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ORIGINAL PAPER

Reappraisal of the Genus *Tapirus* (Perissodactyla, Tapiridae): Systematics and Phylogenetic Affinities of the South American Tapirs

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Abstract The record of the genus *Tapirus* in South America is associated with the faunistic events of the Great American Biotic Interchange (GABI). The taxon is considered an immigrant of Holarctic origin. Although remains are scarce and incomplete during the Pleistocene, an analysis of these materials allowed us to consider valid seven fossil species : *Tapirus tarijensis*, *T. cristatellus, T. greslebini*, *T. rioplatensis, T. oliverasi, T. mesopotamicus,* and *T. rondoniensis.* A phylogenetic analysis was carried out in order to elucidate the relationships of the American fossil and extant species. Our result is consistent with a paraphyletic hypothesis for South American tapirs and suggests that a second dispersal event would have occurred from South America to North America, of a form closely related to *T. cristatellus*, resulting in the derived forms of North America.

Keywords *Tapirus* · South America · Pleistocene · Tapiridae · Phylogeny · Systematics

Introduction

The tapirs are currently represented by one genus and four species that occur in the Neotropical region (*Tapirus bairdii*, *T. pinchaque,* and *T. terrestris*) and in the Oriental region (*T. indicus*).

The origin of the family Tapiridae in America is Holarctic, and its oldest record is probably from the Eocene of North America (Eberle 2005). The earliest records of *Tapirus* in North America are late Miocene (late Clarendonian) (Hulbert 2005). Although there are suggestions that tapirs entered South America in the late Miocene (Campbell et al. 2010), the evidence suggests that the genus appeared in South America from the faunistic events known as the Great American Biotic Interchange (GABI) (GABI 2 from Woodburne 2010). The oldest confident record of the genus *Tapirus* is from the early Pleistocene to about 2.6–1.0 Ma (Tonni 1992).

Remains of *Tapirus* are scarce and incomplete from South America, comprising almost exclusively dental and postcranial fragments. However, in the last decade, significant finds of more complete cranial and postcranial materials have been made (Ferrero and Noriega 2007; Holanda et al. 2007, 2011), allowing a reevaluation and reinterpretation of the evolutionary history of the genus in South America. This article summarizes the different species from South America, discusses their validity, describes new material of *T. mesopotamicus,* and performs a cladistic analysis in an effort to interpret the phylogenetic relationships of the family.

Material and Methods

The type specimens of South American species were reevaluated and compared, when possible, with living and fossil species from North America housed at the collections visited by the authors (see Institutional Abbreviations).

A phylogenetic analysis was performed in order to elucidate the relationships of the American fossil species and extant species. This analysis comprises a total of 51

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characters and 18 terminal taxa including the outgroups (Appendix 1–2). Outgroups include five species of Tapiridae sensu Colbert (2005): *Colodon occidentalis*, *Nexuotapirus marslandensis*, *Miotapirus harrisonensis*, *Plesiotapirus yagii*, and *Paratapirus helvetius*. Following Hulbert and Wallace (2005), the root is placed in *C. occidentalis*. We consider as terminal taxa the living species of the genus *Tapirus* (*T. bairdii*, *T. terrestris, T. pinchaque,* and *T. indicus*); three Miocene species from North America (*T. johnsoni*, *T. webbi,* and *T. polkensis*); three Pliocene–Pleistocene species from North America (*T. lundeliusi*, *T. haysii,* and *T. veroensis*); and three South American fossil taxa (*T. mesopotamicus*, *T. rondoniensis,* and *T. cristatellus*).

The criterion of maximum parsimony was followed using the TNT program (Goloboff et al. 2003). Bremer support (Bremer 1994) was calculated with the same program. The multistate character # 42 was codified as unordered. The data matrix is shown in Appendix 2. The descriptive statistics were done using the last available version of Palaeontological Statistics–PAST software (Hammer et al. 2001).

The temporal distribution of the species established in Fig. 4 follows Colbert (2005)–*C. ociddentalis*; Hulbert (2010)–*N. marslandensis*, *M. harrisonensis*, *P. yagii, T. johnsoni*, *T. webbi, T. polkensis*, *T. lundeliusi*, *T. haysii*, and *T. veroensis*; and Scherler et al. (2011)–*P. helvetius*. The temporal distribution of the South American fossil taxa follows this work.

Institutional Abbreviations

CICYTTP, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Argentina; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MCL, Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MLP, Museo de 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; PVL, Paleontología Vertebrados, Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina; UF, Florida Museum of Natural History, Gainesville, United States; UNIR, Universidade Federal de Rondônia, Porto Velho, Brazil.

Results

Summary of Systematics

Analysis of the material described from the Pleistocene of South America permitted us to consider valid the following species.

Tapirus tarijensis Ameghino, 1902

In the original contribution, Ameghino (1902) illustrated the material, a left dentary with the p2-4, without specifying a number of the collection or a repository (Ameghino 1902: plate V, fig. 2a–b). However, we found that MACN 1523 (Fig. 1b) corresponds to the specimen figured in Ameghino (1902). This material comes from the Tarija Valley, Bolivia, "formación pampeano" (sensu Carles 1888) and later identified as Tolomosa Formation, late Pleistocene (Coltorti et al. 2007). Later, Rusconi (1928) assigned to this taxon the specimen MACN 604, a left metacarpal III from the same locality.

Tapirus tarijensis was described as having a larger tooth row size when compared to *T. terrestris* and a high dentary whose ventral margin is more concave than convex (Ameghino 1902). The specimen MACN 1523 bears cuspids that are rather fragmented, which makes the observation of diagnostic characters difficult. Even so, a mesial cingulid on p3 is well developed; this character is not present in *T. terrestris* or any other living tapirs included in this study. However, when tooth measurements are compared, this material differs from *T. terrestris* in size and overlaps the largest size of North American forms, such as *T. haysii* and *T. webbi* (Table 1).

Tapirus cristatellus Winge, 1906

Winge (1906) published the photograph of a fragment of skull (plate VIII, p. 198) and designated this material, as well as postcranial and dentary remains associated with it but not figured in his work, as *Tapirus cristatellus* (Fig. 1c). *Tapirus cristatellus* is recorded from the karstic region of Minas Gerais State, Brazil, late Pleistocene–Holocene. It is distinct from *T. terrestris* in having larger skull and teeth, flat frontal and parietal, later fusion of the cranial sutures, absence of deltoid process on the humerus, and medial malleolus of the tibia slightly marked (Winge 1906).

New findings attributed to this species were made in Gruta dos Brejões and Toca dos Ossos caves, Bahia State (Holanda et al. 2007). Among the South American species described, *T. cristatellus* seems to be more similar to the North American forms and to *T. pinchaque* due to the pattern of development of the sagittal crest. The juveniles of *T. cristatellus* bear parasagittal ridges, and during the ontogenetic development these ridges meet at the dorsal midline and fuse into a single and low sagittal crest in the adult (Holanda et al. 2007).

Tapirus greslebini Rusconi, 1934

The fossil material comes from the "Puelchan" sands of Villa Ballester, Buenos Aires Province, Argentina. The

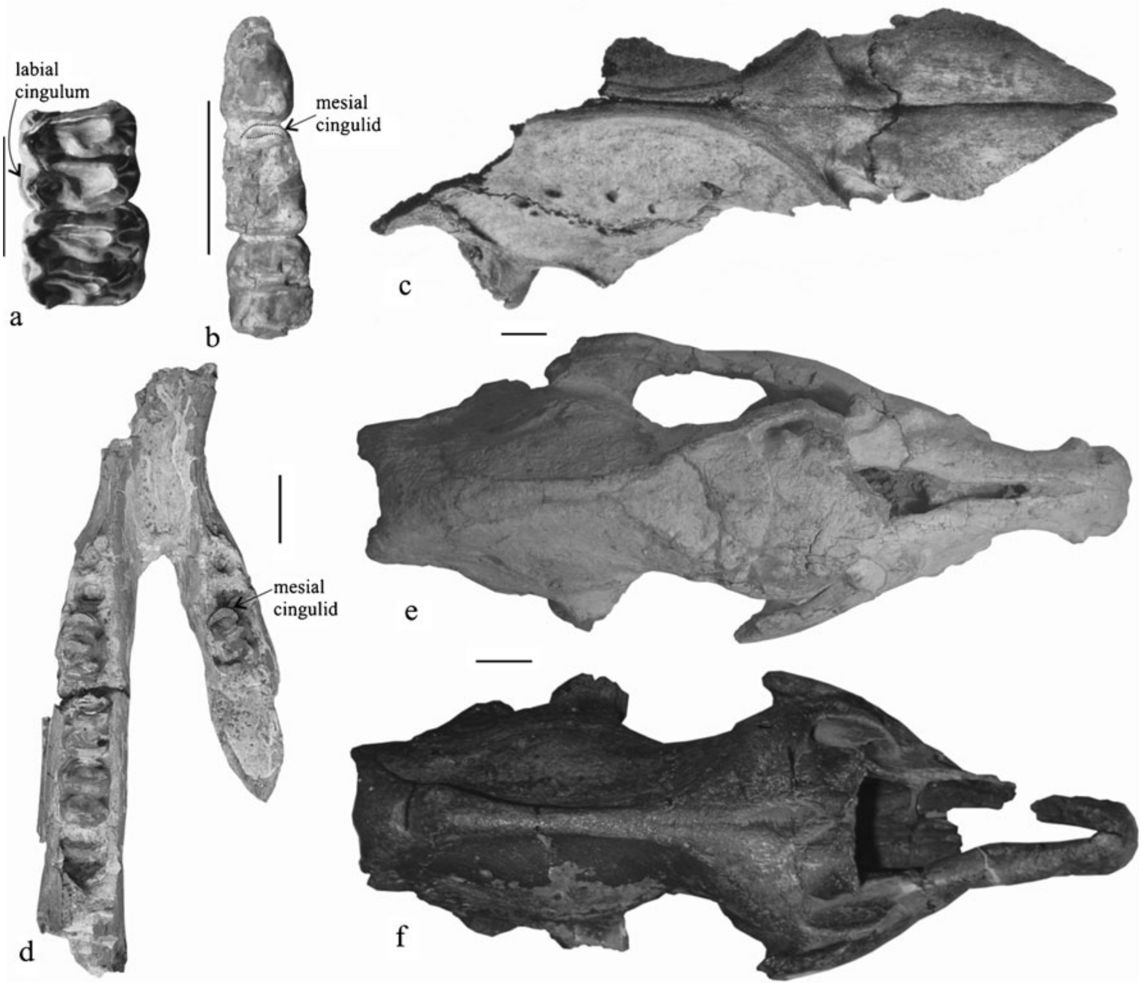

Fig. 1 The fossil species of *Tapirus* from South America. **a** *T. greslebini*, PVL 718, right maxilla fragment with M1 and M2 in occlusal view; **b** *T. tarijensis*, MACN 1523, left dentary fragment with p2-4 in occlusal view; **c** *T. cristatellus*, skull fragment, from Winge (1906) in dorsal view; **d** *T. rioplatensis*, MACN 15735, mandibular fragment with p3, dp4, m1, and m2 in alveolus in occlusal view; **e** *T. mesopotamicus*, CICYTTP-PV-M-1-23, incompleted skull in dorsal view; and **f** *T. rondoniensis*, UNIR-PLV-M009, incomplete skull in dorsal view. Scale bars = 30 mm

specimens lack stratigraphic context because they were obtained from a drilling operation by suction pumps. Despite the difficulty to precisely age the fauna, Pascual et al. (1965) noted the presence of faunistic elements of post Chapalmalalan and Ensenadan age (Pliocene–Pleistocene). *Tapirus greslebini* was based on two upper molars, M1 and M2 [PVL 718 (ex Rusconi collection 562)], besides a fragment of upper molar [PVL 717 (ex Rusconi collection 713)] and an occipital fragment (Rusconi collection 1035, unfound) having been assigned to the species. The molars display some morphological characters with systematic importance that distinguish *T. greslebini* from extant and fossil South American tapirs (Fig. 1a). Both molars showed a mesial subcingulum in the base of the parastyle that reaches the mesolabial wall of the paracone. There is a well-marked labial cingulum developed from the distal wall of the paracone to the labiodistal portion of the metacone of M1 and M3. At the base of the interloph there is also a small lingual cingulum between the protocone and hypocone. According to the original measurements published by Rusconi (1934), it is evident that the molars belonged to a tapir larger than *T. terrestris*, within the size range of *T. haysii,* a North American species (Table 2).

Tapirus rioplatensis Cattoi, 1957

The specimen came from an excavation in Buenos Aires city, Argentina. The fossils were dug from 17 m depth and are Pleistocene in age, according to Cattoi (1957). Recently, Soibelzon (2008) confirmed the stratigraphic location corresponding to the early Pleistocene (Ensenadan Stage/Age from Cione and Tonni 2005).

The holotype (MACN 15735) is a fragment of mandibular symphysis and pelvis. The left mandibular portion

Table 1 Measurements in millimeters of the lower cheek teeth of *Tapirus*. Abbreviations: L, length; W, maximum width. Maximum width is distal width for p2-4, and mesial width for m1-3. Data of *T. oliverasi* from Ubilla (1983), and *T. cristatellus* from Winge (1906). When N > 1, the first line represents the mean, and the second line indicates the observed range (size of the sample)

		p2	p3	p4	m1	m2	m3
T. tarijensis (MACN 1523)	L	22.65	21.85	22.2	–	–	–
	W	14.75	17.1	18.3	–	–	–
T. rioplatensis (MACN 15735)	L	–	30	27.1	30	–	–
	W	–	21	21	23.2	–	–
T. oliverasi (MNA-CPO-183)	L	–	–	–	26.6	29.5	30.3
	W	–	–	–	21.4	22.8	23.3
T. cristatellus (Esc.5)	L	–	–	–	–	25.19	26.6
	W	–	–	–	–	19	20
T. cristatellus (Esc.11)	L	–	–	–	–	24.50	26
	W	–	–	–	–	19	20
T. terrestris	L	21.48	20	20.4	20.53	23.46	24.25
		19.4–24.24 (49)	17.85–23.45 (49)	18.2–22,7 (42)	17–22.6 (50)	19,45–26.72 (46)	22.35–27.76 (27)
	W	13.39	15.12	17.52	16.56	18.07	18.73
		11.2–16 (49)	13–18 (49)	14.9–20.4 (42)	14.7–18.45 (49)	16–20.5 (45)	17.3–20.6 (27)
T. webbi	L	23.61	22.42	21.8	23.36	26.48	26.88
		22.3–25.5 (9)	21.2–24.5 (13)	20.3–23.2 (10)	22.4–25.3 (12)	24.8–29.4 (11)	25.1–27.8 (9)
	W	14.35	15.35	18.34	17.75	19.32	19.4
		13–17.3 (9)	13.8–16.9 (13)	17.3–19.6 (10)	16.6–19.2 (12)	18.3–20.85 (11)	18–21.9 (9)
T. haysii	L	26.88	23.82	24.22	25.6	28.23	29.48
		25.5–28.6 (5)	22.5–25.5 (5)	22.7–27.1 (5)	23.7–27.3 (6)	25.6–30.3 (6)	26–32.1 (6)
	W	17.9	17.06	21.98	21.6	22.43	22.28
		16.4–19 (5)	16.2–17.4 (5)	21.1–23.3 (5)	20.7–22.4 (6)	21.6–23.7 (6)	21.4–23.8 (6)

contains the p3, dp4, m1, and m2 within the alveolus; the right portion bears only the p3 (Fig. 1d). The specimen was identified as a new species of *Tapirus* considering mainly its size and proportions. *Tapirus rioplatensis* is remarkably larger and more robust when compared to other living or fossil South American tapirs (Table 1). Although deciduous teeth are still present in MACN 15735, it is very probable that the animal had reached its definitive size. A mesial cingulid on p3 is present. This character is also found in *T. tarijensis* and differs from *T. terrestris,* where the cingulid on p3 is poorly developed.

Tapirus oliverasi Ubilla, 1983

The species was described based on a right dentary with m1-3 from the Department of Montevideo, Uruguay, Libertad? Formation, early Pleistocene (Ubilla 1983). The type specimen is missing from the collection where it was housed (M. Ubilla, personal communication). *Tapirus oliverasi* differs from *T. terrestris* only because of its larger size and robustness, but is smaller than *T. rioplatensis* (Table 1). Due to the fragmentary nature of the specimen, it is difficult to define a diagnostic character that permits distinguishing *T. oliverasi* from other fossil tapirs previously described for South America, as it is the case for *T. tarijensis* and *T. rioplatensis*.

Tapirus mesopotamicus Ferrero and Noriega, 2007

This species was described based on cranial material and a right mandible fragment (Fig. 1e) reported from the Department of Diamante, Province of Entre Ríos, Argentina, at Salto Ander Egg Formation (Brunetto et al. 2009), late Pleistocene. In this contribution, we include postcranial elements that were not published in the original paper (Ferrero and Noriega 2007), but were found associated with the type (Fig. 2).

Tapirus mesopotamicus differs from *T. terrestris* in having a robust and long skull, a more or less straight suture between nasals and frontals, dorsal table of frontals relatively broad, rostrolateral process of frontal robust, strong lambdoid crests that are highly projected backwards, posterior to the condyles,

Table 2 Measurements in millimeters of the upper cheek teeth of *Tapirus*. Abbreviations: L, length; W, maximum width. Maximum width corresponds to the distal width in P1-4, and mesial width in M1-3. Data of *T. greslebini* from Rusconi (1934), and T. *cristatellus* from Winge (1906). When N > 1, the first line represents the mean, and the second line indicates the observed range (size of the sample)

		P1	P2	P3	P4	M1	M2	M3
T. greslebini (PVL 718)	L	–	–	–	–	25.5	26	–
	W	–	–	–	–	30	31	–
T. cristatellus (Esc.1)	L	20.1	21.5	23	23.5	24.5	26.5	–
	W	17	23	25	27	26.5	29	–
T. cristatellus (Esc.5)	L	–	20	21.66	23	23.5	26	26
	W	–	24	26.75	27.5	26.66	28.75	27.25
T. mesopotamicus (CICYTTP-PV-M-1-23)	L	15.6	17.5	18.2	20	20.2	23.74	24.3
	W	16.22	22.5	25.74	27.5	–	28.74	28.1
T. rondoniensis (UNIR-PV-M009)	L	–	18	19.3	18.5	19.8	21	22
	W	–	20.70	22	23.8	23.1	25.5	23.5
T. terrestris	L	16.86	17.84	19.25	19.81	20.25	22.85	22.88
		14.5–21 (47)	14.6–20.35 (51)	16.3–21.74 (53)	16.70–22.45 (45)	16.15–23.55 (52)	19.1–25.36 (48)	20–26 (26)
	W	15.53	21.13	22.78	24.59	23.32	25.85	26.14
		12.2–19.8 (47)	18.35–23.95 (51)	20.4–25.3 (53)	21–27.4 (45)	21.5–27.7 (52)	22.84–30.9 (48)	23.75–29.7 (26)
T. webbi	L	18.63	20.77	21.25	21.48	23.56	25.56	24.3
		18–20 (6)	19.4–23.1 (8)	20.3–22.7 (6)	20.4–22.8 (7)	21.6–26.4 (9)	23.8–27.6 (8)	21.7–27.4 (4)
	W	16.18	22.93	24.76	25.46	26.38	27.66	25.17
		14.1–18.5 (6)	21.9–25.2 (8)	22.9–26.5 (6)	24.3–26.8 (7)	24.3–28.8 (9)	26.3–29.4 (8)	18.9–27.8 (4)
T. haysii	L	22.63	21.66	22.27	23.56	25	27.22	27.66
		20.9–24.1 (4)	19.6–24.1 (6)	21–23.7 (5)	22.4–25.3 (6)	22.7–27.94 (10)	25.9–28.2 (8)	26.1–28.2 (6)
	W	21.33	26.58	27.08	29.93	28.96	31.96	32.35
		20.21–22.7 (4)	23.8–27.9 (6)	25.3–28.1 (5)	27.8–31.7 (6)	26.4–30.3 (10)	29.5–32.7 (8)	31.3–33.2 (6)

the posterior process of premaxilla ends about midway over C-P1 diastema, and maxilla and base of the zygomatic process strikingly robust (Ferrero and Noriega 2007).

Postcranial elements correspond to several articulated bones of a right foot, including the distal portion of MT II, MT III and MT IV, first and second phalanges of MTII, III and IV, and ungual phalanges of MTII and MTIV (Fig. 2). The foot is clearly more robust than that observed in *T. terrestris* and the difference in size is more evident when considering the MT III dimensions (Table 3).

Tapirus rondoniensis Holanda et al., 2011

The species was recently named after material collected in the locality of Araras, Nova Mamoré Municipality, Rondonia State, Brazil, Rio Madeira Formation, late Pleistocene (Holanda et al. 2011). The specimen comprises a nearly complete skull of a young adult, with the M3 in eruption (Fig. 1f). *Tapirus rondoniensis* differs from *T. terrestris* in

Fig. 2 Incomplete right foot of *Tapirus mesopotamicus,* CICYTTP-PV-M-1-23. Scale bar =30 mm

having external frontal crests that meet very close to the frontoparietal suture to form a true sagittal crest restricted to the parietals, in possessing a dorsal table of frontals broad and inflated, and a weakly molarized P2, with a reduced protocone without a protoloph.

Tapirus terrestris (Linnaeus, 1758)

Currently it is the most widely distributed species in the tropical zones of mainland South America, being found from Rio Grande do Sul, Brazil and the Gran Chaco of Argentina and Paraguay, until the Amazonian region of Brazil, Bolivia, Peru, Ecuador, Colombia, Guianas, Surinam, and Venezuela (Padilla and Dowler 1994). However, in the late Pleistocene it is recorded until Uruguay (Ubilla 1996) and the Province of Entre Ríos, Argentina (Tonni 1992; Ferrero et al. 2007), about 32 °S (Fig. 3). This latter is the southernmost record of *T. terrestris* for South America.

Tapirus terrestris is characterized mainly by an intermediate size between *T. pinchaque* and the fossil North American species, *T. haysii* and *T. webbi,* in having P2 entirely molariform, a high sagittal crest, convex anteroposteriorly and elevated dorsally to the nasals, and narrow and inflated frontals.

Considerations on Tapiridae Phylogeny

A single most parsimonious tree (MPT) was obtained by exhaustive searching (Fig. 4), with 110 steps under equal weights, consistency index (CI) of 0.47, and a retention index (RI) of 0.67. The monophyly of the genus *Tapirus* is corroborated. Members of this clade share the p2 hypoconid and entoconid connected by hypolophid, as well as a long lower diastema, and the protocone and hypocone of P3 and P4 widely separated. Similar to Colbert (2005), *N. marslandensis* is the sister-group of clade *Tapirus*. *Tapirus webbi* shows a close relationship with the extant tapirs and derived fossil tapirs from South and North American. This node exhibits a high Bremer support value (Fig. 4) and is supported by six unambiguous synapomorphies: mental foramen is located directly ventral to p2 (character 30); cheek teeth with tall crowns (33); P2 AW/PW ratio more than 0.85 (35); well separated transverse lophs on P2-P4 and p2-p4 (37); i1 much larger than i2, very procumbent and spatulate (44); and protolophid and hypolophid on premolars are approximately equal in height (47).

The group composed by *T. pinchaque* (Node 4), Neotropical fossil tapirs, extant tapirs, and derived North American species is defined by two unambiguous synapomorphies: anterolateral margin of nasal distinctly concave (character 9) and infraorbital foramen dorsal to P3 or P2 (16). This node is strongly supported by a high Bremer value (Fig. 4). The clade composed of *T. mesopotamicus*, *T. terrestris*, and *T. rondoniensis* shares a narrow and deep supraorbital groove for the nasal diverticulum (character 13).

Tapirus cristatellus appears as sister-group of the clade composed of *T. bardii*, *T. indicus* and derived North American species, *T. polkensis*, *T. lundeliusi*, *T. haysii*, and *T. veroensis*. Members of this clade (Node 8)

Table 3 Measurements in millimeters of the metatarsals of *Tapirus*. Abbreviations: MDB, mediolateral diameter of body; MDD, mediolateral diameter of distal portion. When N > 1, the first line represents the mean, and the second line indicates the observed range (size of sample)

		MT II	MT III	MT IV
T. mesopotamicus (CICYTTP-PV-M-1-23)	MDB	16.74	28.7	16.81
	MDD	23.6	37.8	23
T. terrestris	MDB	17.78	24.38	18.05
		15–21 (11)	22.36–27. 1 (13)	16–20.1 (12)
	MDD	26.95	31.96	26.75
		24–29 (11)	29.22–37.1 (13)	21–30.4 (12)
T. webbi	MDB	19.17	26.64	20.14
		16–22.8 (7)	24.1–29.8 (21)	17.9–22.3 (12)
	MDD	29.68	35.53	25.82
		28–32 (7)	32.4–38.8 (21)	22.4–31 (12)
T. haysii	MDB	19	28.3	18.36
		17.6–21.4 (3)	26.4–30.5 (3)	17–20.1 (3)
	MDD	27.7	36.9	25.56
		26.1–29 (3)	35.2–39.1 (3)	24.7–26 (3)

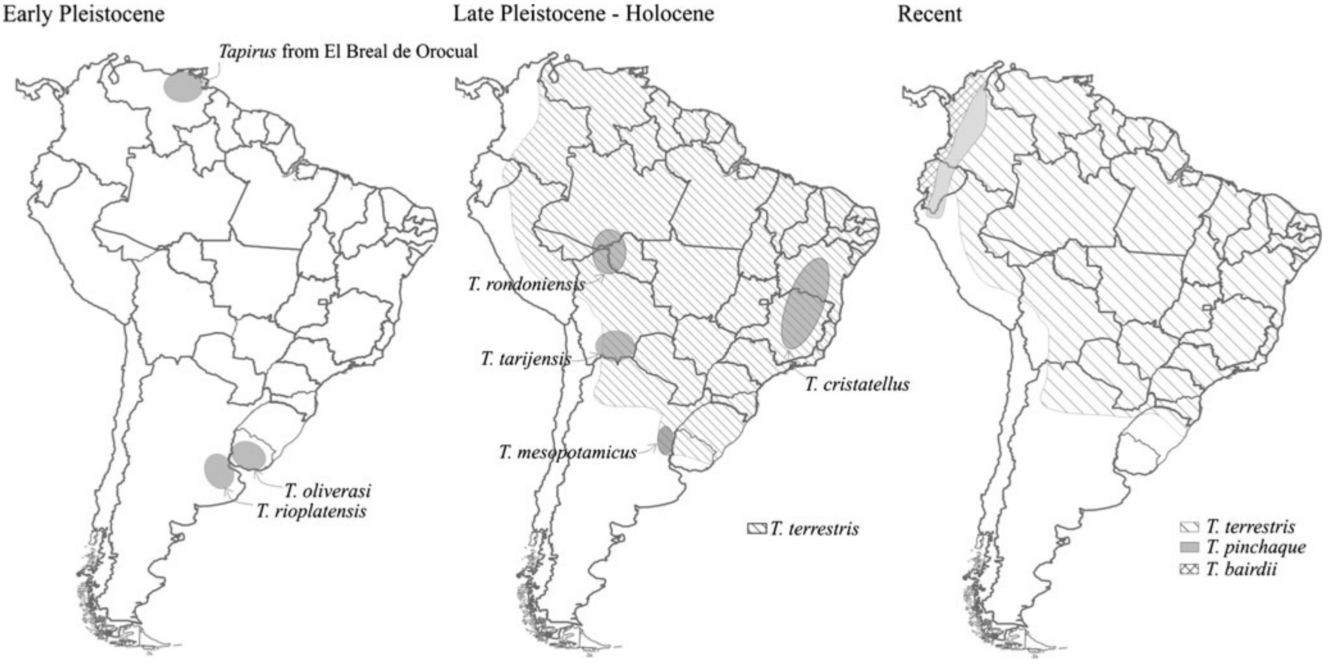

Fig. 3 Geographical distribution of the species of the genus *Tapirus* for the Quaternary of South America

share: fusion of the interparietal with the occipital occurring late in ontogeny (character 7, reversed in *T. lundeliusi*); fossa for meatal diverticulum on dorsal table of frontal possessing a broad exposure with distinct poste-

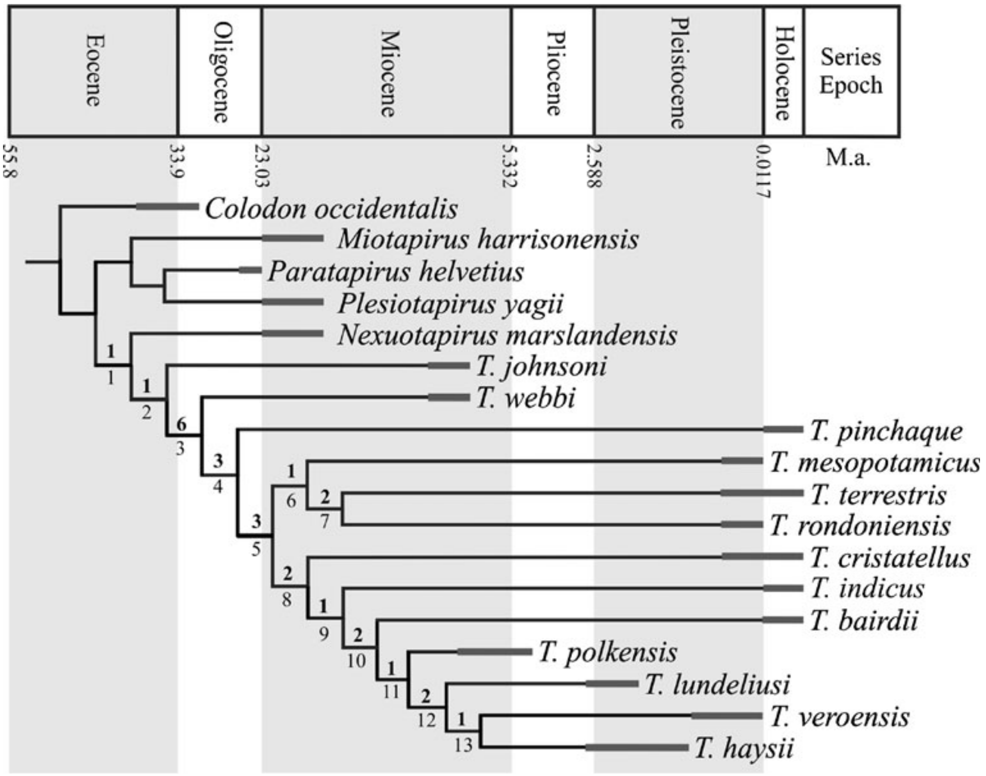

Fig. 4 Recovered cladogram and temporal distribution of the taxa. Numbers below the branches indicate: Node 1: 24 (1); Node 2: 46 (1); Node 3: 30 (1). 33(1), 35(1), 37(1), 44(1), 47(1); Node 4: 9(1), 16(1); Node 5: 48(1); Node 6: no unambiguous synapomorphies; Node 7: no unambiguous synapomorphies; Node 8: no unambiguous synapomorphies; Node 9: 10(1), 11(1); Node 10: 18(0); Node 11: no unambiguous synapomorphies; Node 12: 22(1), 31(1); Node 13: 21(1), 40(1). Only unambiguous synapomorphies are indicated–character number (character state). Numbers above branches indicate the Bremer support values. The temporal distribution of the species follows Colbert (2005), Hulbert (2010), and Scherler et al. (2011)

rior margin (12, reversed in *T. lundeliusi*); and lambdoidal crests in adults projected posterolaterally, with notable lateral flair (15).

The clade composed of *T. indicus, T. bairdii*, and the derived North American species (Node 9) is supported by two unambiguous synapomorphies: fossa for meatal diverticulum on nasal is deep and with distinct margins (10); and very extensive fossa for meatal diverticulum on posterior dorsal surface of nasal, reaching few milimeters of the midline (11). *Tapirus bairdii* and the derived North American species (Node 10) share the lateral exposure of the anteromedial process of the maxilla well exposed in lateral view, dorsal to the premaxilla (character 18).

Discussion

Some of the species described for the Pleistocene of South America based on isolated teeth were invalid and they were only assigned to *Tapirus* sp. due to the impossibility of differentiating them from *T. terrestris*, as it is the case of *Tapirus australis* Rusconi, 1928, and *Tapirus dupuyi* Cattoi, 1951, both from the early Pleistocene, southeast of the Province of Buenos Aires (Ubilla 1983; Tonni 1992).

Recently, Rincón et al. (2009) assigned to the latest Pliocene or early Pleistocene of Venezuela some maxillary and dentary fragments, assigning them to a possible new species of *Tapirus* that has close affinities with *T. webbi*. Holanda and Rincón (2009) emphasized the morphological difference of this material, but treated with care the designation of a new species based on fragmentary remains. If the age of El Breal de Orocual tar seep is confirmed as Pliocene–Pleistocene, these remains would represent the earliest record of tapir in intertropical South America (Fig. 3).

Ubilla (1983), using the dental characters of Cattoi (1957), considered as diagnostic features of *T. oliverasi* some characteristics that may be in fact modifications suffered by the animal, due to the degree of wear of the molars or individual variation. In this case, the only character that distinguishes *T. oliverasi* from *T. terrestris* is its larger size (Table 1). However, large-sized species, such as *T. rioplatensis* and *T. tarijensis*, bear a mesial cingulid, or a labial cingulum as *T. greslebini*, features not observed in *T. terrestris* (Fig. 1a–b, d). *Tapirus mesopotamicus* and *T. rondoniensis*, though clearly well defined by cranial characters, present teeth dimensions that overlap the size range of *T. terrestris* (Table 2). Therefore, similar to the North American species (Ray and Sanders 1984), South American ones fall in two size groups: one within the size range of *T. terrestris*, including *T. rondoniensis* and *T. mesopotamicus,* and another group, composed of larger forms, such as *T. tarijensis*, *T. rioplatensis*, *T. greslebini*, and *T. cristatellus.* In contrast to the early Pleistocene, the late Pleistocene shows an increased diversity of *Tapirus* in South America (Fig. 3). However, the diversity observed in relation to the early Pleistocene could reflect only the greater number of sites discovered in this age.

Our cladogram (Fig. 4) differs from the previous phylogenies proposed by Hulbert and Wallace (2005) and Hulbert (2010) for the New World *Tapirus* because the South American tapirs, *T. pinchaque* and *T. terrestris,* do not form a monophyletic group in our analysis. Ferrero and Noriega (2007), in a preliminary cladistic analysis following Hulbert and Wallace (2005), included *T. mesopotamicus* and proposed a South American monophyletic group. The topology obtained here, which included more fossil species from South America than previously considered in other works, is consistent with a paraphyletic hypothesis for South American tapirs, given that *T. pinchaque*, *T. terrestris, T. mesopotamicus, T. rondoniensis*, and *T. cristatellus* do not form a monophyletic group. In addition, *T. terrestris* and *T. rondoniensis* belong to the same clade, and *T. mesopotamicus* is the sister taxon of it. Unlike Hulbert and Wallace (2005) and Hulbert (2010), in our study *T. polkensis* is the sister-group of the North American species from the Pliocene-Pleistocene, *T. lundeliusi, T. haysii*, and *T. veroensis* (clade *Helicotapirus* of Hulbert 2010), and not *T. bairdii.* According to our phylogenetic hypothesis, *T. bairdii* and *T. indicus* would represent the living tapirs with more derived morphological characters.

Conclusions

A possible close relationship between *T. webbi* from the late Miocene of Florida and the extant South American species was first tentatively proposed by Hulbert (1995; *Tapirus simpsoni,* later renamed as *T. webbi*), and later emphasized by Hulbert (2010). Our hypothesis suggests a Miocene dispersal of a *T. webbi* closely related form to South America, followed by in situ evolution. A second dispersal event would have occurred from South America to North America, from a *T. cristatellus* closely related form, resulting in the derived forms of North America.

In the last decade a large diversity of tapirs was discovered from the Pleistocene-Holocene of South America

(Cozzuol and Holanda 2007; Ferrero and Noriega 2007; Holanda et al. 2011), despite the temporal gap between the Pliocene and early Pleistocene, when there are no records of tapir from the northernmost Intertropical South America or there are very fragmentary remains like those reported from Argentina and Uruguay, being in some cases, of uncertain stratigraphic provenance (Fig. 3). Rincón et al. (2009) recently found some remains of the late Pliocene–early Pleistocene of Venezuela and noted that this material shared similarities with *T. webbi*. The evolutionary history of tapirs, traditionally considered as one of the only lineages that have diversified in South America and remained there, represents an example of the great biodiversity that new discoveries in the Intertropical region can elucidate.

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Appendix 1. Description of Characters Used for Phylogenetic Analysis

The characters and character states are adapted from the character set originally developed by Hulbert and Wallace (2005), with phylogenetically uninformative characters deleted. Original numbering scheme of characters is retained in parentheses.

0. width of sagittal crest in adult specimens: (0) narrow; (1) broad [modified from Hulbert 1995: #2].

1 (3). temporal crests meet to form sagittal crest: (0) at or posterior to the frontoparietal suture; (1) anterior to the frontoparietal suture.

2 (4). dorsal table of frontal: (0) relatively narrow or small; (1) relatively broad.

3 (5). frontal inflation: (0) weak or absent; (1) strong.

4 (6). nasal-frontal lateral profile: (0) nasals and frontals approximately on the same plane; (1) nasals notably stepped down from frontals.

5 (7). size of interparietal bone compared to the parietal: (0) large, interparietal occupying more than 1/3 length of parietal in sagittal plane; (1) small, interparietal occupying less than 1/3 length of parietal in sagittal plane [modified];

6 (8). shape of interparietal bone: (0) typically polygonal (hexagonal or diamond shaped); (1) typically triangular.

7 (9). interparietal fusion with occipital: (0) occurs early in ontogeny (before loss of DP4); (1) occurs late in ontogeny (after eruption of P4).

8 (10). nasal length: (0) long (longer than 1.5 times the width of combined nasals); (1) short (shorter than 1.5 times the width of combined nasals).

9 (11). anterolateral margin of nasal: (0) relatively straight; (1) distinctly concave.

10 (14). fossa for meatal diverticulum on nasal: (0) shallow and without distinct margins; (1) deep and with distinct margins.

11 (15). fossa for meatal diverticulum on posterior dorsal surface of nasal: (0) not extensive, does not near midline; (1) very extensive, approaches within a few mm of midline.

12 (16). development of fossa for meatal diverticulum on dorsal table of frontal: (0) very limited; (1) broad exposure with distinct posterior margin.

13 (17). supraorbital groove for nasal diverticulum: (0) broad and shallow; (1) narrow and deep.

14 (18). posterodorsal process of maxilla widely exposed dorsal to orbit, forming base of trough for meatal diverticulum: (0) yes; (1) no.

15 (20). orientation of lambdoidal crests in adults: (0) mostly posteriorly, little or no outward flair; (1) posterolateral orientation, with notable lateral flair.

16 (22). location of infraorbital foramen relative to cheek teeth: (0) dorsal to P4; (1) dorsal to P3 or P2.

17 (24). anteromedial process of maxilla: (0) absent; (1) present.

18 (25). lateral exposure of anteromedial process of maxilla: (0) maxilla well exposed in lateral view dorsal to premaxilla; (1) maxilla covered

by premaxilla, not visible in lateral view or barely so.

19 (26). dorsal maxillary flange: (0) absent; (1) present [modified].

20 (28). width of maxillary bar between infraorbital foramen and lacrimal: (0) narrow, less than 5 mm; (1) wide, more than 5 mm.

21 (29). shape of lacrimal: (0) narrow, much taller than long; (1) broad, about as long as it is high.

22 (30). facial surface of lacrimal: (0) flat or convex; (1) concave.

23 (31). anterior lacrimal process(es): (0) absent or very weak; (1) present, well developed.

24 (32). posterior (preorbital) process of lacrimal: (0) absent; (1) present.

25 (33). posterior process of lacrimal: (0) broad and flat; (1) slender, pointed or knobby.

26 (34). typical number of lacrimal foramen: (0) two; (1) one.

27 (35). lacrimal foramen visible in lateral view: (0) yes, at least one; (1) no, not visible in lateral view.

28 (36). incisive foramen: (0) terminates posteriorly about midway between canine and P1; (1) terminates posteriorly at P1 or more posterior.

29 (37). relative diastema length: (0) short (ldl/p2m3L < 0.40); (1) long (ldl/p2m3L ≥ 0.40) [ldl = lower diastema length; p2m3L = length from the anterior end of p2 to the posterior end of m3]. [modified]

30 (38). relative location of mental foramen: (0) anterior to the p2; (1) directly ventral to the p2.

31 (39). orientation of anterior margin of ascending ramus of mandible in lateral view: (0) projects vertically and posteriorly, not anteriorly (does not overlie the m3); (1) projects anteriorly as well as vertically below the coronoid process, often lies dorsal to m3.

32 (40). depth of horizontal ramus below m3: (0) shallow (m3 depth <18 % mandible length); (1) deep (m3 depth > 18 % of mandible length) [modified from Hulbert 2010: #40].

33 (41). relative height of crown in cheek teeth: (0) short, relatively brachydont; (1) taller.

34 (42). morphology and size of I3: (0) I3 incisiform, about same size as I2; (1) I3 caniniform, much larger than I2 [Colbert 2005: #3].

35 (45). P2 AW/PW ratio (anterior width/posterior width): (0) on average, less than or equal to 0.85; (1) on average, more than 0.85.

36 (46). P2 lingual cingulum: (0) complete; (1) absent or “broken” [modified from Colbert 2005: #29]

37 (47). transverse lophs on P2-P4 and p2-p4: (0) poorly separated; (1) well separated.

38 (48). P2 protoloph: (0) does not reach ectoloph; (1) just reaches base of ectoloph.

39 (49). P3 protoloph: (0) does not reach ectoloph or just reaches base of ectoloph; (1) merges midway or higher onto ectoloph [modified].

40 (51). P2 metaloph: (0) does not reach ectoloph or just reaches base of ectoloph; (1) merges midway or higher onto ectoloph [modified].

41 (54). P3 and P4 protocone and hypocone: (0) closely appressed and merged with wear; (1) widely separated.

42 (55). parastyle development in P3-M3: (0) moderate, parastyle height less than 50 % of paracone height; (1) strong, parastyle height more than 50 % of paracone height, but parastyle smaller than paracone; (2) very strong, parastyle height equal to paracone height [modified].

43 (56). labial cingulum on posterior half of upper cheek teeth: (0) present on half or more of P3-M3; (1) absent or very rare in P3-M3.

44 (67). i1 morphology and size: (0) i1 larger than i2, not procumbent or slightly procumbent; (1) i1 much larger than i2, very procumbent and spatulate. [modified].

45 (69). length of p2 relative to p3: (0) short, (p2 L)/(p3 L) less than 1.1; (1) long, (p2L)/(p3L) ratio more than 1.1.

46 (70). p2 hypoconid and entoconid: (0) not joined by complete hypolophid; (1) connected by hypolophid.

47 (72). relative height of unworn protolophid and hypolophid (or hypoconid/entoconid if no hypolophid) in premolars: (0) protolophid distinctly taller than hypolophid; (1) the two are approximately equal in height.

48 (73). cristid obliqua on p3: (0) strong, blocks interlophid valley labially; (1) very weak or absent.

49 (74). cristid obliqua on p4: (0) strong, blocks interlophid valley labially; (1) very weak or absent.

50 (78). relative length of limbs (comparing length of femur and dentary): (0) relatively long limbs (femur greatest length longer than that of dentary); (1) relatively short limbs (femur length less than or equal to that of dentary).

Appendix 2. Taxon-Character Matrix

Table 4 Character numbers in top row correspond to those in Appendix 1. "?" indicates an unknown or non applicable character state. *a*=0 or 1. Numbers in bold correspond to character states revised and coded different from the original matrix of Hulbert and Wallace (2005) or Ferrero and Noriega (2007)

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Colodon occidentalis	0	0	**0**	0	0	?	?	?	?	?	0	0	0	0	0	?	0	1	0	0	0	0	0	0	0	?	?
Nexuotapirus marslandensis	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	?
Miotapirus harrisonensis	?	?	?	?	?	?	?	?	0	0	0	0	?	0	?	?	0	0	?	0	0	0	0	0	?	?	?
Plesiotapirus yagii	0	?	?	0	0	?	?	?	1	?	0	0	0	0	0	?	?	?	?	0	?	0	0	?	?	?	0
Paratapirus helvetius	0	?	0	0	0	?	?	?	0	0	0	0	0	0	0	?	0	0	?	0	1	0	0	0	0	?	?
Tapirus johnsoni	0	**1**	0	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	1	1	0
T. webbi	?	?	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	?	1	1	0
T. polkensis	a	0	1	0	0	0	1	1	0	0	1	1	1	0	0	1	1	1	0	1	1	0	0	0	1	0	1
T. lundeliusi	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	1	0	1	0	1
T. haysii	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	0	0	0	1	1	0	1	0	1
T. veroensis	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	0	0	**1**	1	1	0	1	0	0
T. mesopotamicus	0	0	1	0	**1**	?	?	?	?	?	0	0	0	1	0	0	1	1	1	0	1	0	0	0	1	1	?
T. cristatellus	0	1	0	0	1	1	1	1	1	1	0	0	1	?	?	1	1	1	1	0	1	0	0	0	?	?	1
T. rondoniensis	0	0	1	1	1	?	?	?	?	?	0	0	0	1	0	0	1	1	1	0	1	0	0	0	1	0	0
T. bairdii	1	?	1	0	1	0	**0**	1	0	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	1	0	**0**
T. pinchaque	0	0	**1**	0	0	1	**1**	0	0	1	0	0	0	0	1	0	1	1	1	0	1	0	0	1	1	1	0
T. terrestris	0	1	0	1	1	?	?	**0**	0	a	0	0	0	1	0	0	1	1	1	0	1	0	0	1	1	1	0
T. indicus	1	?	1	1	0	1	0	1	1	1	1	1	1	0	0	1	1	1	1	0	1	0	0	0	1	1	0

	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Colodon occidentalis	?	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0
Nexuotapirus marslandensis	0	0	0	0	?	?	0	1	?	1	0	0	0	0	0	0	0	0	1	0	0	0	0	?
Miotapirus harrisonensis	?	1	0	0	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	?
Plesiotapirus yagii	0	?	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	1	?
Paratapirus helvetius	?	?	0	?	?	?	0	1	0	0	0	1	1	0	0	0	0	?	?	?	0	?	?	?
Tapirus johnsoni	0	0	1	0	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0
T. webbi	0	?	1	1	0	0	1	1	1	1	1	0	0	0	1	1	0	1	0	1	1	0	1	0
T. polkensis	1	1	0	1	0	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	0	1	?
T. lundeliusi	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	2	1	1	1	1	1	0	1	1
T. haysii	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1
T. veroensis	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	0
T. mesopotamicus	?	1	?	?	?	?	1	1	1	1	?	1	?	0	1	1	0	?	?	?	?	?	?	?
T. cristatellus	0	?	?	?	?	?	1	1	1	1	1	1	1	0	1	1	0	?	?	?	?	?	?	?
T. rondoniensis	0	?	?	?	?	?	1	1	1	1	1	0	1	0	1	1	1	?	?	?	?	?	?	?
T. bairdii	0	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	**1**	1	0
T. pinchaque	0	1	1	1	0	0	1	1	1	1	1	0	0	0	1	1	0	1	0	?	1	0	?	0
T. terrestris	0	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	0
T. indicus	0	1	1	1	0	0	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	?

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