

## A NEW UPPER PLEISTOCENE TAPIR FROM ARGENTINA: REMARKS ON THE PHYLOGENETICS AND DIVERSIFICATION OF NEOTROPICAL TAPIRIDAE

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**ABSTRACT**—A complete skull of a fossil tapir (Perissodactyla: Tapiridae) was recovered from outcrops of the Arroyo Feliciano Formation (Late Pleistocene; Lujanian Age) in the Argentine Mesopotamia and is here recognized as a new species. The phylogenetic relationships of this new taxon, *Tapirus mesopotamicus* sp. nov., are revealed by cladistic character analysis using several extinct and extant taxa. The taxa included in the analysis are the extinct genera *Miotapirus*, *Paratapirus*, and *Plesiotapirus*, five North American paleospecies *Tapirus veroensis*, *T. haysii*, *T. johnsoni*, *T. webbi*, and *T. polkensis*, and all the living species of the genus *Tapirus* (*T. terrestris*, *T. pinchaque*, *T. bairdii*, and *T. indicus*). *Tapirus mesopotamicus* sp. nov. is diagnosed by having a robust and long skull with short rostrum relative to total length of cranium, a single and not arched sagittal crest, broad table of frontals on the anterior skull roof, temporal crests converging very near the frontal-parietal suture, palate very arched, premaxilla deeply notched above canine, maxilla and base of zygomatic process strikingly robust, P1 short and quadrangular, and mandibular condyle slender with posterior wall flat or somewhat concave. The resulting cladogram depicts a well-supported clade comprising the South American tapirs. The new taxon *T. mesopotamicus* sp. nov. groups with its sister taxon *T. pinchaque*, and together with *T. terrestris*, form a sister clade to *T. bairdii* and three North American fossil tapirs.

### INTRODUCTION

Living tapirs (Perissodactyla: Tapiridae) comprise four species traditionally included in the genus *Tapirus* Brünnich, 1772. Three species are distributed throughout the Neotropical Region—*T. bairdii* (Gill, 1865), *T. pinchaque* (Roulin, 1829), and *T. terrestris* (Linnaeus, 1758)—and the fourth species *T. indicus* Desmarest, 1819 is endemic to the Oriental region. The earliest fossil record of *Tapirus* is from the early to middle Miocene of Europe (Guerin and Eisenmann, 1994). The first appearance of *Tapirus* in North America occurs in the late middle Miocene (early Clarendonian NALMA) and reflects an immigration from Asia (Hulbert, 1995). The history of the family in South America began with the Great American Biotic Interchange across the Panamanian Isthmus (Marshall et al., 1984; Webb, 1985), with the oldest secure record of the genus *Tapirus* dating from the early Pleistocene (Tonni, 1992; Irvingtonian age when correlated with Ensenadan SALMA) of Argentina. Supposed earlier occurrences in South America during the Pliocene require substantiation (Tonni, 1992).

Controversy about the systematics and phylogenetic relationships of living and Pleistocene tapirs remains active, and may be attributed to their striking osteological homogeneity and dental conservatism (Simpson, 1945; Hershkovitz, 1954; Ray and Sanders, 1984; Hulbert, 1995). Consequently, most of the fragmentary fossil specimens and isolated teeth recovered from Pleistocene sediments of North America are inadequate for rigorous specific identification (Ray and Sanders, 1984).

Alternative approaches using cladistic character analysis (Hulbert, 1995; Hulbert and Wallace, 2005; Colbert, 2005) and mo-

lecular phylogenies (Ashley et al., 1996; Norman and Ashley, 2000) recently appeared, have made important contributions to resolve the taxonomy of tapirids at different hierarchical levels.

Fossil South American species have also been described based on fragmentary materials, mainly isolated teeth—i.e., *Tapirus australis* Rusconi, 1928, *T. dupuyi* (C. Ameghino, 1916), *T. rioplatensis* Cattoi, 1957—or material with a dubious stratigraphic provenance such the case of *T. tarijensis* Ameghino, 1902. This article describes the first nearly complete skull of a tapir recovered from levels with accurate stratigraphic provenance referred to the late Pleistocene at the Mesopotamia region of Argentina, and recognized as a new species in a phylogenetic context of the family.

### MATERIALS AND METHODS

The specimen herein studied belongs to the paleontological collections of the Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Argentina, CICYTTP-PV-M-1-23. It includes the skull of an adult specimen lacking the right zygomatic arch and a proximal fragment of the right mandible.

The morphological and metrical descriptions follow Simpson (1945), Ray and Sanders (1984), Colbert (2005), and Hulbert and Wallace (2005).

A cladistic methodology is used to perform the phylogenetic analysis (see Cladistic Analysis).

**Abbreviations**—NALMA, North American Land Mammal Age; SALMA, South American Land Mammal Age; TBR, Tree bisection reconnection; P1 TW/L, ratio of transverse width to length for P1; P2 ATW/PTW, ratio of anterior transverse width to posterior transverse width for P2.

**Institutional Abbreviations**—CML, Colección Miguel Lillo, Instituto Miguel Lillo, Tucumán, Argentina; CICYTTP, Centro

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de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Argentina; **MACN**, Museo Argentino de Ciencias Naturales, Argentina; **MLP**, Museo de La Plata, Argentina; **ANPCYT**, Agencia Nacional de Promoción de Científica y Tecnológica.

#### SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758  
Order PERISSODACTYLA Owen, 1848  
Family TAPIRIDAE Burnett, 1830  
Genus *TAPIRUS* Brünnich, 1772  
*TAPIRUS MESOPOTAMICUS*, sp. nov.  
(Figs. 1–3, Table 1)

**Holotype**—CICYTTP-PV-M-1-23, skull and proximal fragment of the right mandible (Figs. 1–3).

**Etymology**—mesopotamicus; between rivers, after its geographic provenance from the Mesopotamian region of Argentina, South America.

TABLE 1. Skull and mandible measurements (mm) of *Tapirus mesopotamicus*, CICYTTP-PV-M-1-23.

Measures	CICYTTP-PV-M-1-23
Distance between prosthion and foramen magnum	390
Distance between prosthion and lambdoid crests	455
Distance between prosthion and choana	205
Distance between prosthion and orbit	185
Height from sagittal crest to basisphenoid	115
Maximal distance between nasal-frontal suture and lambdoid crests	201
Minimal distance between nasal-frontal suture and lambdoid crests	198
Width at the base of zygomatic arches	166
Height of occipital face from basioccipital to supraoccipital	111.92
Height of occipital face from basioccipital to foramen magnum	95.3
Maximal width between occipital condyles	87.2
Width of foramen magnum	32.92
Length of maxillary diastema	49.3
Distance between prosthion and P1	82
Width of the maxilla at the level of canines in palatal view	65.58
Width of premaxilla anterior to canines in palatal view	54.60
Width of maxilla anterior to P1 in palatal view	49.93
Width of palate at the level of P1	48.35
Width of palate at the level of P3	49.60
Width of palate at the level of M1	54.5
Width of palate at the level of M3	63.05
Minimal width between parietal crests	17.8
Minimal distance between frontals, anterior to supraorbital tubercles	84.85
Width between supraorbital tubercles	108.4
Width between postorbital processes	72.4
Length of upper cheek tooth row	139.85
Length of upper premolar series	70.15
Length of upper molar series	69.87
Greatest width of condyle through articular surface	49.8
Height from occlusal surface of m2 to lower edge of ramus	63.5
Width of the ascending surface just below condyle	82.2
Greatest labio-lingual depth of mandible at the level of m2	34.1
Height from articular surface of condyle to lower edge of mandible	146.7

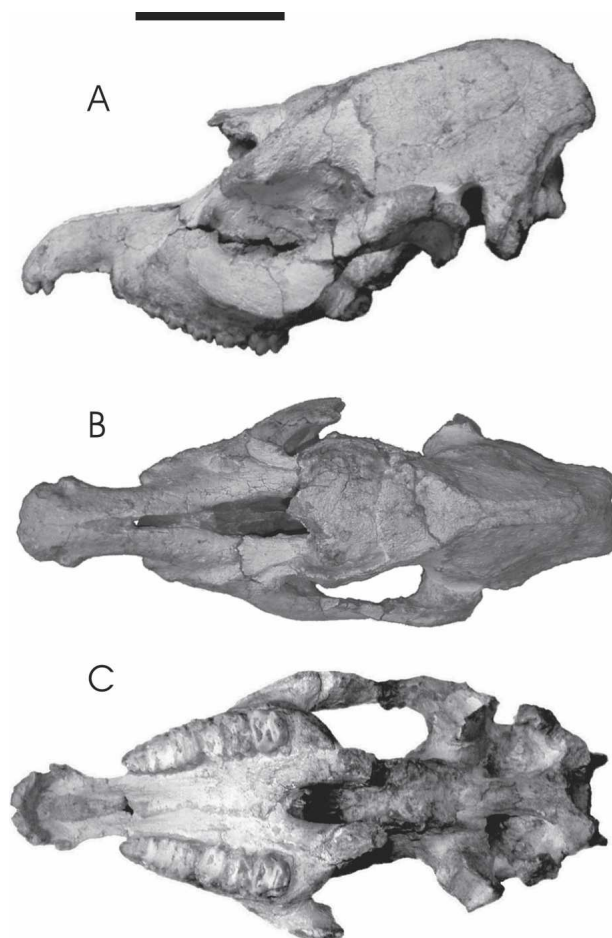


FIGURE 1. Skull of *Tapirus mesopotamicus* sp. nov., CICYTTP-PV-M-1-23. **A**, lateral view; **B**, dorsal view; **C**, ventral view. Scale bar equals 10 cm.

**Diagnosis**—A unique association of characters included the cladistic analysis (apomorphies, occurring together with some plesiomorphies), combined with other descriptive characters not shown in the phylogeny, is regarded as diagnostic for *T. mesopotamicus*. Apomorphies: Suture between nasals and frontals more or less straight; supraorbital grooves for nasal diverticulum narrow and deep; dorsal table of frontals relatively broad; rostrolateral process of frontal robust; lambdoid crests strong and well projected backwards, markedly posterior to condyles; posterior process of premaxilla ends about midway over C-P1 diastema; ascending process of premaxilla short, with moderately acute end, and situated anteriorly to P1; anteromedial process of maxilla present; anteromedial process of maxilla covered by premaxilla, not visible in lateral view or barely so; infraorbital foramen anterior to cranial edge of P3; narrow and closed narial aperture delimited by maxilla; cranial fragment of jugal (in lateral view) broad; lachrymal foramen not visible in lateral view; relative crown height of cheek teeth tall; P2 ATW/PTW ratio on average, greater than 0.85; P3 and P4 protocone and hypocone widely separated; strong parastyle development on P3-M3; posterior surface of articular condyle convex and rather flat. Plesiomorphies: fossa for meatal diverticulum on posterior dorsal surface of nasal not extensive and far from midline; nasals and frontals approximately on the same plane; development of fossa for meatal diverticulum on dorsal table of frontal very limited; single sagittal crest of moderate height; dorsomedial border of maxilla sharp, mostly directed medially; dorsal maxillary flange

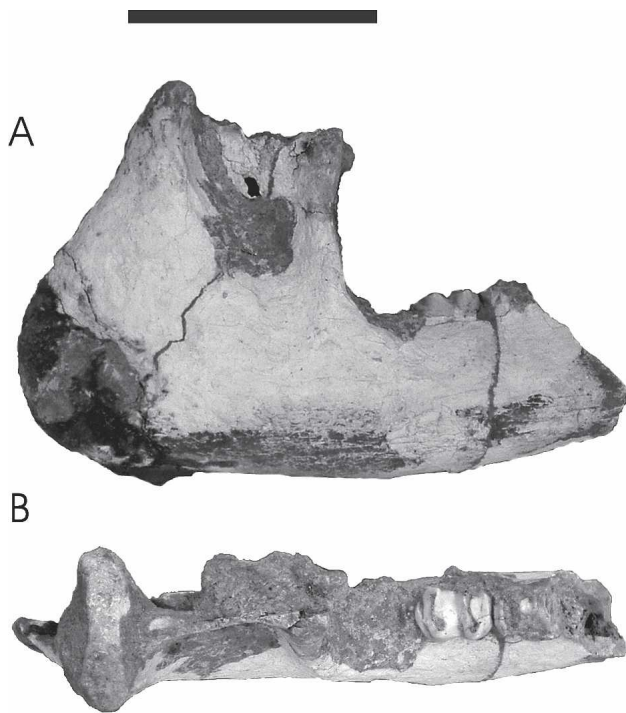


FIGURE 2. Mandible of *Tapirus mesopotamicus* sp. nov., CICYTTP-PV-M-1-23. **A**, lateral view; **B**, occlusal view. Scale bar equals 10 cm.

absent; narrow shaped lachrymal, much taller than long; facial surface of lachrymal flat; posterior (preorbital) process of lachrymal slender and rugous; labial cingulum on posterior half or more of P3-M3; protoloph just reaches to base of ectoloph; P1 TW/L ratio on average greater than 0.80. Descriptive characters: robust and long skull with short rostrum relative to total length of cranium; premaxillary-maxillary suture (in lateral view) located anterior to canine alveolus; ascending process of maxilla dorsally exposed; palate very arched; upper incisors opisthodont; premaxilla deeply notched above canine; maxilla and base of zygomatic process strikingly robust; convergence of temporal crests on dorsal aspect very near the frontal-parietal suture; in-

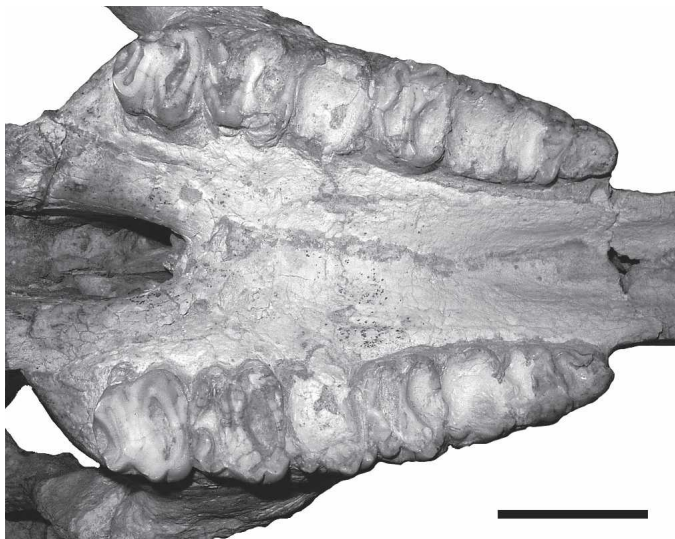


FIGURE 3. Dentition of *Tapirus mesopotamicus* sp. nov., CICYTTP-PV-M-1-23, in palatal aspect. Scale bar equals 5 cm.

terparietal bone absent; depth of nasal notch (in dorsal view) at level of the orbit; anterior lachrymal process well developed; P1 short and quadrangular; P1 with large posterolingual cusp, sometimes with accessory cusps and often with some development of a transverse loph; P1 well laterally exposed; P2 well molarized; P2 lingual cingulum absent; P4 protoloph merges midway or higher onto ectoloph; P4 metaloph merges midway or higher onto ectoloph; M1 metaloph joins the ectoloph at or near metacone; M1 ectoloph essentially straight, joining vertically implanted or slightly distally tilted paracone; M2 parastyle well separated from paracone; M2 ectoloph essentially straight, joining vertically implanted or slightly distally tilted paracone; M3 metaloph joins the ectoloph at or near metacone; M3 metaloph directed primarily linguolabially, forming obtuse angle with ectoloph; M3 parastyle well separated from paracone; M3 ectoloph essentially straight, joining vertically implanted or slightly distally tilted paracone; upper and lower molars without accessory crochets and cristids.

**Horizon, Age, and Locality**—The fossil material comes from the Arroyo Feliciano Formation that crops out along the major rivers and streams of the Entre Ríos Province as the highest terrace (Iriondo et al., 1985; Iriondo, 1996). This geologic unit is assigned to the Lujanian Stage/Age (Late Pleistocene; Cione and Tonni, 1999) based on the biochronology of the included mammals (Noriega et al., 2004). The finding locality is situated on the north bank of the Ensenada stream, at 15 kilometers east of Diamante city, Department of Diamante, Entre Ríos Province, Argentina (Fig. 4).

#### Comparative Description

The sagittal crest is single, low, and not arched as in *T. veroensis* Sellards, 1918 and *T. pinchaque*, different from that of *T. terrestris* where it is arched. The temporal crests converge very near the frontal-parietal suture, more posteriorly than in *T. terrestris* but less than *T. veroensis*, being the least width of frontals

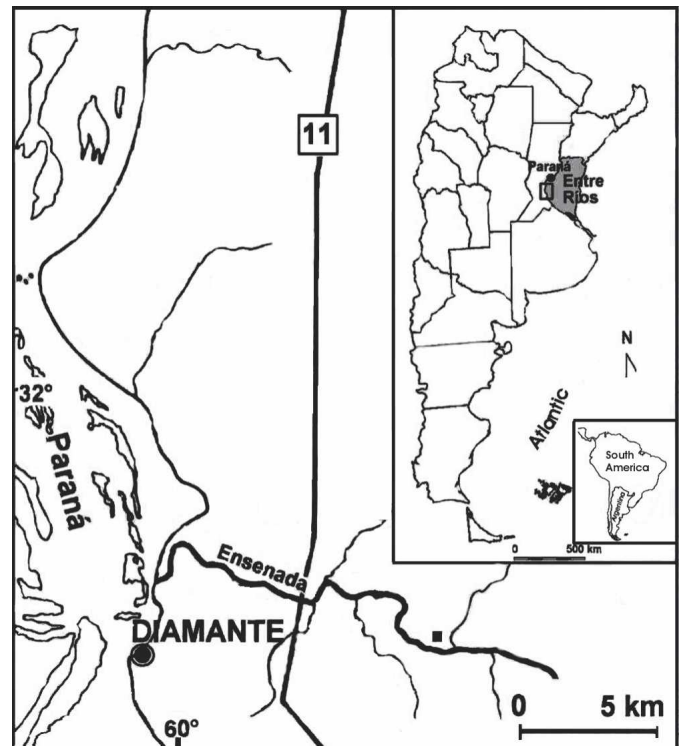


FIGURE 4. Geographic provenance of *Tapirus mesopotamicus* sp. nov. from Entre Ríos Province, Argentina, South America. The black square shows the finding site.



allocated in an intermediate position. The temporal crests in *T. bairdii* are double and subparallel, not forming a single sagittal crest.

The upper contour of the skull, formed by the dorsal margins of nasals, frontals, parietals and supraoccipital, is low and flattened, nearly parallel to basicranium as in *T. pinchaque* and *T. veroensis*. In *T. terrestris* and *T. bairdii*, the nasals are abruptly set down below the level of the frontals, with a high dorsal profile of the skull, more curved and ascending posteriorly. The condition in *T. veroensis*, *T. pinchaque*, and the new species is different, having their nasals in the same horizontal plane as frontals. The dorsal part of the frontals on the skull roof is larger than in *T. terrestris* and *T. bairdii*, similar to that of *T. veroensis* and *T. pinchaque*. The suture between nasals and frontals is nearly straight as in *T. pinchaque* while it is W-shaped in *T. terrestris*, *T. bairdii*, and *T. veroensis*, forming an anteromedial process of the frontal extending between nasals.

In lateral view, the rostral process of the frontal is robust as in *T. pinchaque*, sloping downward at an angle of about 45° to meet the lachrymal and maxilla and forming a robust lateral wall that borders the meatal diverticulum fossa laterally. The dorso-lateral margin of this wall presents a knobby rugosity (see Witmer et al., 1999 for details of muscular attachments on this process). The rostral process of the frontal is more slender in *T. veroensis*, *T. terrestris*, and *T. bairdii*. A conspicuous lateral supraorbital process erects caudoventral to the latter.

The dorsally exposed extension of the maxilla, medial to the ascending process of the premaxilla, is less developed as in *T. pinchaque* and *T. bairdii*, with a smoothly rounded edge in the latter. This extension is well developed and has a somewhat recurved edge in *T. veroensis*, while it is smaller and sharply elevated in *T. terrestris*. The ascending processes of the maxillae are broad, robust, dorsally exposed, and subparallel, bordering a narrow nasal area as in *T. veroensis* and *T. pinchaque*. These processes are narrow, but laterally oriented in *T. bairdii*. In *T. terrestris* they are narrower, more slender, and their divergence from midline delimit a broader and open nasal region, although they tend to twist more strongly laterally at the dorsal portion.

The lachrymal is narrow, much taller than long, with a flat facial surface as in the living species compared. The anterior lachrymal process is very weak, as in *T. bairdii*, while it is well developed in *T. terrestris* and *T. pinchaque*. The posterior lachrymal process is knobby, similar to that of *T. terrestris* and *T. pinchaque*, while it is broad and flat in *T. bairdii*. Lachrymal foramen is not visible in lateral view.

In ventral view of the diastema, the latero-ventral edge of the maxilla ends abruptly at the medial side of P1 as in *T. veroensis* and *T. terrestris*. Consequently, P1 locates relatively more lateral or external than in *T. pinchaque* and *T. bairdii*, where this edge merges gently with the lateral side of P1. The posterior edges of the palatines reach at the boundary between M2 and M3.

The lateral or supraorbital grooves for nasal diverticulum leading up to the spiral grooves are deep and narrow as in *T. terrestris* and *T. bairdii*. They are broad and shallow in *T. veroensis* and *T. pinchaque*. The spiral grooves excavated on nasals and frontals are not extensive and far from the midline as in *T. terrestris* and *T. pinchaque*; these grooves are nearly meeting at midline in *T. veroensis* and *T. bairdii*.

The lambda crests are strong, well separated and projected backward posterior to condyles, as in *T. veroensis*, *T. terrestris*, and *T. pinchaque*; differing from those of *T. bairdii* that reach at the same level or project hardly anterior to condyles.

The upper cheek tooth series are subparallel and almost complete in *T. mesopotamicus*, but show an important degree of abrasion in most of its elements that makes the recognition of loph difficult. This abrasion was mainly due to natural wear and, in a lesser degree, to erosion during taphonomic process or dam-

age during preparation, taking into account that the whole palate and teeth were originally covered by a strong carbonatic matrix.

As stated by Simpson (1945:59), the molarization of P1-2 is the most important qualitative dental character in the genus *Tapirus*. P1 of *T. mesopotamicus* is more quadrangular than in *T. terrestris*, *T. bairdii*, *T. veroensis*, and much more than in *T. pinchaque*, but is not very well molarized as in *T. haysii*. The length of P1 is short and distinct for the new species (Table 2). The presence of basal tubercles on the inner and/or outer faces of the cheek teeth in tapirs is a character of rather poor taxonomic value because of its high variability. A basal tubercle can be located between the protocone and the hypocone at the inner end of the median valley and/or between the paracone and the metacone on the outer side. In *T. mesopotamicus* a distinct tubercle is developed on the outer side of P3-4 and M1-3. M2 and M3 have a well marked rounded basal swelling like a cingulum on the anterior and posterior sides.

In lateral aspect, the third incisor is opisthodont in relation to the plane of the molariform tooththrow (see Hershkovitz, 1954; Ray and Sanders, 1984).

Dental dimensions of *T. mesopotamicus*, *T. terrestris*, *T. veroensis*, and *T. haysii* are compared in Table 2.

The preserved fragment of the mandible of *T. mesopotamicus* has M<sub>2</sub> with the metaconid broken and M<sub>1</sub> with the anterior lophid lacking. The condyle is more slender than in *T. terrestris*, with its posterior wall—just below the articular surface—rather flat or somewhat concave, while it is clearly convex in *T. terrestris*.

Skull and mandible measurements of *T. mesopotamicus* are described in Table 1.

## RESULTS

### Cladistic Analysis

The phylogenetic analysis comprises a total of 34 characters and 13 terminal taxa including the outgroups (see Appendix 1, 2).

We consider as terminal taxa all living species of the genus *Tapirus* (*T. terrestris*, *T. pinchaque*, *T. bairdii*, and *T. indicus*); a

TABLE 2. Dental dimensions in millimeters of *Tapirus mesopotamicus*, *T. terrestris* (from Simpson, 1945: 44–45; Table 2 and 3, respectively), *T. veroensis* (from Ray and Sanders, 1884: 294; Table 2), and *T. haysii* (“*T. copei*” of Simpson, 1945:68–69; Tables 12 and 14, respectively).

	<i>T. mesopotamicus</i>	<i>T. terrestris</i>	<i>T. veroensis</i>	<i>T. haysii</i>
LP1	13.53	14.6–17.7	17.5–20.8	22.4–24.9
WP1	16.43	14.7–16.7	14.9–18.6	19.6–21.5
LP2	17.42	16.1–18.9	18.7–21.1	21.9–24
AntWP2	21.18	17–20.3	19.6–23.2	25.5–26.5
PostWP2	22.23	17.7–22.3	22.8–25.8	27.4–27.9
LP4	21.04	18.3–21.7	20–22.9	24.1–26.4
AntWP4	27.52	22.6–28.1	24.2–28.6	29.9–31.8
PostWP4	26.24	21.1–26.2	22.5–28.9	28.4–30.1
LM2	23.6	21.4–26.2	23.5–27	27.3–29.7
AntWM2	29.67	23.4–29	26.3–31.1	31.3–34.9
PostWM2	25.76	20.7–26	23.8–28.4	28–31.5
LM3	23.92	20.5–26.5	23.5–26.1	26.8–29.2
AntWP3	28.34	24.5–28.4	28–32.1	31–34.1
PostWM3	23.17	20–22.2	23.1–28.1	26.5–29
LM2	25.77	21.4–26	22.5–29	27.4–30.8
AntWM2	—	16–20.2	18.4–23.4	20.5–24.1
PostWM2	18.41	15.5–18.3	17.8–22.8	18.3–22.8

**Abbreviations:** LP1, length of P1; WP1, width P1; LP2, length of P2; AntWP2, anterior width of P2; PostWP2, posterior width of P2; LP4, length of P4; AntW4, anterior width of P4; PostWP4, posterior width of P4; LM2, length of M2; AntWM2, anterior width of M2; Post WM2, posterior width of M2; LM3, length of M3; AntWM3, anterior width of M3; PostWM3, posterior width of M3; LM2, length of M2; AntWM2, anterior width of M2; PostWM2, posterior width M2.

Miocene species from Nebraska, U.S.A., *T. johnsoni* (Schultz, Martin and Corner, 1975), and other two Miocene species from Florida, *T. polkensis* (Olsen, 1960) and *T. webbi* (Hulbert, 2005); two Pleistocene species from North America, *T. veroensis* and *T. haysii*, Leidy, 1860 (= *T. copei* sensu Ray and Sanders, 1984), and the herein reported new species (*T. mesopotamicus*). Several North and South American fossil taxa, which are based on fragmentary elements and isolated teeth, are excluded from the analysis (e.g. *T. californicus* Merriam, 1913; *T. merriami* Frick, 1921; *T. tennesseae* Hay, 1920; *T. australis*, *T. rioplatensis*, *T. dupuyi*) because complete comparisons of cranial and dental features are needed to develop the phylogenetic hypothesis. This analysis includes no Asiatic or European fossil species of the genus *Tapirus*. It assumes that *T. indicus* is more closely related to other Asiatic and Tertiary European species than living American tapirs (Desmarest, 1819; in Tonni, 1995), and that the few similarities *T. indicus* shares with Neotropical *Tapirus* represent homoplasy (Hulbert 1995). We believe it will be necessary to include more fossil European and Asiatic taxa to resolve the phylogenetic relationships between the American tapirs (fossils and recent) and *T. indicus*. However, this fact exceeds the scope of our analysis.

Outgroups include three paleospecies of Tapiridae: *Miotapirus harrisonensis* (Schlaikjer, 1937), *Plesiotapirus yagii*, and *Paratapirus helveticus*. Following Hulbert and Wallace (2005), the root is placed in *M. harrisonensis*.

We use the stem-based definition of *Tapirus* of Hulbert (2005) that considers *Tapirus* as the taxon comprised of *T. terrestris* and all species that share a more recent common ancestor with *T. terrestris* than with the type species of the remaining genera in the family Tapiridae as defined by Colbert (2005).

The cladistic analysis is developed under the principle of parsimony and is conducted using the TNT computer program (Goloboff et al. 2003). A total of 100 replications with TBR, holding 10 trees per replicate (hold 1000; mult 100 = hold 10), are performed.

Bremer support (Bremer, 1988, 1994) is calculated with TNT computer program (Goloboff et al. 2003).

The analysis results in only one most parsimonious tree (Fig. 5) of 66 steps (MPTs) under equal weights. This tree has a consistency index (CI) of 0.621 and a retention index (RI) of 0.638.

The monophyly of the genus *Tapirus* is corroborated. The cladogram shows *T. indicus* as the sister taxon of all the remaining species of *Tapirus*. The clade of *Tapirus* is supported by three characters: Posterior process of premaxilla terminates dorsal to or just in front of P1 (11<sup>1</sup>), relative crown height of cheek teeth tall (19<sup>1</sup>), and ATW/PTW ratio on average greater than 0.85 (21<sup>1</sup>). This node exhibits a high Bremer support value (Fig. 5).

The group composed by *T. mesopotamicus* and *T. pinchaque* is defined by three synapomorphies: suture between nasals and frontals nearly straight (26<sup>1</sup>), broad cranial fragment of jugal (30<sup>0</sup>), and rostralateral process of frontal robust (32<sup>0</sup>). *Tapirus terrestris* appears as the sister taxon of the latter, exhibiting the lambdoidal crests well projected backwards, markedly posterior to condyles (5<sup>0</sup>), the lateral exposure of the anteromedial process of maxilla not visible in lateral view or barely so (9<sup>1</sup>), and the posterior process of premaxilla ending about midway over C-P1 diastema (11<sup>2</sup>), as derived characters shared with them.

Three autapomorphies are defined for *T. mesopotamicus*: dorsal table of frontal relatively broad (1<sup>1</sup>), lachrymal foramen not visible in lateral views (18<sup>1</sup>), and narrow and closed narial aperture delimited by maxilla (28<sup>1</sup>).

*Tapirus polkensis* together with *T. terrestris*, *T. haysii*, and *T. veroensis* are members of a clade supported by four synapomorphies: fossa for meatal diverticulum on posterior dorsal surface of nasal very extensive, approaching a few millimeters of midline (3<sup>1</sup>); fossa for meatal diverticulum on dorsal table of frontal broad with distinct posterior margin (4<sup>1</sup>); posterior process of

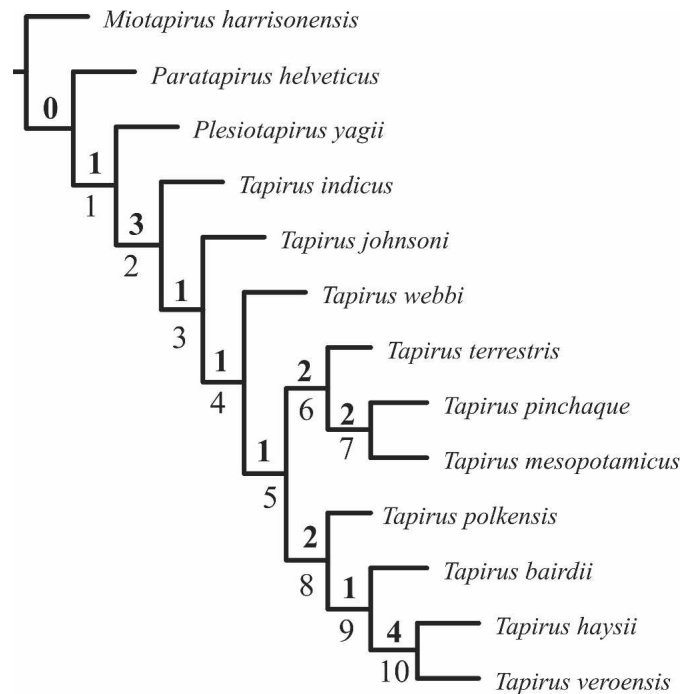


FIGURE 5. Cladogram obtained with TNT program. Numbers below branches indicate: Node 1: 23<sup>1</sup>; Node 2: 11<sup>1</sup>, 19<sup>1</sup>, 21<sup>1</sup>; Node 3: 33<sup>1</sup>; Node 4: 24<sup>1</sup>; Node 5: 7<sup>1</sup>; Node 6: 5<sup>0</sup>, 9<sup>0</sup>, 11<sup>1</sup>; Node 7: 26<sup>1</sup>, 30<sup>1</sup>, 32<sup>1</sup>; Node 8: 1<sup>1</sup>, 3<sup>1</sup>, 4<sup>1</sup>, 16<sup>0</sup>; Node 9: 12<sup>0</sup>. Node 10: 0<sup>1</sup>, 13<sup>1</sup>, 14<sup>1</sup>, 24<sup>2</sup>, 25<sup>1</sup>. Only non-ambiguous synapomorphies are indicated. Numbers above branches indicate Bremer support values.

lachrymal broad and flat (16<sup>0</sup>); and dorsal table of frontal relatively broad (1<sup>1</sup>). This node is strongly supported by a high Bremer support value (Fig. 5).

The Pleistocene species from North America, *T. veroensis* and *T. haysii*, are grouped by having a low sagittal crest (0<sup>1</sup>), a broad shaped lachrymal (13<sup>1</sup>) with its facial surface concave (14<sup>1</sup>), a strong parastyle development on P3-M3 (24<sup>2</sup>), and very rare or absent labial cingulum on posterior half of P3-M3 (25<sup>1</sup>).

## Remarks

Our cladogram differs from the previous phylogeny of the New World *Tapirus* proposed by Hulbert (1995) in the fact that the Neotropical tapirs appeared as a monophyletic group in the latter analysis. However, a more recent cladistic analysis performed by Hulbert and Wallace (2005) is highly congruent with our results, showing overall similarities among the topologies of the different cladograms: *T. bairdii* has a sister relationship with the North American clade of *T. haysii* and *T. veroensis*, being *T. polkensis* related with the whole group in both analyses. The clade of *T. haysii* and *T. veroensis* has a high Bremer support value (Fig. 5). In addition, *Tapirus terrestris* and *T. pinchaque* resulted in the same clade, as in Hulbert and Wallace (2005) cladograms, but with *T. mesopotamicus* more closely related with *T. pinchaque*.

The relationships of *Paratapirus helveticus*, *T. webbi*, and *T. polkensis* are well resolved and not collapsed in our cladogram, being the latter the sister taxon of the group composed by *T. terrestris*, *T. haysii*, and *T. veroensis*.

## DISCUSSION AND CONCLUSIONS

*Tapirus mesopotamicus* belongs to a mammal fauna from the Late Pleistocene of the Entre Ríos Province in the Mesopo-

tamian region of Argentina that had included until now only the fossil record of the living *T. terrestris* among the family (Tonni, 1992). The latter is the common South American tapir which is nowadays widely distributed throughout the continent from Colombia to northern Argentina. A definite character that differentiates *T. mesopotamicus* from *T. terrestris* is the shape of the sagittal crest. In a similar sense, Simpson (1945) stated that "The aspect of this region happens to be the most diagnostic single character among recent and, as far as it is known in them, Pleistocene tapirs, and it alone unmistakably, distinguishes all the sufficiently defined species." Simpson (1945), based on the morphology of *T. terrestris*, considered that the sagittal crest and sagittal tables in tapirs are characteristics that are not related ontogenetically. Hershkovitz (1954) considered the striking sagittal crest of *T. terrestris* to be an extreme development of a condition that is incipient in *T. pinchaque*, having been clearly demonstrated that the latter species and *T. veroensis* undergo the primitive pattern of crest development (Lundelius and Slaugher, 1976; Holbrook, 2002). In this context, it is probable that *T. mesopotamicus* has had the same developmental pattern as in most fossil and extant species of American tapirs, excepting *T. terrestris*. So, the shape of the crest in *T. mesopotamicus* and *T. terrestris* is interpreted as a primitive and derived developmental pattern, respectively. These primitive characters, in combination with those more advanced which rise from the cladistic analysis, give a clear support to the erection of *T. mesopotamicus* as a new species.

A great similarity in morphology and metrics of the teeth is observed among the different species of fossil and living *Tapirus*, with the exception of *T. haysii* whose measurements are clearly larger. Likewise, Ray and Sanders (1984) postulated that the three extant species of tapirs which inhabiting the North of Colombia (*T. terrestris*, *T. pinchaque*, and *T. bairdii*) are clearly separated by cranial osteology, but they overlap in most of dental characters. As Simpson (1945:51) pointed out, P1-M3/p2-m3 in the tapirs are homodynamic series which work as units without any clear functional differentiation within the cheek row teeth, exhibiting a tendency of morphological modification only in the most anterior element (i.e., anterior terminalization of P1) and very slight evidence of posterior terminalization of M3. Consequently, the ranges of variation overlap widely between adjacent teeth among all members of the family, and *T. mesopotamicus* is not the exception.

Simpson (1945), Hulbert (1995), and Ray and Sanders (1984) stated that the molarization of premolars, apart from size in only few cases, is the most useful morphological feature of the dentition for separating the species of tapirs. In addition, Hulbert (1995:530) states that, excluding the size and the strong molarization of P1 and P2, the dentition of *T. haysii* is almost undistinguishable from those of *T. veroensis* and the living Neotropical tapirs. P1 of *T. mesopotamicus* is more quadrangular than in extant species of *Tapirus* and *T. veroensis*; but we consider, regardless of the difficulty of interpreting its abraded cusps, that it is less molarized than in *T. haysii*.

Recent phylogenetic analyses (Norman and Ashley, 2000; Hulbert and Wallace, 2005) recovered a sister taxon relationship between the two endemic South American tapirs species, *T. terrestris* and *T. pinchaque*. The high similarity between *T. pinchaque* and *T. terrestris* based on molecular data suggests that they had a recent common ancestor and the possibility that a single tapir lineage dispersed to South America following the formation of the Panamanian Isthmus during late Pliocene times and subsequently speciated (Norman and Ashley, 2000). Our morphological comparisons and the phylogeny presented herein do not contradict this conclusion, placing the new taxon *T. mesopotamicus* in this South American clade.

The more outstanding conclusion of our cladistic analysis, besides the grouping of *T. mesopotamicus* with *T. pinchaque*, is that

it confirms the monophyly of the genus *Tapirus* and strongly rejects a monophyletic grouping of the Neotropical tapirs. Accordingly, the Central American *T. bairdii* is included in a different clade together with several North American fossil species.

In sum, our phylogenetic analysis which includes the first well-preserved skull of a fossil tapir with precise stratigraphic provenance constitutes a preliminary approach to elucidate the relationships and history of the Neotropical tapirs. The possibility of obtaining more accurate phylogenetic and paleobiogeographic hypotheses to explain the South American diversification of the group will depend on the description of those complete fossil tapirs recently recovered in Amazonia (Holanda et al. 2004) and on new findings of early Pleistocene age coming from northern localities in the continent.

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#### APPENDIX 1. Description of characters used for phylogenetic analysis.

- (0) Adult height of sagittal crest: moderate (0); low, less than 2 mm (1); very high, more than 10 mm (2).
- (1) Dorsal table of frontal: relatively narrow or small (0); relatively broad (1).
- (2) Nasal-frontal lateral profile: nasals and frontals approximately on same plane (0); nasals notably stepped down from frontals (1).
- (3) Fossa for meatal diverticulum on posterior dorsal surface of nasal: not extensive, does not near midline (0); very extensive, approaches within a few mm of midline (1).
- (4) Development of fossa for meatal diverticulum on dorsal table of frontal: very limited (0); broad exposure with distinct posterior margin (1).
- (5) Posterior projection of lambdoidal crests in lateral view: well projected backwards, markedly posterior to condyles (0); less projected backwards, at the same level or hardly anterior to condyles (1).
- (6) Dorsomedial border of maxilla: sharp border that is mostly directed medially (0); rounded border that is directed ventromedially (1); border up-turned and expanded as an extension of dorsal flange (2).
- (7) Location of infraorbital foramen relative to the cheek teeth: posterior to anterior edge of P3 or dorsal to P4 (0); anterior to anterior edge of P3 (1).
- (8) Anteromedial process of maxilla: absent (0); present (1).
- (9) Lateral exposure of anteromedial process of maxilla: maxilla well exposed in lateral view dorsal to premaxilla (0); maxilla covered by premaxilla, not visible in lateral view or barely so (1).
- (10) Dorsal maxillary flange: absent (0); present (slight or extensive) (1).
- (11) Length of posterior process of premaxilla: long, terminates posterior to P1 (0); terminates dorsal to or just in front of P1 (1); ends about midway over C-P1 diastema (2); very short, terminates well anterior to midway point of diastema (3).
- (12) Width of maxillary bar between infraorbital foramen and lacrimal: narrow, usually less than 5 mm (0); wide, more than 5 mm (1)
- (13) Shape of lacrimal: narrow, much taller than long (0); broad, about as long as it is high (1).
- (14) Facial surface of lacrimal: flat or convex (0); concave (1).
- (15) Anterior lacrimal process(es): absent or very weak (0); present, well developed (1).
- (16) Posterior process of lacrimal: broad and flat (0); slender, pointed or knobby (1).
- (17) Typical number of lacrimal foramen: two (0); one (1).

- (18) Lachrymal foramen visible in lateral view: yes, at least one (0); no, not visible in lateral view (1).
- (19) Relative crown height of cheek teeth: short, relatively brachydont (0); taller (1).
- (20) P1 TW/L ratio: on average, less than or equal to 0.80 (0); on average, greater than 0.80 (1).
- (21) P2 ATW/PTW ratio: on average, less than or equal to 0.85 (0); on average, greater than 0.85 (1).
- (22) P2 protoloph: does not reach ectoloph (0); just reaches to base of ectoloph (1).
- (23) P3 and P4 protocone and hypocone: closely oppressed and merge with wear(0); widely separated (1).
- (24) Parastyle development on P3-M3: moderate (0); strong (1); very strong (2).
- (25) Labial cingulum on posterior half of upper cheek teeth: present on half or more of P3-M3; present on half or more of P3-M3 (0); absent or very rare on P3-M3 (1).
- (26) Suture between nasal and frontals: W-shaped (0); nearly straight (1).
- (27) Sagittal crest: single (0); double (1).
- (28) Narial aperture delimited by maxilla: broad and open (0); narrow and closed (1).
- (29) Upper incisors: pro-odont (0); opisthodont (1); orthodont (2).
- (30) Cranial fragment of jugal in lateral view: broad (0); narrow (1).
- (31) Supraorbital groove for nasal diverticulum: broad and shallow (0); narrow and deep (1).
- (32) Rostrolateral process of frontal: robust (0); slender (1)
- (33) Relative diastema length: short ( $ldl / p2m3L < 0.40$ ) (0); medium

( $0.40 \leq ldl / p2m3L < 0.50$ ) (1); long ( $ldl / p2m3L \geq 0.50$ ) (2). [ $ldl$  = lower diastema length;  $p2m3L$  = length from anterior point of  $p2$  to posterior point of  $m3$ ]

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis.

	0	5	10	15	20	25	30
<i>Miotapirus harrisonensis</i>	---	0--	000-	000000-	---	0100000-	-----
<i>Plesiotapirus yagii</i>	0-	000-	1---	00-00-	---	000101100-	0---0-0
<i>Paratapirus helveticus</i>	-	0000-	000-	001000-	---	0001000-	0---0-0
<i>Tapirus johnsoni</i>	00000-	0010111	100001001	11111100-	-----	0-1	
<i>Tapirus webbi</i>	--	000-	001001100-	1001110110-	-----	0-1	
<i>Tapirus polkensis</i>	01011-	0110-	110--	0111111110-	-----	0-1	
<i>Tapirus haysii</i>	110111011002011	10111111121-	-----	0-0			
<i>Tapirus veroensis</i>	110110011001011000011111	12100010010					
<i>Tapirus bairdii</i>	01111121101300000--	111111001021112					
<i>Tapirus terrestris</i>	20100011110210011001111111100001111						
<i>Tapirus pinchaque</i>	0000000111021001100101011010010001						
<i>Tapirus mesopotamicus</i>	01000001110210001-	111111101011010-					
<i>Tapirus indicus</i>	0100010011011000100111110001021110						

APPENDIX 3. Revised materials used for anatomical comparisons.

*Tapirus terrestris*: MLP 1681; MLP 1399 MACN 3327; MACN 31231; MACN 10.25; MACN 33221; MACN 4386; MACN 7.6; MACN 4329; MACN 4738; MACN 2889; MACN 10.24; MACN 47386; MACN 19147; MACN 48330; CML 06346; CML 06347; CML 04933. *Tapirus bairdii*: MLP 1451. *T. indicus*: MACN 29926; MACN 12.9; MACN 30351; MACN 25.53; MACN 4347; MACN 2544.