.M. 2011. New *Tapirus* species (Mammalia: Perissodactyla: Tapiridae) from the upper Pleistocene of Amazonia, Brazil. *Journal of Mammalogy* 92: 111–120.
- Holbrook, L.T. 2002. The unusual development of sagittal crest in the Brazilian tapir (*Tapirus terrestris*). *Journal of Zoology* 256: 215–219.
- Hue, E. 1907. *Musée Ostéologique—étude de la faune quaternaire. Ostéométrie des mammifères*. 50 pp. Schleicher Frères, Paris.
- Hulbert, R.C., Jr., 2005. Late Miocene *Tapirus* (Mammalia, Perissodactyla) from Florida, with description of a new species, *Tapirus webbi*. *Bulletin of the Florida Museum of Natural History* 45: 465–494.
- Hulbert, R.C., Jr., 2010. A new early Pleistocene tapir (Mammalia: Perissodactyla) from Florida, with a review of Blancan tapirs from the state. *Bulletin of the Florida Museum of Natural History* 49: 67–126.
- Hulbert, R.C., Jr., Wallace, S.C., Klippel, W.E., and Parmalee, P.W. 2009. Cranial morphology and systematic of an extraordinary sample of the late Neogene dwarf tapir, *Tapirus polkensis* (Olsen). *Journal of Paleontology* 83: 238–262.
- Marshall, L.G., Berta, A., Hoffstetter, R., Pascual, R., Reig, O.A., Bombin, M., and Mones, A. 1984. Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary of South America. *Palaeovertebrata, Mémoire Extraordinaire*: 1–76.
- Radinsky, L.B. 1965. Evolution of the tapiroid skeleton from *Heptodon* to *Tapirus*. *Bulletin of the Museum of Comparative Zoology* 134: 69–106.
- Ray, C.E. and Sanders, A.E. 1984. Pleistocene Tapirs in the Eastern United States. In: H.H. Genoways and M.R. Dawson (eds.), *Contributions in Quaternary Vertebrate Paleontology. Special Publication of Carnegie Museum of Natural History* 8: 283–315.
- Rincón, A.D. 2003. Los mamíferos fósiles del Pleistoceno de la Cueva del Zumbador (Fa. 116) estado Falcón, Venezuela. *Boletín de la Sociedad Venezolana de Espeleología* 37: 18–25.
- Rincón, A.D., Parra, G.E., Prevosti, F.J., Alberdi, M.T., and Bell, C.J. 2009. A preliminary assessment of the mammalian fauna from the Pliocene–Pleistocene El Breal de Orocal locality, Monagas State, Venezuela. *Museum of Northern Arizona Bulletin* 64: 593–620.
- Rincón, A.D., Prevosti, F.J., and Parra, G.E. 2011. New saber-toothed cat records (Felidae: Machairodontinae) for the Pleistocene of Venezuela, and the Great American Biotic Interchange. *Journal of Vertebrate Paleontology* 31: 468–478.
- Rusconi, C. 1928. *Nueva especie fosil de tapir de la Argentina Tapirus australis n. sp. con una nota sobre Tapirus tarijensis*, *Ameghino*, 3–15. Imprenta M.L. Rañó, Buenos Aires.
- Simpson, G.G. 1945. Notes on Pleistocene and recent Tapirs. *Bulletin of the American Museum of Natural History* 86: 34–81.
- Torres, D.A. and Gutiérrez, E.E. 2001. The genus *Tapirus* in Venezuela: distribution and suggestions for its conservation. *First International Tapir Symposium, Book of Abstracts, Costa Rica*, 17. IUCN/SSC apir Specialist Group, San Jose.
- Ubilla, M. 1983. Sobre la presencia de tapires fosiles en el Uruguay (Mammalia, Perissodactyla, Tapiridae). *Revista de la Facultad de Humanidades y Ciencias* 1: 85–104.
- Winge, H. 1906. Jordgundne og nulevende Hoydyr (Ungulata) fra Lagoa Santa, Minas Gerais, Brasilien. *E Museo Lundii* 3:1–239.
- Woodburne, M.O. 2010. The Great American Biotic Interchange: Dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution* 17: 245–264.
- Woodburne, M.O., Cione, A.L., and Tonni, E.P. 2006. Central American provincialism and the 73 Great American Biotic Interchange. In: O. Carranza-Castañeda and E.H. Lindsay (eds.), *Advances in late Tertiary vertebrate paleontology in Mexico and the Great American Biotic Interchange. Universidad Nacional Autónoma de México, Instituto de Geología and Centro de Geociencias, Publicación Especial* 4: 73–101.

Appendix 1

Cranial, dental and postcranial material used for anatomical comparisons and morphometric analyses:

Tapirus terrestris: MLP01, MLP 754, MLP 755, MLP 1349, MLP 1402, MLP 1681, MLP 4IV0013, MACN 7.6, MACN 31211, MACN 33276, MACN 50559, MCN 1315, MCN 2532, MCN 2750, MCN 2848, MNRJ 18, MNRJ 600, MNRJ 1605, MNRJ 53701, MNRJ 57062, MNRJ 57067, MNRJ 64437, MNRJ 64572, MNRJ 64652, MNRJ 70698, MNRJ 71599, MZUSP 106, MZUSP 3232, MZUSP 3266, MZUSP 3268, MZUSP 3269, MZUSP 3727, MZUSP 3728, MZUSP 3758, MZUSP 5701, MZUSP 6139, MZUSP 6140, MZUSP 6575, MZUSP 7005, MZUSP 7006, MZUSP 7007, MZUSP 7700, MZUSP 9604, MZUSP 9712, MZUSP 9714, MZUSP 10715, MZUSP 22421, MZUSP 22422, MZUSP 20034, MZUSP 20035, MZUSP 20037, MZUSP 29085, MZUSP 31983, UNIR 17, UNIR 20, UNIR 68, UNIR 83;

Tapirus bairdii: MLP 1451;

Tapirus indicus: MACN 29926; MACN 129; MACN 30351; MACN 2553; MACN 4347;

Tapirus webbi: UF10994, UF10977, UF11005, UF11007, UF11100,

UF11134, UF26162, UF 26177, UF26179, UF 26185, UF26186, UF26190, UF26191, UF26195, UF26198, UF26206, UF26213, UF26218, UF26219, UF26220, UF26221, UF26225, UF26237, UF26245, UF26246, UF26963, UF28014, UF32082, UF32083, UF32085, UF39818, UF87228, F:AM37402, F:AM37403;

Tapirus veroensis: UF/FGS277 (holotype), UF2560, UF3991, UF 3995, UF3996, UF3997, UF4389, UF4849, UF11310, UF14834, UF14968, UF18702, UF18947, UF49659, UF121941, UF135772, UF146081, UF210878, UF210879, UF210890, UF213842, UF 242050;

Tapirus johnsoni: F:AM37305, F:AM37320, F:AM37323, F:AM 167104;

Tapirus haysii: UF8225, UF60872, UF60874, UF62601, UF80446, UF80973, UF82782, UF82783, UF83580, UF84190, UF87228, UF87231, UF89539, UF115948, UF223920, UF243500;

Tapirus tarijensis: MACN 1523 (holotype), AMNH55999, UF91589;

Tapirus rioplatensis: MACN15735 (holotype);

Tapirus mesopotamicus: CICYTTP-PV-M-1-23 (holotype).