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A taxonomic and biogeographic review of the fossil tapirs from Bolivia

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Fossil remains of South American tapirs are often fragmentary and scarce compared with those of other mammals that entered South America during the "Great American Biotic Interchange". Here, we review and add to the Pleistocene tapir remains from the Tarija Valley (Bolivia), and provide a taxonomic re-evaluation of *Tapirus tarijensis*. *T. tarijensis* was a large-sized animal, approximating the size of the living Malaysian *T. indicus* and the extinct North American *T. haysii.* The geographical distribution of Pleistocene records of *Tapirus* in South America indicates that *T. tarijensis* was the only known species inhabiting the Tarija Valley during this time.

Key words: Mammalia, Perissodactyla, tapirs, *Tapirus tarijensis*, Quaternary, Tarija Valley, South America.

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Introduction

Fossil tapirs (Perissodactyla: Tapiridae) are known from Europe, North America, South America and Southeast Asia, including China (e.g., Cerdeño and Ginsburg 1988; Hulbert 2005; Tong 2005; Ferrero and Noriega 2007; Holanda et al. 2011, Medici 2011, Scherler et al. 2011). In South America, the family is only represented by *Tapirus* Brisson, 1762, with the oldest reliable records of the genus dating to the Early–Middle Pleistocene of the Pampean region of Argentina (see Tonni 1992; Soibelzon 2005; Soibelzon et al. 2008). All of the living tapirs occurring in South America today (*T. bairdii* [Gill, 1865]; *T. pinchaque* [Roulin, 1829] and *T. terrestris* [Linnaeus, 1758]) also belong to this genus.

Although remains of *Tapirus* are often fragmentary and scarce compared with other mammalian migrants that took part in the "Great American Biotic Interchange" (Woodburne et al. 2006; Webb 2006), the fossil record of South American tapirs has substantially improved in recent years, and now comprises material from Argentina, Brazil, Peru, Uruguay, and Venezuela (e.g., Ubilla 1983, 2004; Marshall et al. 1984; Hoffstetter 1986; Tonni 1992; Ferrero and Noriega 2003, 2007; Holanda and Cozzuol 2006; Ubilla and Rinderknecht 2007; Holanda et al. 2007, 2011; Ferrero et al. 2007, 2009; Holanda and Rincón 2012).

In Bolivia, finds of fossil tapirs are restricted to the Tarija Valley (Fig. 1). The first tapirid specimen from this locality was described by Ameghino (1902), who erected the new species *Tapirus tarijensis* based on a poorly preserved mandibular fragment bearing pm2–pm4 in situ. Subsequent studies generally followed this assignment (e.g., Hoffstetter 1963; Marshall and Sempere 1991; Takai et al. 1982, 1984), but did not discuss the diagnostic features of this species, with the exception of its relatively large size (Boule and Thevenin 1920).

Here, we provide a detailed morphological description of the holotype and new referred material of *Tapirus tarijensis*,

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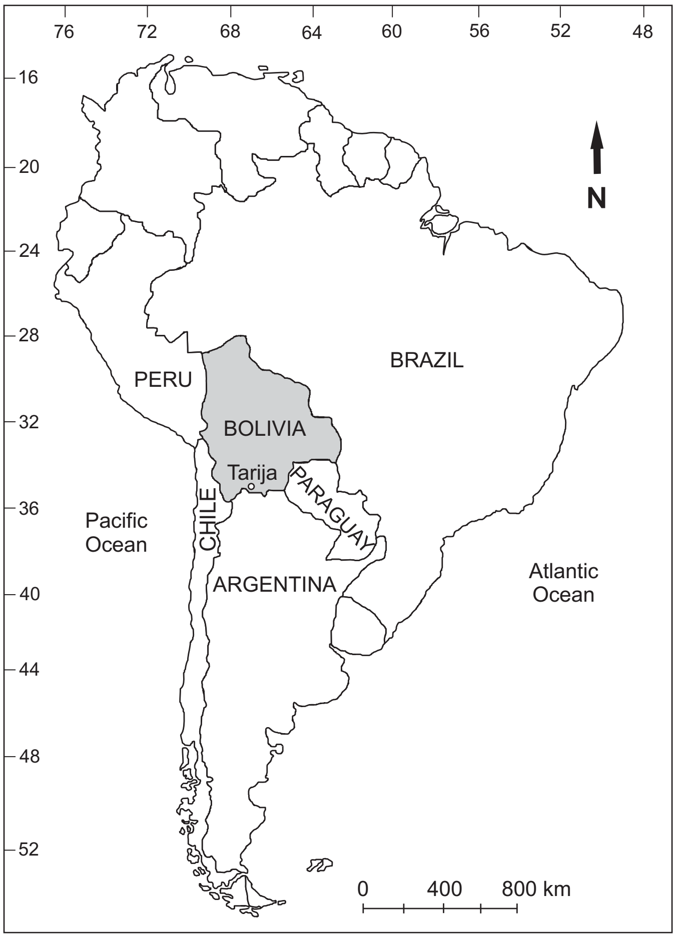

Fig. 1 Geographic map showing the location of Tarija Valley within Bolivia.

and discuss its diagnostic features and taxonomy. In addition, we describe some additional material referable to *Tapirus* sp. from the Tarija Valley, and briefly comment on the geographical distribution of the genus during the Pleistocene–Holocene of South America.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CICYTTP, Colección Paleontológica, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Argentina; CRK, Coleção de Referência Zoológica Renato Kipnis, Laboratório de Estudos Evolutivos e Humanos, Universidade de São Paulo, São Paulo, Brazil; F:AM, Frick Fossil Mammal Collection, American Museum of Natural History, New York, USA; MACN-M, Colección de Mastozoología del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MACN-PV, Colección Paleontología Vertebrados del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Estado do Rio Grande do Sul; MHN, Museu de História Natural, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Museo Nacional de Historia Natural de Montevideo, Uruguay; MNHN-TAR, Museum national d'Histoire naturelle de Paris, France, Tarija Collection; MNPA-V, Museo Nacional Paleontológico-Arqueológico, Universidad Autónoma Juan Misael Saracho, Tarija, Bolivia; MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; UNIR, Universidade Federal de Rondônia, Porto Velho, Brazil; UF, Florida Museum of Natural History, Gainesville, USA; UFMG, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil.

Other abbreviations.—PCA, Principal Component Analysis.

Material and methods

The present analysis is mainly based on specimens collected from 1978 to 1980 by researchers of The Research Institute of Evolutionary Biology located in Tokyo, Japan (see Takai et al. 1982, 1984), as well as material that arose from expeditions organized by staff of the University of Florida, USA (MacFadden et al. 1983, 1994; MacFadden and Shockey 1997; MacFadden 2000). Measurements of teeth and metapodial elements were obtained using calipers, following Simpson (1945) and Hulbert (2005), and are reported in Tables 1–4 and the Supplementary Online Material (SOM available at http://app.pan.pl/SOM/app59-Ferrero_etal_SOM.pdf). Where sample size permitted, the material from Tarija was compared with *T. terrestris* using Student's t-tests, performed in PAST v. 2.16 (Hammer et al. 2001). In addition, we used Principal Component Analysis (PCA) to quantify the observed variation in the dental measurements, and compare *T. tarijensis* with a range of other living and fossil tapirs, including *T. indicus*, *T. haysii*, *T. johnsoni*, *T. rondoniensis*, *T. simpsoni*, *T. terrestris*, *T. veroensis*, and *T. webbi* (Fig. 6, Table 5). *T. cristatellus*, *T. greslebini*, *T. mesopotamicus*, and *T. rioplatensis* could not be included in our PCA owing to their relatively poor or incomplete state of preservation.

Geological setting

The age of the sediments from the Tarija Valley is controversial (Tonni et al. 2009; Soibelzon et al. 2011). Despite discrepancies regarding the chronology of the fossil-bearing sediments, and especially the disparity between fossil-bearing localities and dated stratigraphic columns, some authors (e.g., Takai et al. 1982, 1984; Alberdi and Prado 2004) assigned the entire fauna exclusively to the Ensenadan (Early Pleistocene) of the Pampean regional time scale (see Fig. 1 in Soibelzon et al. 2009) or to the "Ensenadan Land Mammal Age" (Marshall et al. 1984; MacFadden 2000), although Marshall et al. (1984: 33) mentioned the possibility "that some fossils from this locality are younger". By contrast, radiocarbon dating of organic levels from several different localities suggests a Late Pleistocene age (between 27180 and 39000 ^{14}C BP) for the fossiliferous strata (Coltorti et al. 2007). Following Tonni et al. (2009), we consider the mammalian fauna of Tarija to represent neither exclusively the Ensenadan Stage/Age (Early to Middle Pleistocene) nor the Lujanian Stage/Age (Late Pleistocene to early Holocene), as it contains several taxa typical of either: at least 3 species only occurring in the Ensenadan *Mesotherium cristatum* Biozone and 10 species typical of the Lujanian *Equus* (*Amerhippus*) *neogaeus* Biozone (see Tonni et al. 2009 and bibliography cited therein).

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Perissodactyla Owen, 1848

Family Tapiridae Burnett, 1830

Genus *Tapirus* Brisson, 1762

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

Tapirus tarijensis Ameghino, 1902

Fig. 3A.

Lectotype: MACN-PV-1523, left mandible with pm2–pm4 (Ameghino 1902: 247–248, pl. 5: 22a, b).

Type locality: Tarija Valley, Bolivia (Fig. 1).

Type horizon: Pleistocene, "Pampean formation" (sensu Carles 1888).

Referred material.—MNPA-V 006038, palatal fragment bearing PM1–M2 and an unerupted M3 (Fig. 3B); MNHN-TAR 843, partial left maxilla bearing PM2–M2 (Fig. 3C); MNHN-TAR 842, left mandible with dpm2–dpm4, m1 (Fig. 3D); MNHN-TAR 847, partial right mandible with fragmentary m1 and complete m2–m3 (Fig. 3E); MNHN-TAR 846 partial left mandible with m1–m2 and broken m3 (root) (Fig. 3F); MNPA-V485, partial right mandible with pm2–pm3 (Fig. 4A); MNPA-V1437, partial right mandible with pm2–m2 (Fig. 4B); MNPA-V1448, partial left mandible with m2?–m3? (Fig. 4C); MNPA-V1446, partial right mandible with pm3–m1 (Fig. 4D); MNPA-V1447, partial left mandible with pm4–m2 (Fig. 4E); MNPA-V1445 partial right mandible with m2? (Fig. 4F); MNPA-V 5942, partial mandible of a juvenile specimen with some molariform teeth and an unerupted left m1?, right m2?, left pm3–pm4, right pm3, mandibular symphysis with right i1–i2 and left i1–i3 (Fig. 4G); MNHN-TAR 844, partial left mandible with m3 (Fig. 5A); MNHN-TAR 845, right mandible with pm4–m3 (Fig. 5B); UF 91589, partial left mandible with partial pm4, m1–m3, mandibular symphysis, and partial right mandible bearing m2–m3 (Fig. 5C); AMNH 55999, left mandible with pm2–m3. Tarija Valley (Bolivia), Pleistocene.

Table 1. Summary statistics for the upper teeth of *Tapirus terrestris* (see Supplementary Online Material) and measurement values for *Tapirus tarijensis*. Abbreviations: AW, greatest anterior width; CV, coefficient of variation; L, length; MAX, maximum; MIN, minimum; N, sample size; PW, greatest posterior width; s, standard deviation; x, sample mean.

	Tapirus terrestris					*Tapirus tarijensis*	
	N	MIN–MAX	x	s	CV	MNPA.V 006038	MNHN–TAR 843
P1 L	47	14.50–21.00	16.85	1.5	9.73	17.00	–
P1 W	47	12.20–19.80	15.53	1.43	9.18	17.70	–
P2 L	51	14.60–20.35	17.84	1.34	7.70	19.00	24.8
P2 AW	51	16.60–21.00	18.81	1.04	6.20	22.00	22.2
P2 PW	51	18.35–23.95	21.13	1.25	6.13	23.00	25.6
P3 L	53	16.30–21.74	19.25	1.15	6.26	22.00	–
P3 AW	53	20.05–25.30	22.69	1.15	5.13	25.60	–
P3 PW	53	20.40–25.30	22.78	1.22	5.49	24.80	–
P4 L	45	16.70–22.45	19.81	1.13	5.96	21.00	–
P4 AW	45	21.00–27.40	24.59	1.39	5.67	26.20	–
P4 PW	45	19.00–27.20	23.66	1.71	7.41	24.10	–
M1 L	52	16.15–23.55	20.25	1.33	6.78	22.67	26.4
M1 AW	52	21.50–27.70	23.32	1.04	4.56	26.06	31.0
M1 PW	52	18.80–24.30	20.96	1.13	5.82	23.40	27.0
M2 L	48	19.10–25.36	22.85	1.42	6.75	25.00	25.8
M2 AW	48	22.84–30.90	25.85	1.59	6.43	30.20	34.8
M2 PW	48	19.00–25.70	22.44	1.31	5.74	22.90	30.2

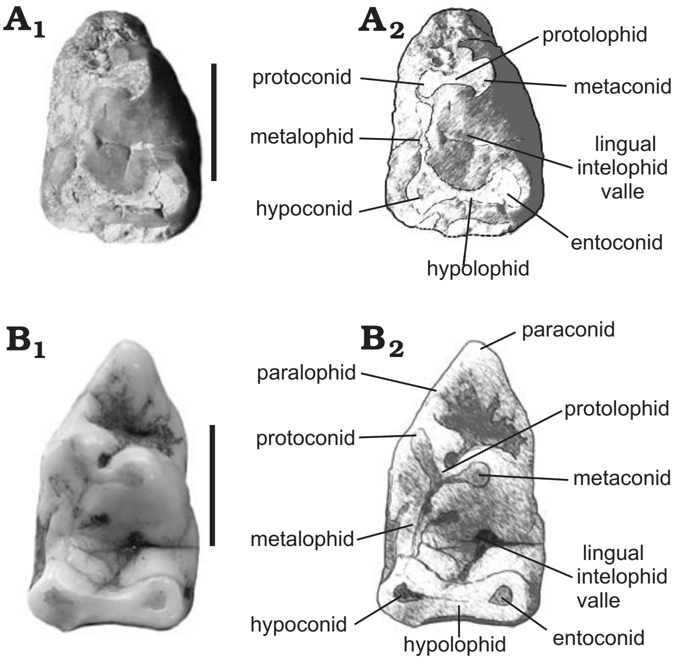

Fig. 2. Photographs (A_1, B_1) and explanatory drawings (A_2, B_2) of the left pm2 of tapirs *Tapirus tarijensis* Ameghino, 1902, MACN-PV-1523 from Tarija Valley (Bolivia), Pleistocene (**A**) and *Tapirus terrestris* (Linnaeus, 1758), CICYTTP-M-1-4, from Parque Nacional Iguazú, Misiones (Argentina), Recent (**B**), in occlusal views. Scale bars 10 mm.

Emended diagnosis.—Differs from all extant tapirs in having an accessory cusp on the lingual side of the paraconid of dpm2, as well as a pm2 characterized by a metalophid (or oblique cristid) originating at the base of the hypoconid and extending anteriorly to the base of the protoconid in an almost straight line, as well as a trapezoidal lingual interlophid valley; differs from *T. mesopotamicus*, *T. rondoniensis*, and extant South American tapirs in its larger size, and from *T. rioplatensis*, *T. mesopotamicus*, and extant South American tapirs in its more robust and dorsoventrally higher

Table 2. Summary statistics for the permanent lower teeth of *Tapirus* (see Supplementary Online Material). The two rightmost columns in *Tapirus tarijensis* show the results of a two-tailed t-test for significant differences in relation to *Tapirus terrestris*. Abbreviations: AW, greatest anterior width; CV, coefficient of variation; (D), deciduous tooth; L, length; MAX, maximum; MIN, minimum; N, sample size; ns, not significant (p >0.05); PW, greatest posterior width; s, standard deviation; x, sample mean. Values marked with an asterisk are from Perini et al. (2011).

	Tapirus terrestris				*Tapirus tarijensis*							*T. rioplatensis*
	N	MIN–MAX	x	s	N	MIN–MAX	x	s	CV	t	p	MACN 15735
p3 L	50	17.85–23.45	20.01	1.20	3	22.80–24.00	23.50	0.62	4.350	4.951	p <0.05	29.00
p3 AW	50	13.00–18.00	15.11	1.03	3	15.30–17.60	16.30	1.18	6.250	1.933	ns	18.00
p3 PW	50	13.00–19.00	15.75	1.24	3	15.00–18.30	16.77	1.66	9.170	1.353	ns	–
p4 L	42	18.20–22.70	20.40	1.15	5	23.00–26.50	24.76	1.29	4.670	7.895	p <0.05	28.00 (D)
p4 AW	42	14.22–18.50	16.78	0.99	5	15.00–21.00	17.62	2.69	14.99	1.419	ns	21.00 (D)
p4 PW	42	14.90–20.40	17.52	1.20	5	13.00–20.10	17.08	3.11	18.54	0.635	ns	20.00 (D)
m1 L	51	17.00–22.60	20.54	1.22	7	22.00–26.20	24.47	1.76	7.020	7.555	p <0.05	28.00
m1 AW	50	14.70–18.45	16.54	0.84	7	17.00–21.20	19.43	1.64	8.220	7.434	p <0.05	23.00
m1 PW	51	13.50–18.80	15.69	0.99	7	16.00–20.00	18.38	1.34	7.410	6.445	p <0.05	20.00
m2 L	46	19.45–26.72	23.45	1.58	7	21.10–29.10	26.56	2.79	10.24	4.323	p <0.05	–
m2 AW	45	16.00–20.50	18.07	0.96	7	20.00–21.70	20.70	0.57	2.620	7.023	p <0.05	–
m2 PW	46	15.30–20.15	17.46	1.08	7	19.10–21.00	19.87	0.69	3.830	5.679	p <0.05	–
m3 L	27	22.35–27.76	24.42	1.42	4	28.30–31.60	29.97	1.49	4.380	7.281	p <0.05	–
m3 AW	27	17.30–20.60	18.73	0.88	4	20.00–21.60	20.97	0.77	2.820	4.804	p <0.05	–
m3 PW	26	15.20–19.00	16.64	1.05	4	17.80–22.00	20.17	1.78	10.44	5.705	p <0.05	–

	*Tapirus pinchaque**				*Tapirus indicus**				*Tapirus bairdi**			
	N	MIN–MAX	x	s	N	MIN–MAX	x	s	N	MIN–MAX	x	s
p2 L	0	–	–	–	8	22.25–26.38	23.92	1.52	7	20.32–22.50	21.32	0.78
p2 A	0	–	–	–	8	12.40–15.70	13.92	0.98	7	11.03–13.40	12.57	0.75
p3 L	3	20.10–20.90	20.57	0.42	8	20.49–25.41	22.71	1.78	8	18.11–21.28	20.24	0.99
p3 AW	3	12.70–14.00	13.47	0.68	8	13.99–16.86	15.76	1.02	8	12.70–14.72	13.69	0.71
p3 PW	3	14.00–15.70	14.87	0.85	8	16.15–18.83	17.57	0.92	8	14.51–17.76	16.42	1.27
p4 L	1	–	20.00	–	7	20.19–23.90	22.15	1.08	8	18.66–21.92	20.59	1.22
p4 AW	1	–	14.60	–	7	17.10–18.53	18.10	0.47	8	14.86–17.05	15.94	0.81
p4 PW	1	–	15.30	–	7	18.20–19.42	18.89	0.47	8	15.63–18.70	17.38	1.19
m1 L	4	20.30–22.70	21.33	1.01	9	19.78–25.15	23.29	1.68	8	18.25–21.46	20.46	1.09
m1 AW	4	15.30–17.40	16.33	1.08	9	17.35–19.31	18.39	0.60	8	15.09–17.68	16.67	0.87
m1 PW	4	14.30–16.20	15.15	0.83	9	15.30–18.00	17.07	0.93	8	14.40–17.13	15.93	0.97
m2 L	3	22.80–23.90	23.20	0.61	6	22.80–27.33	24.95	1.79	8	20.10–23.47	22.14	1.10
m2 AW	3	17.10–18.30	17.60	0.62	6	19.20–20.86	19.93	0.69	8	16.17–18.78	17.74	0.89
m2 PW	3	15.60–17.70	16.60	1.05	6	18.15–19.47	18.80	0.55	8	15.70–18.88	17.27	1.23
m3 L	0	–	–	–	6	23.70–27.38	25.86	1.24	7	21.33–24.28	22.88	1.08
m3 AW	0	–	–	–	6	17.50–21.26	19.68	1.30	7	16.78–18.51	17.82	0.61
m3 PW	0	–	–	–	6	15.70–18.86	17.71	1.10	7	15.63–17.52	16.56	0.72

mandible; shares a well-developed cingulid on pm3 with *T. rioplatensis*, *T. veroensis*, *T. haysii*, and *T. lundeliusi*, but not *T. webbi*, *T. jonhsoni*, and *T. polkensis*; resembles *T. indicus*, *T. haysii*, *T. oliverasi*, *T. cristatellus*, *T. greslebini*, and *T. rioplatensis* in terms of size; shares with all other tapirs a mesial cingulid better developed on pm3 than on pm4; resembles all other tapirs except *T. greslebini* in the morphology of the upper molars.

Description.—The lectotype comprises a partial left mandible bearing pm2–pm4 (Figs. 2A, 3A; SOM: table S1). The mandible is robust and every tooth is worn. The pm2 is broken anterior to the protoconid (the paralophid and paraconid are not preserved). In occlusal view, the metaconid and the protoconid are transversely aligned (Fig. 2A), unlike in other tapirs, in which the protoconid is located more mesially (Fig. 2B). The metaconid is developed as a strong, high cusp. The metalophid (or oblique cristid) originates at the base of the hypoconid and extends anteriorly to the base of the protoconid in an almost straight line, thus resulting in a trapezoidal lingual interlophid valley (Fig. 2A). By contrast, the metalophid follows an oblique route and terminates between the protoconid and the metaconid in other tapirs (Fig. 2B). The pm3 is worn and broken at the level of the protolophid. The hypoconid is not preserved. The mesial cingulid is prominent and better developed than in extant South American tapirs. The pm4 is the best preserved tooth, and

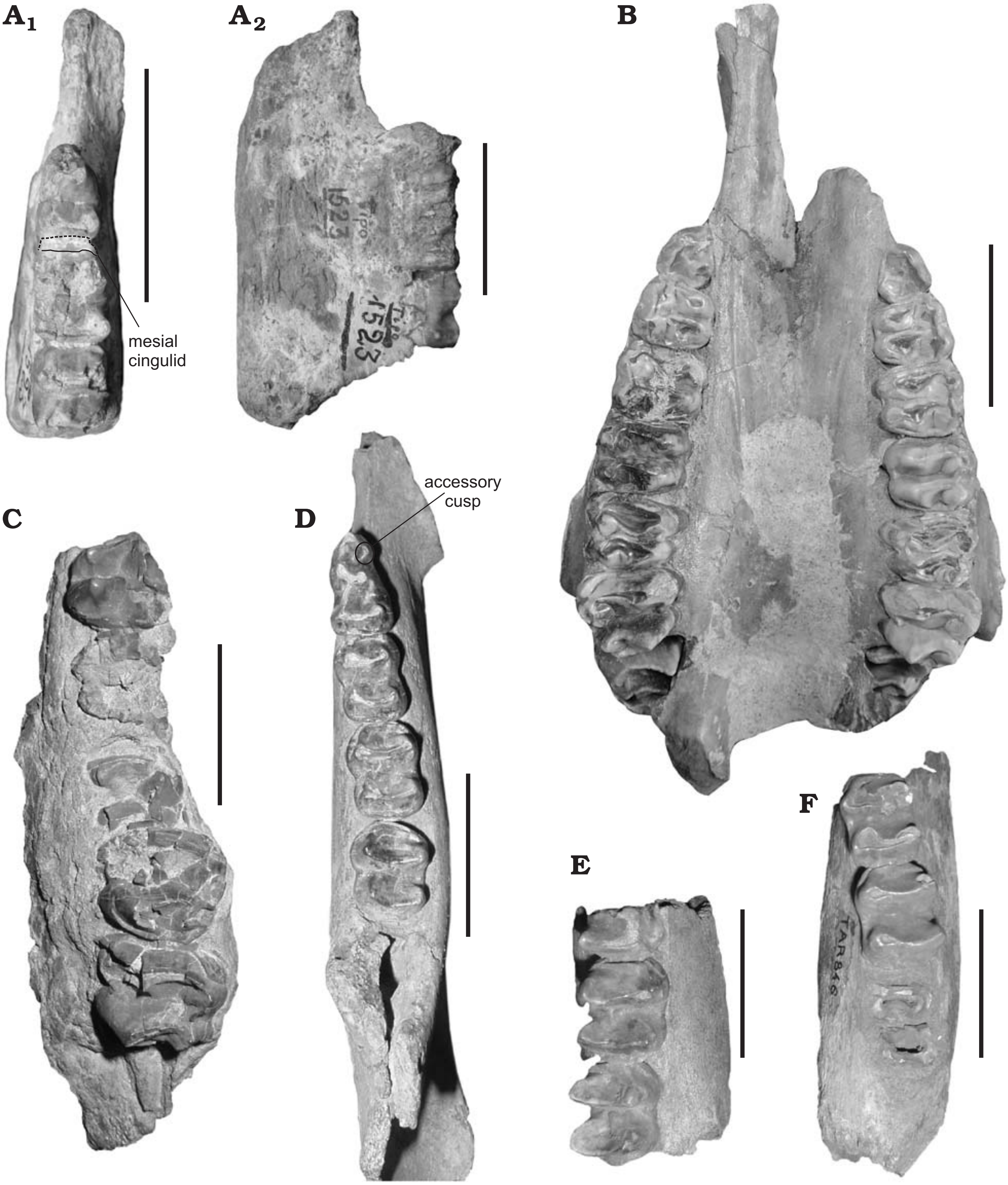

Fig. 3. Pleistocene tapir *Tapirus tarijensis* Ameghino, 1902, from Tarija Valley (Bolivia). **A**. MACN-PV-1523, left mandible, in dorsal (A_1), and lateral (A_2) views. **B**. MNPA-V 006038, palatal fragment, in ventral view. **C**. MNHN-TAR 843, partial left maxilla, in ventral view. **D**. MNHN-TAR 842, left mandible, in dorsal view. **E**. MNHN-TAR 847, partial right mandible, in dorsal view. **F**. MNHN-TAR 846, partial left mandible, in dorsal view. Scale bars 50 mm.

bears a mesial cingulid less developed than that of pm3, as also seen in *T. terrestris.* The posterior border of pm4 bears a poorly developed distal cingulid, showing a subtle slope where its dorsalmost portion would have approximated the base of the hypoconid.

Comparative description.—Most of the studied specimens represent incomplete cranial and mandibular fragments. Judging from the dental measurements (Tables 1–3; Fig. 6; SOM), *Tapirus tarijensis* is larger than *T. mesopotamicus*, *T. rondoniensis* and all of the extant South American tapirs,

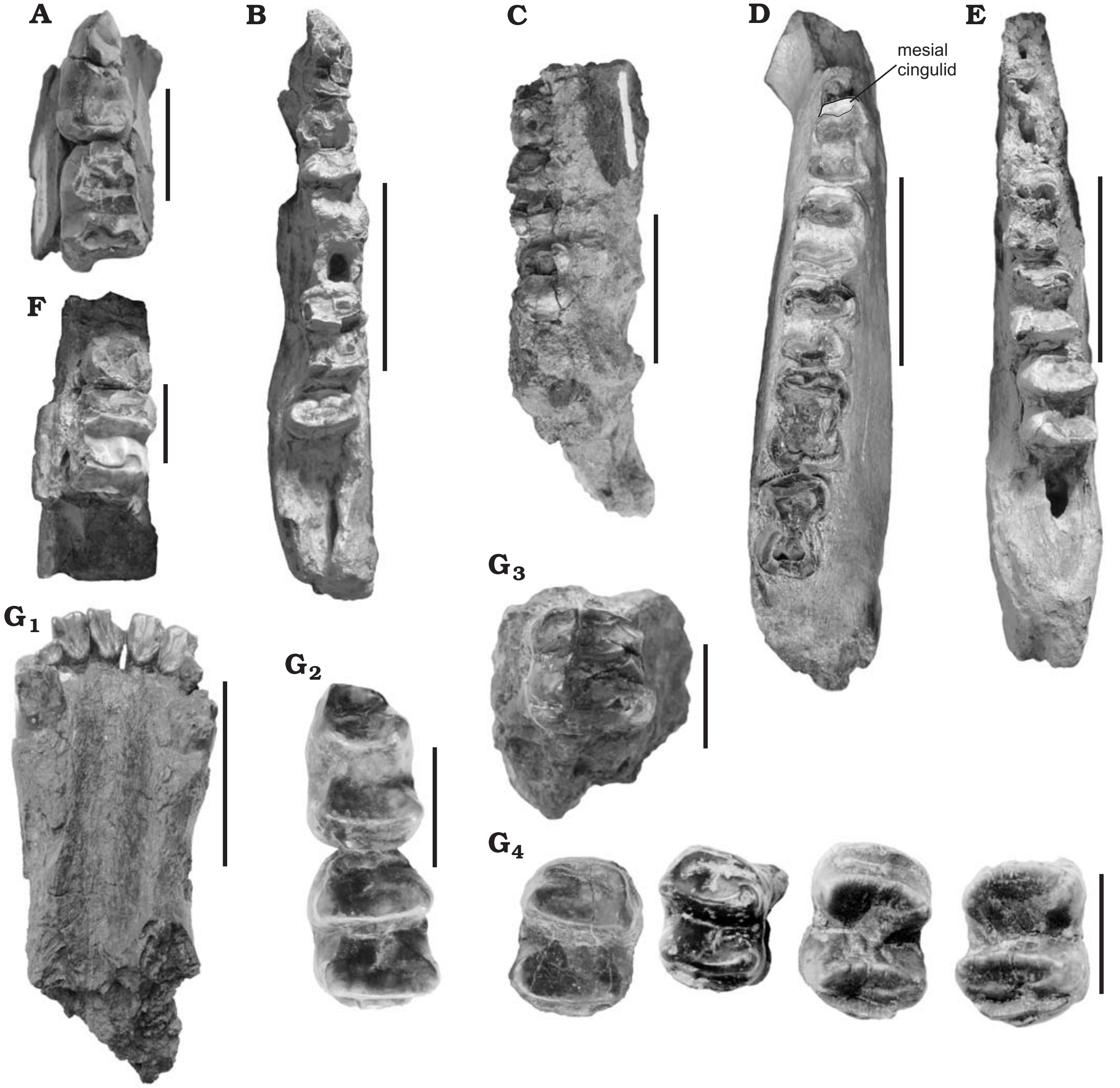

Fig. 4. Pleistocene tapir *Tapirus tarijensis* Ameghino, 1902, from Tarija Valley (Bolivia). **A**. MNPA-V485, partial right mandible, in dorsal view. **B**. MNPA-V1437, partial right mandible, in dorsal view. **C**. MNPA-V1448, partial left mandible, in dorsal view. **D**. MNPA-V1446, partial right mandible, in dorsal view. **E**. MNPA-V1447, partial left mandible, in dorsal view. **F**. MNPA-V1445, partial right mandible, in dorsal view. **G**. MNPA-V 5942, mandibular symphysis (G_1); left pm3–pm4 (G_2); right M2? (G_3); right pm3, left m1? and two unerupted m1? (G_4); all in dorsal/occlusal view. Scale bars in A, F, and G_2–G_4,10 mm; in B–E and G_1, 50 mm.

slightly smaller than *T. rioplatensis*, and at least partially overlaps with the size range of *T. cristatellus*, *T. greslebini* (see Holanda and Ferrero 2013), *T. oliverasi*, and *T. indicus*. Its PM1 resembles that of other species of *Tapirus* (except *T. pinchaque*) in being subtriangular in occlusal view and in bearing a well-developed hypocone. The PM2 is molariform and characterized by a well-developed protocone and hypocone. As in all living and fossil American tapirs except *T. pinchaque* and *T. rondoniensis*, the protoloph reaches the base of the ectoloph. The parastyle is poorly developed on PM2, better developed on PM3–PM4, and strongly developed on M1 and especially M2, similar to all other American tapirs. It is presently unclear whether a well-developed parastyle also occurs on M3, since the latter is so far only known from unerupted teeth (e.g., MNPA-V 006038); however, it is likely that M3 resembles M2 in this regard. As in other tapirs, there are no lingual cingula on any of the cheek teeth. The morphology of the upper molars resembles that of other

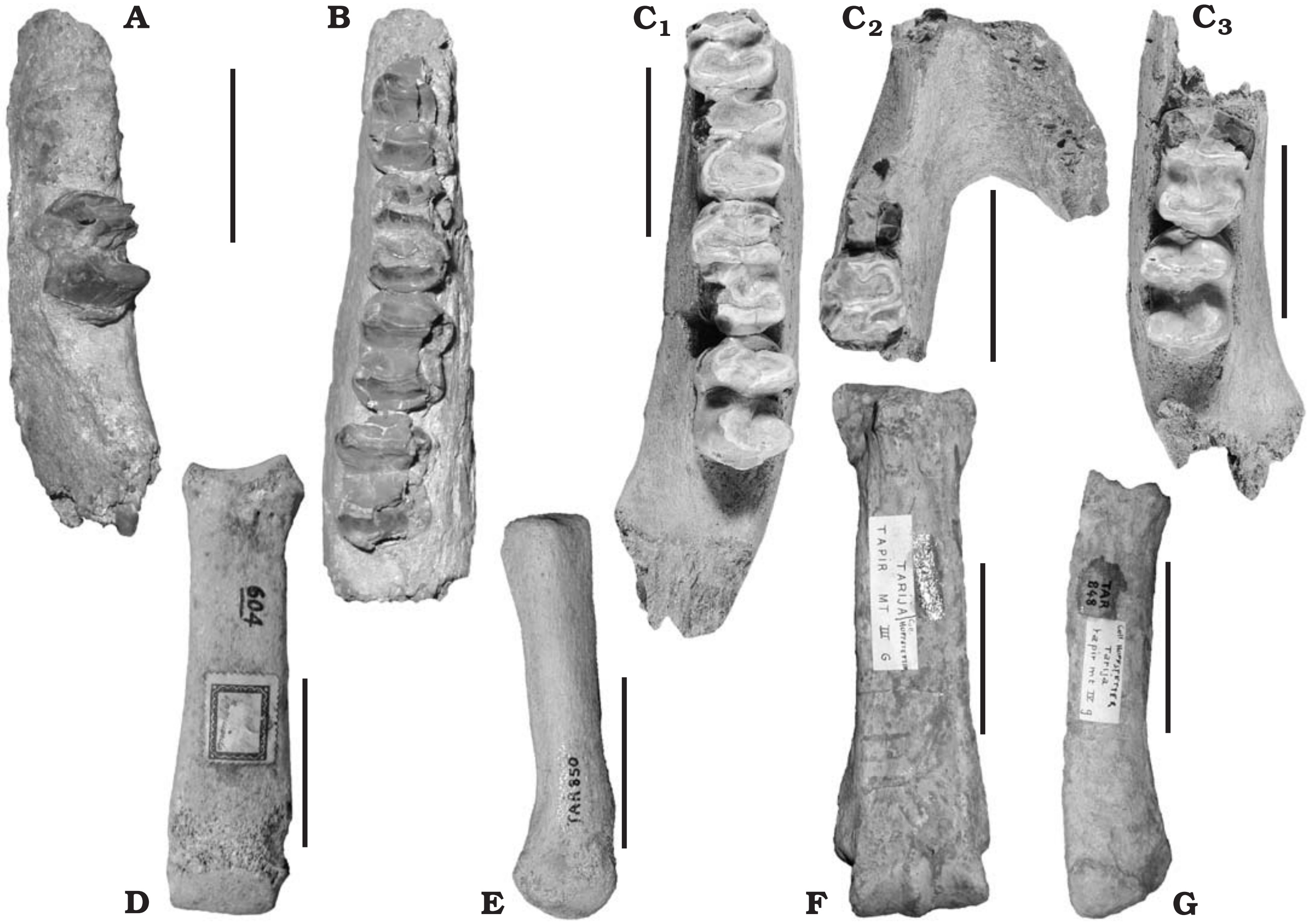

Fig. 5. Pleistocene tapirs from Tarija Valley (Bolivia). **A**–**C**. *Tapirus tarijensis* Ameghino, 1902. **A**. MNHN-TAR 844, partial left mandible, in dorsal view. **B**. MNHN-TAR 845, right mandible, in dorsal view. **C**. UF 91589, partial left mandible (C_1), mandibular symphysis (C_2), and partial right mandible (C_3), all in dorsal view. **D**–**G**. *Tapirus* sp. **D**. MACN-PV-604, left MC III, in anterior view. **E**. MNHN-TAR 850, right MT IV, in anterior view. **F**. MNHN-TAR 849, left MC III, in anterior view. **G**. MNHN-TAR 848, left MT IV, in anterior view. Scale bars 50 mm.

species of *Tapirus* except *T. greslebini*, which is uniquely distinguished by a mesial subcingulum at the base of the parastyle, a well-marked labial cingulum between the distal wall of the paracone and the labiodistal portion of the metacone, and a small lingual cingulum between the protocone and the hypocone (Holanda and Ferrero 2013).

The lower border of the mandibular body is somewhat concave (MACN-PV 1523, MNPA-V 1447, 1437) or straight (AMNH 55999, MNPA-V 1446). The mandible of the juvenile specimen (MNHN-TAR 842) is robust and approximately 20% higher (at the level of m1) than that of *T. terrestris* at a comparable ontogenetic stage (Table 3). The dpm2 is rectangular in occlusal view, relatively robust and, unlike in any other species of *Tapirus*, bears an accessory cusp on the lingual side of the paraconid, with the two being connected by a relatively low, oblique crest. An accessory crest on dpm2 also occurs in other perissodatyles, such as rhinoceroses, in which it, however, corresponds to a bifurcation of the paralophid (Cerdeño and Sánchez 2000: 284). The dpm3 and

Table 3. Summary statistics for the deciduous premolars and the mandibular height of *Tapirus terrestris* (see Supplementary Online Material), and measurement values for *Tapirus tarijensis*. Abbreviations: AW, greatest anterior width; CV, coefficient of variation; Hm, dorsoventral height of the body of the mandible, measured at the level of m1; L, length; MAX, maximum; MIN, minimum; N, sample size; PW, greatest posterior width; s, standard deviation; W, width; x, sample mean.

	Tapirus terrestris					*T. tarijensis*
	N	MIN-MAX	x	s	CV	MNHN-TAR 842
dp2 L	11	17.35–24.85	23.13	2.07	8.96	24.10
dp2 W	11	12.00–18.00	14.06	1.78	12.68	20.10
dp3 L	11	19.50–22.00	20.56	0.77	3.76	28.00
dp3 AW	11	12.40–18.00	13.88	1.50	10.78	22.70
dp3 PW	11	12.40–19.00	14.20	1.72	12.12	20.30
dp4 L	14	19.90–22.70	21.46	0.88	4.08	25.90
dp4 AW	14	13.40–20.80	15.18	1.78	11.73	22.70
dp4 PW	14	13.24–18.70	14.69	1.29	8.81	22.10
Hm	14	29.50–54.00	40.12	8.42	20.99	55.00

Table 4. Summary statistics for the metapodials of *Tapirus terrestris* (see Supplementary Online Material), and measurement values for *Tapirus* sp. from Tarija and *Tapirus mesopotamicus*. Abbreviations: CV, coefficient of variation; DDP, dorsopalmar diameter of proximal portion of metacarpal and dorsoplantar diameter of metatarsals; L, length; MAX, maximum; MDB, mediolateral diameter of the body; MDD, mediolateral diameter of distal portion; MDP, mediolateral diameter of proximal portion; MIN, minimum; N, sample size; s, standard deviation; x, sample mean.

	Tapirus terrestris					*Tapirus* sp.		*T. mesopotamicus*
	N	MIN-MAX	x	s	CV			
Metacarpal III						MACN 604		
L	12	107.30–127.60	119.32	5.59	4.69	131.50		
DDP	12	20.30–25.60	23.39	1.36	5.81	26.00		
MDP	12	28.00–31.00	29.61	1.06	3.59	32.20		
MDB	12	23.60–27.30	25.57	1.15	4.49	28.00		
MDD	12	29.70–36.00	32.46	1.98	6.10	34.70		
Metatarsal III						MNHN-TAR 849		
L	13	106.6–125.5	119.05	4.77	4.01	148.20		–
DDP	13	24.30–29.00	26.76	1.45	5.42	–		24.30
MDP	13	27.20–31.00	28.98	1.34	4.62	40.00		–
MDB	13	22.36–27.10	24.38	1.42	5.83	30.10		28.70
MDD	13	29.22–37.10	31.96	2.24	7.01	43.30		37.80
Metatarsal IV						MNHN-TAR 848	MNHN-TAR 850	
L	12	97.10–110.10	102.94	3.38	3.29	123.10	113.20	–
DDP	12	18.40–24.40	21.33	1.67	7.85	–	–	25.00
MDP	12	18.30–24.70	21.57	1.89	8.74	29.30	25.90	–
MDB	12	16.00–20.10	18.05	1.39	7.68	23.00	20.30	16.81
MDD	12	21.00–30.40	26.75	2.74	10.25	29.60	30.00	23.00

dpm4 of *T. tarijensis* bear well-developed mesial cingulids, as also seen in deciduous teeth of *T. terrestris*.

Only two specimens (MNPA-PV-485 and AMNH 55999) preserve a complete pm2, which is characterised by a more robust talonid than in the extant South American species. No pm2 has been found for any of the other South American fossil tapirs (*T. mesopotamicus*, *T. rondoniensis*, *T. cristatellus*, *T. oliverasi, T. greslebini*, and *T. rioplatensis*).

The pm3 of *T. tarijensis* (MNPA-V485, 5942, 1437, 1446) resembles that of *T. rioplatensis, T. veroensis, T. haysii,* and *T. lundeliusi* in having a well-developed, mesiolingually extending cingulid originating at the level of the protoconid. By contrast, the mesial cingulid is less developed and originates at a more ventral position relative to the protoconid in all of the living and some fossil North American species, such as *T. webbi*, *T. jonhsoni*, and *T. polkensis*. No pm3 has yet been found for *T. mesopotamicus*, *T. oliverasi*, *T. greslebini*, *T. rondoniensis*, and *T. cristatellus*.

The pm4 is rectangular in occlusal outline and bears a well-developed cingulid, although the latter is less sharp and lower than that of pm3. This tooth is nearly indistinguishable in its morphology from that of other fossil and extant South American tapirs. Similarly, the lower molars of *T. tarijensis* generally resemble those of other members of the genus.

Stratigraphic and geographic range.—Pleistocene, Tarija Valley, Bolivia.

Tapirus sp.

Fig. 5D–F.

Referred material.—MACN-PV-604, left metacarpal III (Fig. 5D); MNHN-TAR 849, left metacarpal III (Fig. 5F); MNHN-TAR 848, left metatarsal IV (Fig. 5G); MNHN-TAR 850 right metatarsal IV (Fig. 5E) from the Tarija Valley, Bolivia, "Pampean formation" (sensu Carles, 1888).

Remarks.—All of referred elements are robustly built, but too worn to discern details of their morphology. Because they were not clearly associated with any dental material, these remains cannot be confidently assigned to *Tapirus tarijensis*.

Morphometric analyses

In terms of the lower tooth measurements, the material assigned to *T. tarijensis* is on average significantly larger than *T. terrestris* (Student's t-test, $p < 0.001$), with the exception of the width of the anterior and posterior lophids of p3 and p4 (Table 2). Small sample sizes prevented us from conducting statistical tests on the lower deciduous and upper tooth data, but the latter still generally seem to corroborate the size difference between the two species. Thus, although MNPA-V 006038 overlaps in its size with the largest specimens of *T. terrestris*, MNHN TAR-843 is 10–20% larger according to all measurements (Table 1). Similarly, MNHN-TAR 842 generally exceeds the size of the largest specimens of *T. terrestris* by 10–21% (Table 3).

In all of the Principal Component analyses, the first two principal components account for more than 80% of the total variation, with PC1 reflecting size in all cases (Fig. 6). The PCA of the upper teeth (Fig. 6A) revealed three groupings, comprising (i) *T. terrestris*, *T. rondoniensis*, *T. johnsoni*, and some specimens of *T. veroensis*; (ii) MNPA-V 006038 (referred to *T. tarijensis*), *T. veroensis*, *T. simpsoni*, *T. webbi*,

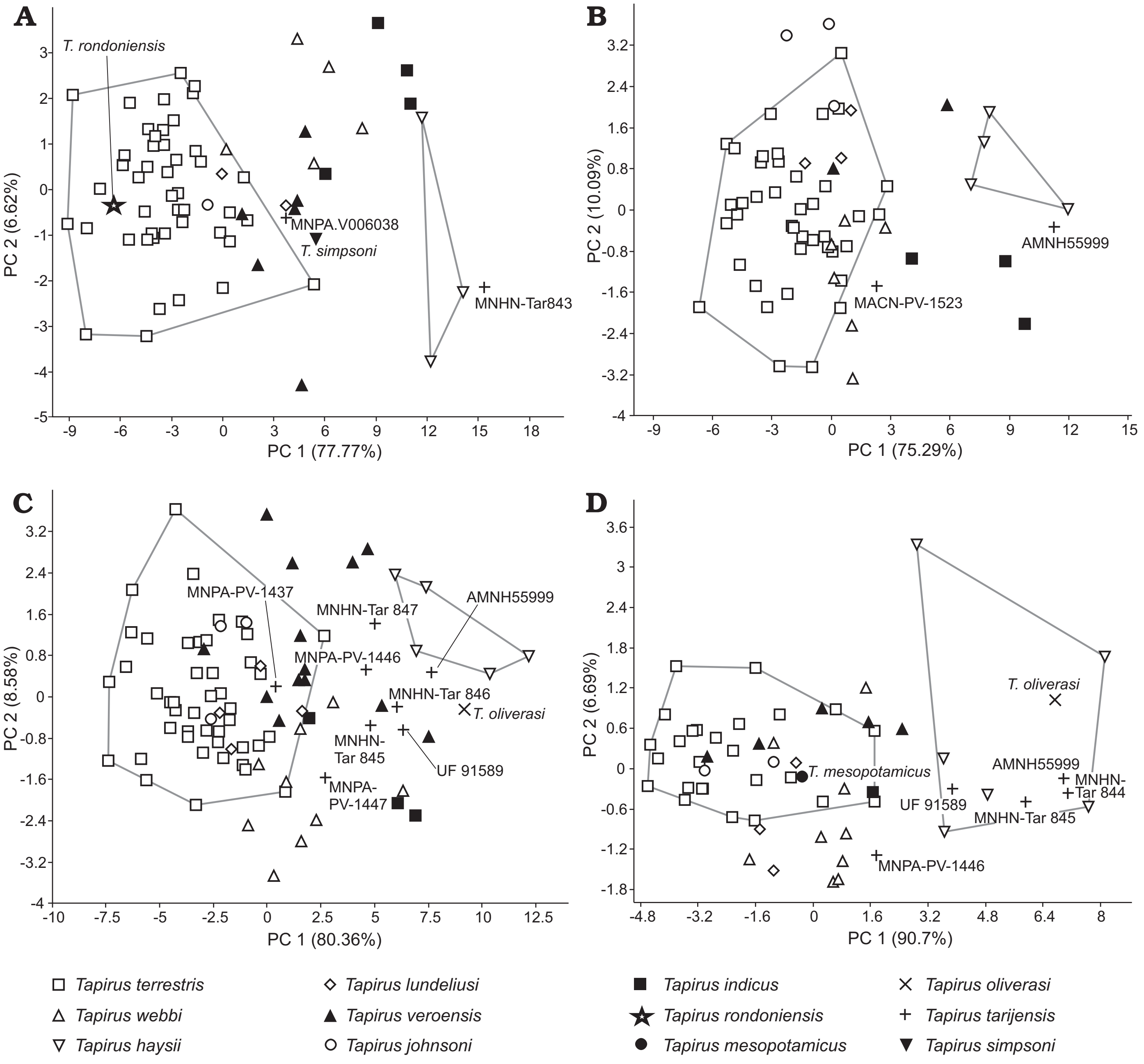

Fig. 6. Principal Component analyses including *Tapirus terrestris*, *T. webbi*, *T. haysii*, *T. lundeliusi*, *T. veroensis*, *T. johnsoni*, *T. indicus*, *T. rondoniensis*, *T. mesopotamicus*, *T. oliverasi*, *T. tarijensis*, and *T. simpsoni*. **A**. Upper dentition (Pm2, M1–M2). **B**. Lower dentition (pm2–pm4). **C**. Lower dentition (m1–m2). **D**. Lower dentition (m3).

and *T. indicus*; and (iii) the largest specimens of *T. indicus*, *T. tarijensis* (MNHN-Tar 843), and *T. haysii*.

The lower tooth data were analyzed using three separate PCAs. In the first analysis (Fig. 6B), which includes all of the measurements preserved in the lectotype of *T. tarijensis* (MACN-PV-1523), *T. terrestris*, *T. lundeliusi*, *T. johnsoni*, and *T. webbi* broadly overlap, with MACN-PV-1523 occupying an intermediate position between them and the larger species *T. veroensis*, *T. indicus*, and *T. haysii*. Although the lectotype falls close to the larger specimens of *T. terrestris* specimens, the two species do not overlap. Another specimen assigned to *T. tarijensis* (AMNH 55999) clusters with *T. haysii*, and indeed represents one of the largest specimens in the analysis; however, it should be noted that the data for this specimen were obtained from a cast. The second PCA of the lower teeth (Fig. 6C) is based on m1 and m2 only, and distinguishes a group comprising *T. terrestris*, *T. lundeliusi* and *T. johnsoni* from a second cluster including *T. tarijensis* along with large specimens of *T. veroensis*, *T. webbi*, *T. indicus*, *T. oliverasi*, and *T. haysii*. A similar pattern is evident in the third analysis (Fig. 6D), which focuses only on m3 and clusters *T. terrestris*, *T. mesopotamicus*, *T. lundeliusi*, some specimens of *T. veroensis* and some of *T. webbi* on the one hand, and *T. tarijensis*, *T. haysii*, and *T. oliverasi* on the other.

Table 5. Factor loadings for the first two principal components arising from the Principal Component analyses of the lower and upper teeth. Abbreviations as in Table 1.

	PC 1	PC 2
Lower teeth (p2–p4)		
p2L	0.4671	-0.2164
p2W	0.3009	0.344
p3L	0.4277	-0.3446
p3AW	0.1584	0.6295
p3PW	0.3742	-0.1077
p4L	0.3573	-0.3154
p4AW	0.3002	0.4003
p4PW	0.3542	0.2202
Lower teeth (m1–p2)		
m1L	0.4678	-0.4728
m1AW	0.3927	0.3499
m1PW	0.3735	0.4633
m2L	0.4808	-0.5573
m2AW	0.3586	0.2042
m2PW	0.3572	0.2952
Lower teeth (m3)		
m3L	0.7252	-0.6864
m3AW	0.4409	0.4016
m3PW	0.5289	0.6063
Upper teeth		
P2L	0.3433	0.383
P2AW	0.2610	-0.1728
P2PW	0.3103	0.1641
M1L	0.3424	0.5399
M1AW	0.3725	-0.0873
M1PW	0.3187	-0.2321
M2L	0.3076	0.2913
M2AW	0.3944	-0.3966
M2PW	0.3317	-0.4488

In terms of the postcranial remains, 8 of our 17 metapodial measurements fall outside the size range of *T. terrestris* (Table 4). Thus, MNHN-TAR 849 is about 18% longer and 30% wider than the largest metatarsal III measured for *T. terrestris*. Similarly, MNHN-TAR 848 exceeds *T. terrestris* by 10% in three of the four measurements of metatarsal IV. Moreover, MNHN-TAR 849 and 848 are about 10% and 25% larger, respectively, than the equivalent elements of *T. mesopotamicus* (Table 4).

Discussion and conclusions

Morphology and taxonomy.—The remarkably small degree of variation in dental morphology across different species of *Tapirus* is well known (Simpson 1945; Hershkovitz 1954; Ray and Sanders 1984; Hulbert 1995, Holanda and Cozzuol 2006; Ferrero and Noriega 2007), and has posed a considerable challenge to the definition of diagnostic characters and, thus, the specific assignment of often fragmentary fossil material. The extant tapirs (*T. terrestis*, *T. pinchaque*, *T. bairdii*, and *T. indicus*) clearly differ in their cranial morphology from South American fossil species, such as *T. mesopotamicus* and *T. rondoniensis,* but, with the exception of the large *T. indicus*, overlap with the latter in terms of their tooth size. In his description of *T. tarijensis*, Ameghino (1902) listed high lophids on the lower molars and a high mandibular body with a concave lower border as diagnostic characters of this species. He furthermore commented that *T. tarijensis* might be slightly larger than *T. americanum* (= *T. terrestris*), but did not provide any data on differences in tooth size. Later, Boule and Thevenin (1920) interpreted all of the remains from Tarija as those of a large tapir resembling *T. terrestris*, and assigned them to *T.* cf. *americanum* (= *T.* cf. *terrestris*), rather than *T. tarijensis*.

Based on our comparisons of the lectotype of *T. tarijensis* (MACN-PV-1523) with the other specimens from Tarija, we consider a concave lower border of the mandibular body to be the result of individual variation, rather than a species-diagnostic character. However, the existence of *T. tarijensis* as a separate species is supported by several unique traits, as detailed above in the emended diagnosis. This conclusion is further corroborated by our morphometric analyses of the teeth, which show *T. tarijensis* to be significantly larger than *T. terrestris*, *T. mesopotamicus*, and *T. rondoniensis*, and similar in size to other large living and fossil tapirs, such as *T. indicus*, *T. oliverasi*, and *T. haysii*. Equally, the metapodials of *Tapirus* sp. from Tarija are clearly more robust that those of *T. terrestris* and *T. mesopotamicus*.

Ray and Sanders (1984) suggested that North American tapirs usually fall into two size groups, including (i) those species similar in size to *T. terrestris* and (ii) those species larger than *T. terrestris*. A similar pattern occurs among South American tapirs, with *T. tarijensis* belonging to the larger size group including *T. greslebini*, *T. oliverasi*, *T. rioplatensis*, and, in some cases, *T. cristatellus* (Holanda and Ferrero 2013).

Biogeographic distribution.—Based on available data, *T. tarijensis* seems to have been endemic to the Tarija Valley, Bolivia. However, it is possible that the species has escaped detection in other regions of South America owing to the difficulty of distinguishing species based on their teeth and the fragmentary nature of much of the described material. Thus, for example, poorly preserved material currently makes it difficult to distinguish *T. oliverasi* from both *T. tarijensis* and *T. rioplatensis* (Holanda and Ferrero 2013). Several other taxa previously proposed to be endemic to Tarija were later also found in the Pampean region of Argentina (e.g., *Scelidodon tarijensis, Arctotherium tarijense*, *A. wingei*; Tonni et al. 2009; Soibelzon et al. 2011), thus adding to an extensive list of species with a wide geographic distribution across several parts of South America (e.g., Alberdi and Prado 1992, 1993; Soibelzon 2004; Prevosti 2007; Gasparini et al. 2009; Tonni et al. 2009, Zurita et al. 2009; Soibelzon et al. 2011). In addition, it is possible that *T. terrestris* may have been distributed alongside *T. tarijensis* in Bolivia, resembling the sympatric occurrence of the three extant South American species in Colombia, or the co-occurrence of *T. cristatellus* and *T. terrestris* in Brazil (Cartelle 1999). Testing such ideas must await the discovery of more informative material.

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References

Alberdi, M.T. and Prado, J.L. 1992. El registro de *Hippidion* Owen, 1869 y *Equus* (*Amerhippus*) Hoffstetter, 1850 (Mammalia, Perissodactyla) en América del Sur. *Ameghiniana* 29: 265–284.

Alberdi, M.T. and Prado, J.L. 1993. Review of the genus *Hippidion* Owen, 1869 (Mammalia: Perissodactyla) from the Pleistocene of South America. *Zoological Journal of the Linnean Society* 108: 1–22.

Alberdi, M.T. and Prado, J.L. 2004. *Los caballos fósiles de América del Sur. Una historia de 3 millones de años*. 269 pp. Serie Monográfica 3. Investigaciones Arqueológicas y Paleontológicas del Cuaternario Pampeano. Universidad Nacional del Centro de la Provincia de Buenos Aires, Olavarría.

Ameghino, F. 1902. Notas sobre algunos mamíferos fósiles nuevos o pocos conocidos del valle de Tarija. *Anales del Museo Nacional de Buenos Aires* 8: 225–261.

Boule, M. and Thévenin, A. 1920. *Mammifères fossiles de Tarija, Vol. 4.* 256pp. Imprimerie Nacional, Paris.

Brisson, M.J. 1762. *Regnum animale in classes IX. distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem divisionem in ordines, sectiones, genera & species. Cum brevi cujusque specie descriptione, citationibus auctorum de iistractantium, Nominibus eis ab ipsis & nationibus impositis, nominibusque vulgaribus. Editio altera auctior.* 296 pp. Lugduni Batavorum, Theodorum Haak, Paris.

Burnett, G.T. 1830. Illustrations of the Quadrupeda, or quadrupeds, being the arrangement of the true fourfooted beasts, indicated in outline. *Quarterly Journal of Scientific Literary and the Arts* 26: 336–353.

Carles, E. de. 1888. Noticias sobre un viaje a Tarija (Bolivia). *Boletín del Instituto Geográfico Argentino* 9 (Cuaderno 1): 35–40.

Cartelle, C. 1999. Pleistocene mammals of the Cerrado and Caatinga of Brazil. *In*: J.F. Eisenbergand and K.H. Redford (eds.), *Mammals of the Neotropics—The Central Neotropics 3*, 27–46. University of Chicago Press, Chicago.

Cerdeño, E. and Ginsburg, L. 1988. Les Tapiridae (Perissodactyla, Mammalia) de l'Oligocène et du Miocène infèrieur europèens. *Annales de Paléontologie* 74: 71–96.

Cerdeño, E. and Sánchez, B. 2000. Intraspecific variation and evolutionary trends of *Alicornops simorrense* (Rhinocerotidae) in Spain. *Zoologica Scripta* 29: 275–305.

Coltorti, M., Abbazzi, L., Ferreti, M., Lacumin, P., Paredes Río, F., Pellegrini, M., Pieruccini, P., Rustioni, M., Tito, G., and Rook, L. 2007. Last Glacial mammals in South America: a new scenario from the Tarija Basin (Bolivia). *Naturwissenschaften* 94: 288–299.

Ferrero, B.S. and Noriega, J.I. 2003. El registro fósil de los tapires (Perissodactyla: Tapiridae) en el Pleistoceno de Entre Ríos. *Ameghiniana* 40: 84S.

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.

Ferrero, B.S., Brandoni, D., Noriega, J.I., and Carlini A.A. 2007. Mamíferos de la Formación El Palmar (Pleistoceno tardío) de la provincia de Entre Ríos, Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia* 9: 109–117.

Ferrero, B.S., Gasparini, G.M., Soibelzon, E., Zurita, A.E., Miño Boilini, A.R., and Soibelzon, L. 2009. Los tapires (Perissodactyla, Tapiridae) del Valle de Tarija, Bolivia. Consideraciones morfométricas e implicancias taxonómicas. *Ameghiniana* 46 (4): 77R–78R.

Gasparini, G.M., Soibelzon, E., Zurita, A.E., and Miño-Boilini, A.R. 2009. The Tayassuidae (Mammalia, Artiodactyla) from Tarija valley, Bolivia. Paleofaunistic update. *Alcheringa* 33 (4): 7–20.

Gill, T.N. 1865. [No title]. *Proceedings of the Academy of Natural Science Philadelphia* 17: 183.

Hammer, O., Harper, D.A.T., and Ryan, P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Paleontologia Electronica* 4: 1–9.

Hershkovitz, P. 1954. Mammals of Northern Colombia, Preliminary Report Nº 7: Tapirs (Genus *Tapirus*), with a systematic review of American species. *Proceedings of the Smithsonian National Museum* 103: 465–496.

Hoffstetter, R. 1963. La faune pléistocéne de Tarija (Bolivie). *Bulletin du Muséum National d'Histoire Naturelle* 35: 194–203.

Hoffstetter, R. 1986. High Andean mammalian faunas during the Plio-Pleistocene. *In*: Vuilleumier F. and M. Monasterio (eds.), *High Altitude Tropical Biogeography*, 218–245. Oxford University Press, New York.

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: 93–200.

Holanda, E.C. and Ferrero, B.S. 2013. Reappraisal of the genus *Tapirus* (Perissodactyla, Tapiridae): systematics and phylogenetic affinities of the South American tapirs. *Journal of Mammalian Evolution* 20: 33–44.

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: 23R.

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

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.

Hulbert, R.C., Jr. 1995. The Giant Tapir, *Tapirus haysii*, from Leysey Shell Pit 1^a and other Florida Irvingtonian Localities. *Bulletin of the Florida Museum of Natural History* 37: 515–551.

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.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 824 pp. Laurentii Salvii, Stockholm.

MacFadden, B.J. 2000. Middle Pleistocene climate change recorded in fossil mammal teeth from Tarija, Bolivia, and upper limit of the Ensenadan Land-mammal age. *Quaternary Research* 54: 121–131.

MacFadden, B.J. and Shockey, B.J. 1997. Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: Morphological and isotopic evidence. *Paleobiology* 23: 77–100.

MacFadden, B.J., Siles, O., Zeitler, P., Johnson, N.M., and Campbell, K.E., Jr. 1983. Magnetic polarity stratigraphy of the middle Pleistocene (Ensenadan) Tarija Formation of southern Bolivia. *Quaternary Research* 19: 172–187.

MacFadden, B.J., Yang, W., Cerling, T.E., and Anaya, F. 1994. South American fossil mammals and carbon isotopes: a 25 million-year sequence from the Bolivian Andes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107: 257–268.

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* 1984: 1–76.

Marshall, L.G. and Sempere, T. 1991. The Eocene to Pleistocene vertebrates of Bolivia and their stratigraphic context: a review. 12. *In*: R. Suarez-Soruco (ed.), *Vertebrados. Revista Técnica de YPFB. Fósiles y Facies de Bolivia, Volumen 1*, 631–652. Santa Cruz de la Sierra, Bolivia.

Medici, E.P. 2011. Family Tapiridae (Tapirs). *In*: D.E Wilson and R.A. Mittermeier (eds.), *Handbook of the Mammals of the World—Hoofed Mammals, Volumen 2*, 182–204. Lynx Editions, Barcelona.

Owen, R. 1848. Description of teeth and portions of jaws in two extinct anthracotheroid quadrupeds (*Hyopotamus vectianus* and *H. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of Pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London* 4: 103–141.

Perini, F.A., Oliveira, J.A., Salles, L.O., Moraes Neto, C.R., Guedes, P.G., Luiz Flamarion, B.O., and Weksler, M. 2011. New fossil records of *Tapirus* (Mammalia, Perissodactyla) from Brazil, with a critical analysis of intra-generic diversity assessments based on lower molar size variability. *Geobios* 44: 609–619.

Prevosti, F.J. 2007. *Grandes cánidos (Carnivora, Canidae) del Cuaternario de la República Argentina: sistemática, filogenia, bioestratigrafía y paleoecología.* 501 pp. Unpublished Ph.D., Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata.

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: a Volume in Memorial to John E. Guilday. *Carnegie Museum Natural History, Special Publication* 8: 283–315.

Roulin, X. 1829. Memoir pour servir a l'histoire du tapir; et description dune espece nouvelle appartenant aux hautes regions de la Cordillere des Andes. *Annales des Science Naturelle Zoologie Paris* 17: 26–55.

Scherler, L., Becker, D., and Berger, J.P. 2011. Tapiridae (Perissodactyla, Mammalia) of the Swiss Molasse Basin during the Oligocene–Miocene transition. *Journal of Vertebrate Paleontology* 31: 479–496.

Simpson, G.G. 1945. Notes on Pleistocene and Recent Tapirs. *Bulletin of the American Museum of Natural History* 86: 36–82.

Soibelzon, L.H. 2004. Revisión sistemática de los Tremarctinae (Carnivora: Ursidae) fósiles de América del Sur. *Revista del Museo Argentino de Ciencias Naturales* 6: 105–131.

Soibelzon, E. 2005. Los mamíferos del Ensenadense (Pleistoceno Inferior a Medio) del Este de la región pampeana: asociaciones faunísticas, bioestratigrafía y diversidad. Una aproximación a su estudio. *In*: Cabaleri N., Cingolani, C.A., Linares, E., López de Luchi, M.G., Ostera, H.A. and Panarello, H.O. (eds.), *Actas del XV Congreso Geológico Argentino*, 233–239.

Soibelzon, E., Gasparini, G.M., Zurita, A.E., and Soibelzon, L.H. 2008. Las "toscas del Río de La Plata" (Buenos Aires, Argentina). Análisis paleofaunístico de un yacimiento paleontológico en desaparición. *Revista del Museo Argentino de Ciencias Naturales* 10: 291–308.

Soibelzon, E., Prevosti, F.J., Bidegain, J.C., Rico, Y., Verzi, D.H., and Tonni, E.P. 2009. Correlation of late Cenozoic sequences of southeastern Buenos Aires province: Biostratigraphy and magnetostratigraphy. *Quaternary International* 210: 51–56.

Soibelzon, E., Rodriguez, S., Avilla L., Soibelzon, L.H., and Zurita, A.E. 2011. Mammals of the Tarija Valley (Southern Bolivia): diversity, endemism and the problem with its antiquity. 71st Annual Meeting of the Society of Vertebrate Paleontology. Las Vegas, USA. *Journal of Vertebrate Paleontology* (Supplement): 197–198 (available online).

Takai, F., Arozqueta, B., Mizuno, T., Yoshida, A., and Kondo, H. 1984. On fossil mammals from the Tarija department, Southern Bolivia. *The Research Institute of Evolutionary Biology* 4: 1–63.

Takai, F., Mizuno, T., Iwasaki, Y., Tanaka, K., and Yoshida, A. 1982. Tarija mammal bearing formation in Bolivia. *The Research Institute of Evolutionary Biology* 3: 1–72.

Tong, H.W. 2005. Dental characters of the Quaternary tapirs in China, their significance in classification and phylogenetic assessment. *Geobios* 38: 139–150.

Tonni, E.P. 1992. *Tapirus* Brisson, 1762 (Mammalia, Perissodactyla) en el Lujanense (Pleistoceno Superior-Holoceno Inferior) de la Provincia de Entre Ríos, República Argentina. *Ameghiniana* 29: 3–8.

Tonni, E.P., Soibelzon, E., Cione, A.L., Carlini, A.A., Scillato Yané, G.J., Zurita, A.E., and Paredes Ríos, F. 2009. Preliminar correlation of the Pleistocene sequences of the Tarija valley (Bolivia) with the Pampean chronological standard. *Quaternary International* 210: 57–65.

Ubilla, M. 1983. Sobre la presencia de tapires fosiles em el Uruguay (Mammalia, Perissodactyla, Tapiridae). *Revista de la Facultad de Humanidades y Ciencias* 1: 85–104.

Ubilla, M. 2004. Mammalian biostratigraphy of Pleistocene fluvial deposits in northern Uruguay, South America. *Proceedings of Geologist's Association* 115: 347–357.

Ubilla, M. and Rinderknech, A. 2007. Fossil tapirs from Uruguay: a review. *Ameghiniana* (Suplement) 44: 42A.

Webb, S.D. 2006. The great American biotic interchange: Patterns and processes. *Annals of the Missouri Botanic Garden* 93: 245–257.

Woodburne, M.O., Cione, A.L., and Tonni, E.P. 2006. Central American provincialism and Great 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, Publicación Especial 4*, 73–101. Universidad Nacional Autónoma de México, Instituto de Geología y Centro de Geociencias, Mexico.

Zurita, A.E., Miño Boilini, A.R., Soibelzon, E., Carlini, A.A., and Paredes Ríos, F. 2009. The diversity of (Xenarthra) in the Tarija valley (Bolivia): systematic, biostratigraphic and paleobiogeographic aspects of a particular assemblage. *Neues Jahrbuch für Geologie und Palantölogie Abhandlungen* 251/252: 225–237.