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Description of a new species of *Sparassocynus* (Marsupialia: Didelphoidea: Sparassocynidae) from the late Miocene of Jujuy (Argentina) and taxonomic review of *Sparassocynus heterotopicus* from the Pliocene of Bolivia

MARÍA ALEJANDRA ABELLO[1], MARTÍN DE LOS REYES[2], ADRIANA MAGDALENA CANDELA[2], FRANCOIS PUJOS[3], DAMIÁN VOGLINO[4] & BERNARDINO MAMANI QUISPE[5]

[1]*Laboratorio de Sistemática y Biología Evolutiva (LASBE), Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata. Paseo del Bosque s/n, B1900FWA, La Plata, Argentina. E-mail: mabello@fcnym.unlp.edu.ar*
[2]*División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata. Paseo del Bosque, B1900FWA La Plata, Argentina. E-mail: delossreyes@yahoo.com.ar, acandela@fcnym.unlp.edu.ar.*
[3]*Dpto. de Paleontología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT–CONICET–Mendoza, Avda.Ruiz Leal s/n, Parque Gral. San Martín, 5500 Mendoza, Argentina. E-mail: fpujos@mendoza-conicet.gov.ar*
[4]*Museo de Ciencias Naturales "Rvdo. P. Antonio Scasso", Don Bosco 580, San Nicolás de los Arroyos, Buenos Aires, Argentina. E-mail: dvoglino@fundacionoga.org.ar*
[5]*Departamento de Paleontología , Museo Nacional de Historia Natural , Calle 26 s/n, Cota Cota, La Paz, Bolivia. E-mail: bmamaniq@hotmail.com*

Abstract

A new species of sparassocynid marsupial, *Sparassocynus maimarai* **n. sp.** from the late Miocene of Maimará Formation (Jujuy Province, Argentina) is described from a left mandibular fragment with a complete p2–m4 series. It differs from the remaining species of the genus *S. bahiai* (Montehermosan—late Miocene/early Pliocene—of Buenos Aires Province, Argentina) and *S. derivatus* (Chapadmalalan and Marplatan–Pliocene of Buenos Aires Province) by its smaller size, the relatively longer m1 with respect to the m4, the presence of a lingual cingulum extended between para- and metaconid on the m1–3, and its more robust entoconids. As part of this study the taxonomic status of *Sparassocynus heterotopicus* (Montehermosan, Umala, Bolivia; Pliocene) was reviewed concluding that this taxon should be referred to as '*Sparassocynus*' *heterotopicus* and considered a Didelphoidea of uncertain affinities. *Sparassocynus maimarai* **n. sp.** is the oldest records of the genus, adding new information to evaluate the origins and early diversification of sparassocynids. *Sparassocynus maimarai* **n. sp.** was recovered with precise stratigraphic control, highlighting its potential biostratigraphic significance to the temporal correlations between Maimará Formation and other Mio–Pliocene stratigraphic units from the northwestern Argentina.

Key words: Neogene, Metatheria, South America

Introduction

The Sparassocynidae are a lineage of South American extinct marsupials included in the Didelphimorphia (Aplin & Archer, 1987). More recently, this order has been considered a non-natural group (see e.g., Ladevèze & Muizon, 2010) within which were included several extinct and extant opossums (i.e., Didelphidae; Voss & Jansa, 2009) as well as stem-metatherians such as pucadelphids and herpetotheriids (Sánchez-Villagra *et al*., 2007, Horovitz *et al*., 2009). Among Didelphimorphia, sparassocynids were proposed as closely related to didelphids and caluromyids, forming a monophyletic group (i.e., Didelphoidea; Goin, 1991, 1995).

Within Sparassocynidae two genera are recognized: *Hesperocynus* Forasiepi, Goin & Martinelli, 2009 and *Sparassocynus* Mercerat, 1898. *Hesperocynus* includes only one species, *H. dolgopolae* (Reig, 1958a), while *Sparassocynus* includes, to date, three species *S. bahiahi* Mercerat, 1898, *S. derivatus* Reig & Simpson, 1972, and *S. heterotopicus* Villarroel & Marshall, 1983. More recently, Forasiepi *et al*. (2009) pointed out that the validity of *S. heterotopicus* is yet under debate as it could be considered a possible didelphid or sparassocynid (the taxonomic status of this species is discussed below).

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The oldest record of sparassocynids comes from the late Miocene (Huayquerian) of central and northwestern Argentina (Forasiepi *et al*., 2009) and is represented by a single species, *Hesperocynus dolgopolae*, from the localities of Chiquimil (=Entre Ríos locality, Catamarca Province, Andalhualá Formation; Reig, 1958a, 1958b; Fig. 1B), and several localities of La Pampa Province (e.g., El Guanaco, Cerro Azul Formation; Goin *et al*., 2000; Abello *et al*., 2002; Fig. 1B). In addition, the more complete remains of this species comes from fossiliferous levels of Puesto Arroyo Seco de la Frazada (Mendoza Province, Aisol Formation; Forasiepi *et al*., 2009), whose age was considered no older than late Miocene (Huayquerian age, Forasiepi *et al*., 2009) or than early Pliocene (Vucetich et al, 2011). During the late Miocene–Pliocene (Montehermosan, Chapadmalalan, and Marplatan ages) the second genus, *Sparassocynus*, is registered in several coastal localities of eastern Argentina (e.g., Montehermoso and Arroyo Lobería) in outcrops of Montehermoso and Chapadmalal formations (Buenos Aires Province; Zárate, 1989; Tomassini *et al*., 2013) (Fig. 1B).

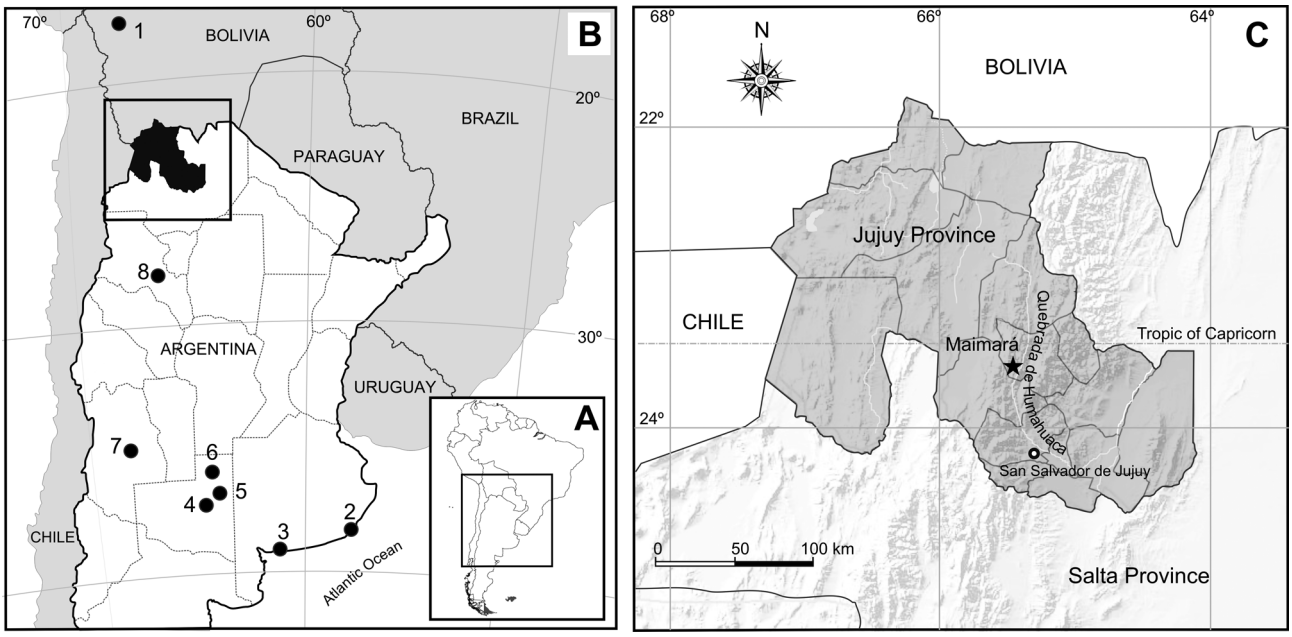

FIGURE 1. Map showing geographical positions of localities mentioned in the text. **A**, boxed area in map of South America showing central and southern Bolivia, and central and northern Argentina. **B**, fossiliferous localities: (1) Umala, (2) Arroyo Lobería, (3) Monte Hermoso, (4) El Guanaco, (5) Quehué, (6) Caleufú, (7) Puesto Arroyo Seco de la Frazada, and (8) Chiquimil. **C**, area of Jujuy Province with the location of the type locality of *Sparassocynus maimarai* **n. sp.**

In this contribution, we describe a new sparassocynid species from the late Miocene Maimará Formation (Quebrada de Humahuaca, Jujuy Province, Argentina Fig. 1C). A comparative study of the new taxa, represented by an incomplete mandible with the premolar and molar series, was made with the remaining Sparassocynidae species recognize up to date, including *S. heterotopicus* from the Pliocene of Umala Formation (Bolivia). As a consequence of this analysis, the taxonomic status of *S. heterotopicus* was reviewed.

The sparassocynid recovered in Maimará Formation represents the first marsupial known from this Mio–Pliocene unit (Pingel *et al*., 2013). In addition, it is one of the first mammals recovered with precise stratigraphic control, highlighting its potential biostratigraphic significance to the temporal correlations between Maimará Formation and other Mio-Pliocene stratigraphic units from the northwestern Argentina.

Particularly, the study of Neogene units from Quebrada de Humahuaca such as the Maimará Formation, and its extinct mammals, plays a significant role in establishing a bioestratigraphic scheme for the Neogene of northwestern Argentina (NWA) and contribute to calibrate the stages of the Great American Biotic Interchange (GABI) (Woodburne, 2010 and cites herein). In contrast to other well-known Neogene units from NWA, an evaluation from a geological-paleontological perspective of the late Miocene Maimará Formation is still in its early days (Pujos *et al*., 2012; Galli *et al*., 2012; Candela *et al*., 2013). Recent geological surveys and paleontological explorations have resulted in the discovery of new fossil mammals, such as the new marsupial remain described in the present study.

Geological setting and age. The Maimará Formation (Salfity *et al.*, 1984) outcrops at the central sector of the

Quebrada de Humahuaca (Humahuaca Basin, Eastern Cordillera, Jujuy Province, Argentina; see Galli *et al*., 2012; Pingel *et al*., 2013), near the Maimará locality (Fig. 1C). The more complete sequence of the Maimará Formation is exposed in the Quebrada de Maimará (Pingel *et al*., 2013), western of the Maimará locality, on the left margin of the Arroyo Huasamayo (Pujos *et al*., 2012). This unit comprises inter-bedded sandstones and conglomerates intercalated with several tuff levels (Fig. 2). The deposits are ordered in an upwardly coarsening sequence developed in an ephemeral fluvial system under arid and semi-arid conditions (Galli *et al*., 2012). Fossil-rich clay beds and siltstones dominate the basal 50 m of this section and contain freshwater ostracods and the charophytes oogonia (Galli *et al*. 2012; Pingel *et al*., 2013).

Traditionally, the Maimará Formation was assigned to the Huayquerian age (late Miocene; see Reguero & Candela, 2011 and bibliography herein) but this assignment was not based on precise biostratigraphic analysis and/or geochronological data. Recently, new $^{206}Pb/^{238}U$ zircon ages obtained from several volcanic ashes from the Humahuaca Basin, indicate that the sediments of the Maimará Formation were deposited since at least 5.92+/-0.12 Ma to 4.18+/-0.11 Ma (Pingel *et al*., 2013), i.e. late Miocene-early Pliocene.

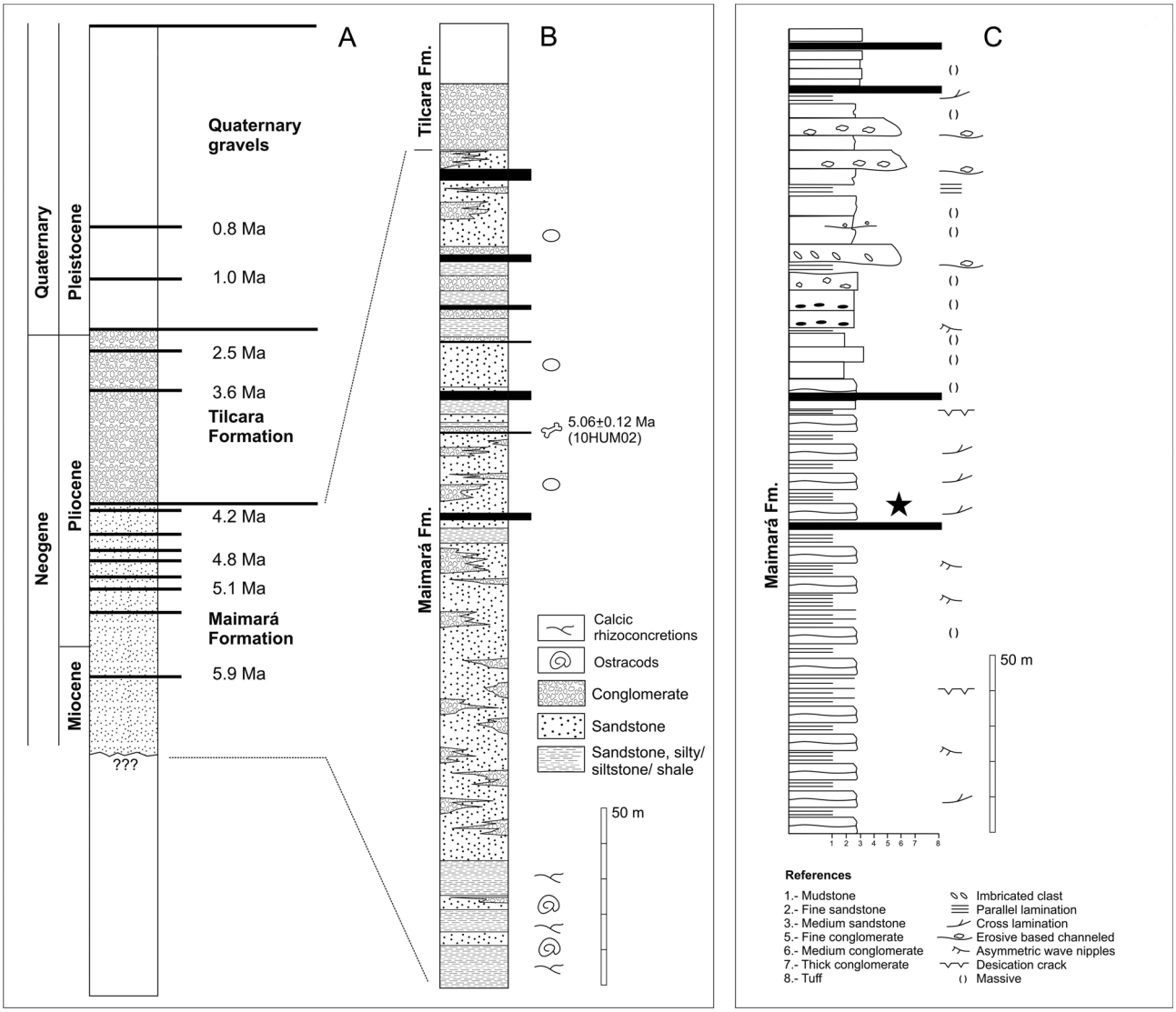

FIGURE 2. A, simplified Cenozoic chronostratigraphy of the area of Humahuaca Basin modified from Pingel *et al.* (2013), showing Maimará and Tilcara formations and $^{206}Pb/^{238}U$ zircon ages obtained from several volcanic ashes in the Humahuaca Basin volcanic rocks. **B**, stratigraphic section located near Incahuasi and in the Quebrada de Maimará, modified from Pingel *et al.* (2013). **C**, stratigraphic section showing the marsupial bearing level (star) and the more basal tuffs of the section, modified from Pujos *et al*. (2012).

The level from which *Sparassocynus maimarai* mandible was retrieved is about 100 m from the base (see profile in Pujos *et al*., 2012: fig. 2; Fig. 2A) between two tuffs exposed at the base of the stratigraphic section outcropping at Quebrada of Maimará. Recently, the two tuffs exposed at the base of the Maimará Formation, 10HUM02 and 10 HUM21, were dated at 5.06 and 5.9 Ma respectively (Pingel *et al*., 2013; Fig. 2B). Taking into account the stratigraphic position in the section of the new specimen and considering that the two more basal tuffs associated with the vertebrate-bearing horizon can be correlated with those recently dated by Pingel *et al*. (2013: fig. 3 a–c; see Fig. 2 A–B), we infer that the new specimen would have an age not younger than 5.06 Ma and not older than 5.9 Ma. The marsupial from Maimará represents a component of the mammalian assemblage that lived close to the Mio–Pliocene limit.

Material and methods

Taxonomy. The new species, *Sparassocynus maimarai*, is recognised based on comparative study of the species of Sparassonynidae and Didelphidae, and assigned to the genus *Sparassocynus* taking into account the features proposed as diagnostic of this genus, which were supported by previous taxonomic studies (e.g., Goin 1991; Forasiepi *et al.*, 2009); thereby, the generic assignation of the new species was made applying alfa-taxonomy. Up to now, there are no analyses including all sparassocynid species within a cladistic framework; hence, the diagnosis of the recognized genera *Sparassocynus* and *Hesperocynus* were not made in terms of genealogy. An integrative cladistic analysis of Sparassocynidae would be not only key to test the diagnosis proposed for both genera described so far, but also to determine the closer phylogenetic relationships of the new species among sparassocynids. This latter would require a detailed character analysis, considering wholly the described sparassocynid species, a study that goes beyond the aim of this work.

Open nomenclature. Usage of open nomenclature follows the recommendations given by Matthews (1973) and Bengtson (1988).

Dental nomenclature. M/m, upper and lower molar; p, lower premolar; StA-D, stylar cusps A to D, respectively.

Institutional abbreviations. FMNH, Field Museum of Natural History, Chicago, USA; JUY-P, Museo de Geología, Mineralogía y Paleontología, Instituto de Geología y Minería, Universidad Nacional de Jujuy, San Salvador de Jujuy, Argentina; MACN-PV, Colección Nacional de Paleovertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales de Mar del Plata, Mar del Plata, Argentina; MNHN-BOL, Museo Nacional de Historia Natural, La Paz, Bolivia.

Revised materials. *Sparassocynus derivatus*: MMP 851 M, right mandible with p1–m4; MMP 412 M, right mandible with p1–m4 (Fig. 3A); MMP 1088, associated left mandible with c–m4 and left maxillary fragment with P2–M4; MMP 1379, left mandible with p1–m4; MACN-PV 17909, left mandible with p3–m4. *Sparassocynus bahiai*: MLP 11–92 (type), skull fragment with left P2–M4 and right P2–M3; MLP 11–119 (type of *Perazoyphium brachignathus,* Fig. 3B), right mandible with root of p1 and complete p2–m4; MLP 86-VI-I-I, fragmentary skull with left M2–3 and right P3–M3; MACN-PV 15403, left mandible with fragment of p2 and complete p3–m4; MACN-PV 2927, incomplete skull with left I1–M4, right I1–C and P3–M4, left mandible with i2–p1 and p3–m4, and right mandible with i4–c. *Hesperocynus dolgopolae*: FMNH 14469 (type), right mandible with p2–m3 (Fig. 3C); MLP 86-VII-10-1, right mandible with p2–m1, fragment of m2, and complete m3–4 (Fig. 3D). '*Sparassocynus*' *heterotopicus*: MNHN-BOL-011896, left M1–3 (Fig. 4A) and left m2–4 (Fig. 4B–C).

Results

Systematics

Supercohort Marsupialia Illiger, 1811

Order Didelphimorphia Gill, 1872

Superfamily Didelphoidea Gray, 1821

Family Sparassocynidae (Reig, 1958a)

***Sparassocynus* Mercerat, 1898**

Type species. *Sparassocynus bahiai* Mercerat, 1898, Montehermosan (late Miocene/early Pliocene; following Reguero & Candela, 2011) Buenos Aires Province, Argentina.

Included species. *Sparassocynus derivatus* Reig & Simpson, 1972, Chapadmalalan (late early Pliocene) and Marplatan (late Pliocene), Buenos Aires Province, Argentina, and *S. maimarai* **n. sp.**

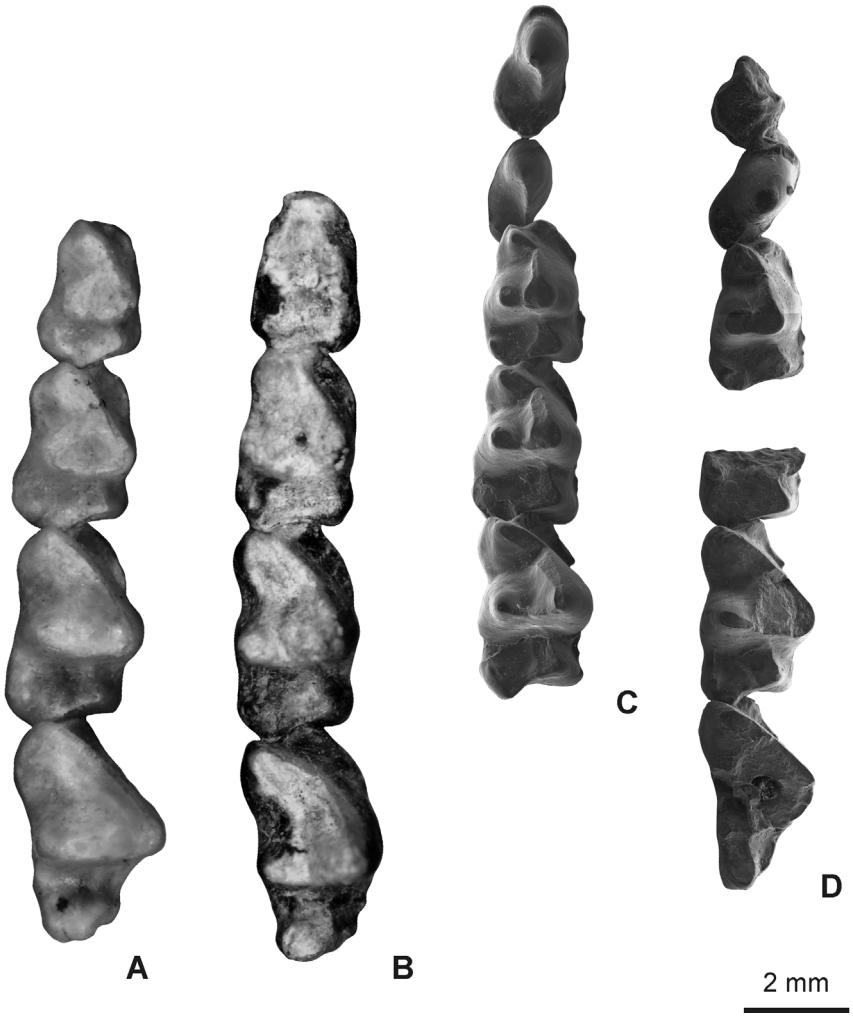

FIGURE 3. Lower dentition of *Sparassocynus* and *Hesperocynus* in occlusal view (anterior towards top). **A**, *Sparassocynus derivatus*, MMP 412 M, right m1–m4; **B**, *Sparassocynus bahiai*, MLP 11-119, right m1–m4; **C**–**D**, *Hesperocynus dolgopolae*, **C**, FMNH 14469 (holotype), right p2–m3; **D**, MLP 86-VII-10-1, right p2–m1, talonid of m2, and complete m3–4.

***Sparassocynus maimarai* new species**
Fig. 5, Tables 1–2

Etymology. "*maimarai*" in reference to the locality of Maimará where the new species was discovered.

Holotype. JUY-P-48, left mandibular fragment with a complete p2–m4 series.

Locality and Horizon. The type specimen was collected in the Maimará Formation (late Miocene-early Pliocene), near the Locality of Maimará, Jujuy Province, Argentina (Fig. 1C).

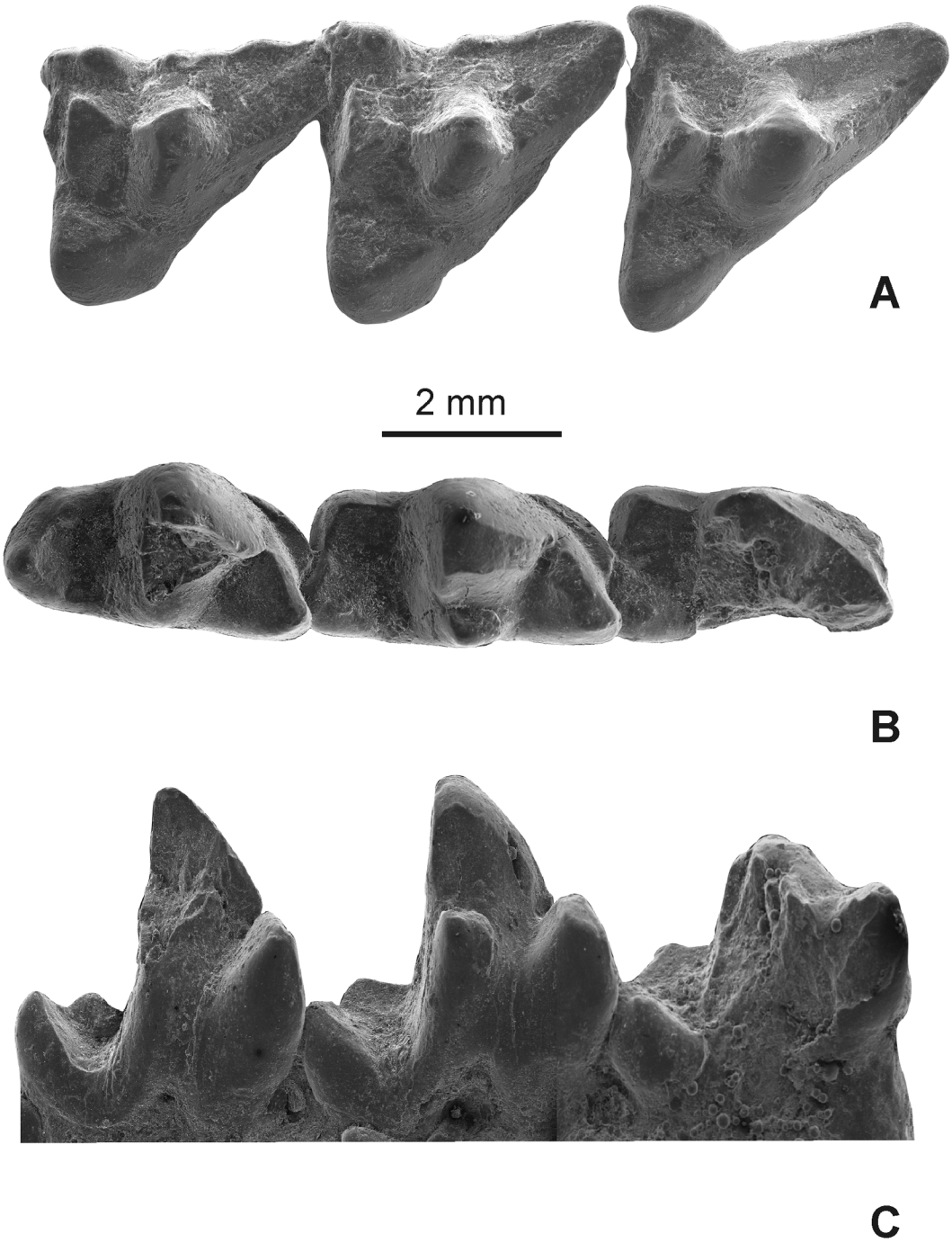

FIGURE 4. Lower dentition of '*Sparassocynus*' *heterotopicus* (cast, MNHN-BOL-011896). **A**, left M1–3 in oclussal view (anterior towards left); **B**–**C**, left m2–4 in oclussal and lingual views respectively (anterior towards left).

Diagnosis. *Sparassocynus maimarai* differs from *S. bahiai* and *S. derivatus* by its smaller size, the relatively longer m1 with respect to the m4, its more robust and conical entoconids, and the presence of a lingual cingulum extended between para- and metaconid on the m1–3.

Comparative description. Considering the mean of m1–3 length as a proxy of species size, *S. maimarai* is 9% smaller than *S. bahiai* and *S. derivatus* (Tables 2 and 3). The horizontal ramus of the dentary is short and deep as in *S. bahiai* and *S. derivatus*, and about a 40% deeper than *Hesperocynus* (Tables 2 and 3). The mandibular symphysis is long, ending posteriorly behind to the p3–m1 boundary (Fig. 5A–C). The ventral border of the horizontal ramus between p2 and m4 is not preserved (Fig. 5A–B) and the possible presence of a well-developed notch mark for the geniohyoid muscle, a diagnostic character of sparassocynids (Goin, 1991), could not be evaluated. On the labial side of the dentary two mental foramina are present, one located below the p2 and the other below the posterior

root of m1. The anterior end of the mandible is broken in front of the p2 (Fig. 5A–B). Behind the root of the canine is the posterior alveolus of p1, which was oblique to the dentary row (Fig. 5C). The p2 is labiolingualy compressed, and has a small posterior cusp; the p3 is narrow posteriorly with a small lingual talon (Fig. C, E). Premolars are slightly imbricated, without diastema between them such as some specimens of *S. derivatus* (e.g., MMP 1088).

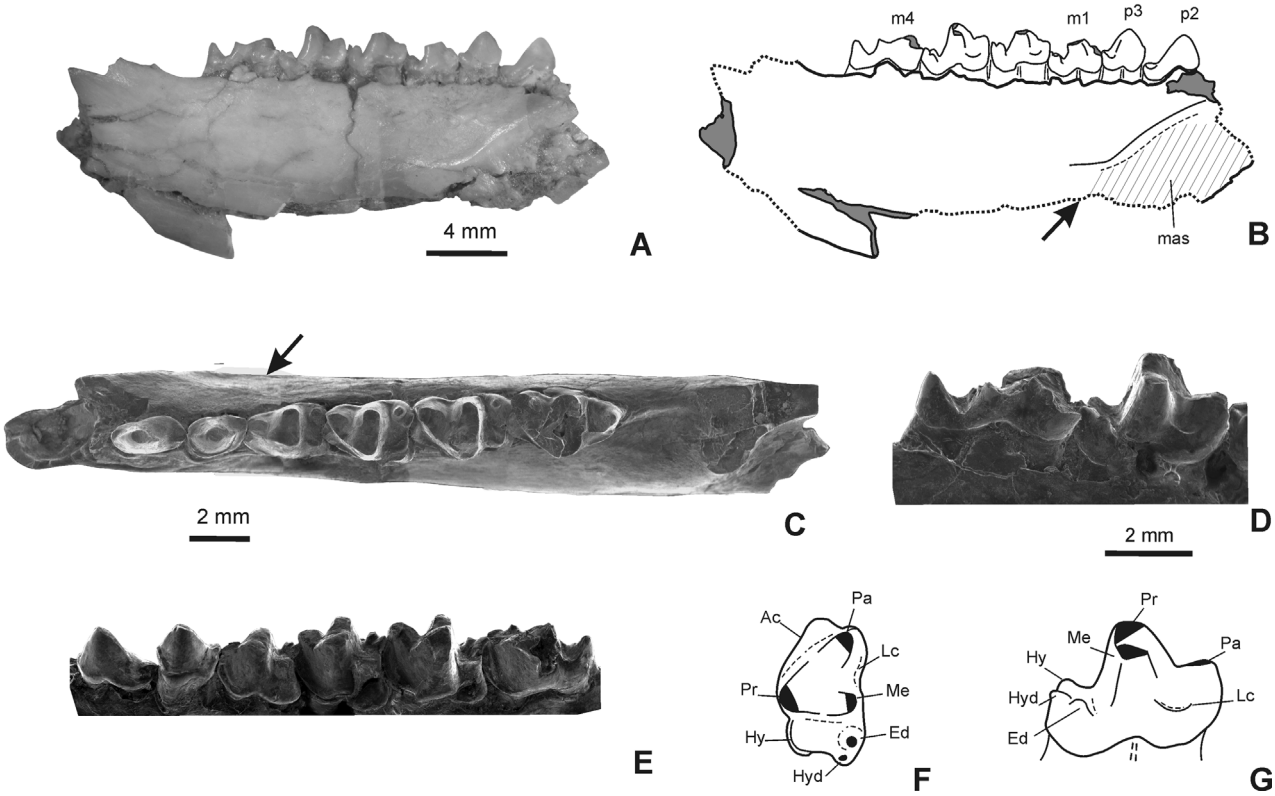

FIGURE 5. *Sparassocynus maimarai* **sp. nov.** (holotype JUY-P-48). **A**–**C**, mandible in lingual (**A**–**B**) and occlusal (**C**) views (arrow indicates the posterior extent of the mandibular symphysis); **D**, detail of m3–4 in lingual view (anterior towards right); **E**, p2–m4 series in labial view (anterior towards left); **F**–**G**, schematic drawings of the m4 in occlusal (**F**) and lingual (**G**) views. **Abbreviations**: **Ac**, anterobasal cingulum; **Ed**, entoconid; **Hy**, hypoconid; **Hyd**, hypoconulid; **Lc**, lingual cingulum; **m1**–**m4**, lower molars; **mas**, mandibular symphysis; **Me**, metaconid; **p1**–**p2**, lower premolars; **Pa**, paraconid; **Pr**, protoconid.

Molars increase in length, and have a proportionally longer and wider trigonids, from m1 to m4. First lower molar is relatively longer with respect to the m4 than it is in *S. bahiai* and *S. derivatus* (Tables 2 and 3). Talonids of *S. maimarai* are shorter and narrower than the trigonids as occur in the remaining *Sparassocynus* species (Fig. 5C; Tables 2 and 3). The talonid of m4 is, in the contact with the trigonid, as wide as that of *S. derivatus* and *S. bahiai* (Figs. 5C and 3A–B), and wider than in *H. dolgopolae* (Fig 3D; Tables 2 and 3). Similarly to the remaining Sparassocynidae, trigonids are higher than talonids (Reig & Simpson, 1972; Goin, 1991). The paraconid is lower than proto- and metaconid; metaconid is reduced compared to the protoconid and partially fused to this cusp (Fig. 5D–E, G). The paraconid is slightly larger than that of *S. bahiai* and *S. derivatus*. Lingually, a basal cingulum is located between para- and metaconid (Fig. 5D, F–G). Anterobasal cinguli are narrow and become anteriorly wider along the paraconid where they form deep hypoconulid notchs. The hypoconids are lingual to the protoconids and do not project labially (Fig. 5C, F). The entoconids are robust and rounded in section (i.e., are not labiolingually compressed; Fig. 5C, F) compared to that of other *Sparassocynus* species. The hypoconulids are well developed, especially on m2–3, and locked in the deep hypoconulid notchs of the respective posterior molars.

TABLE 1. Dental measurements (in millimeters) of studied specimens of Sparassocynidae and '*Sparassocynus*' *heterotopicus*. MH, mandibular height taken below the m4; L, length; W, width; trig., trigonid; tal., talonid. An asterix (*) means that the measurement is approximate; (**) measurement taken from Reig (1958a).

Taxon	Col. number	MH	Lp2	Wp2	Lp3	Wp3	Lm1	Ltalm2
Sparassocynus maimarai	JUY-P-48	9	2.7	1.4	2.2	1.5	2.6	0.8
Sparassocynus derivatus	MMP 851 M	8.5	2.9	1.7	2.6	1.5	2.8	0.8
Sparassocynus derivatus	MMP 412 M	10	2.7	1.7	2.5	1.7	2.9	0.8
Sparassocynus derivatus	MMP 1088	9	2.5	1.3	2.5	1.5	2.5	0.8
Sparassocynus derivatus	MMP 1379 M	11	2.7	1.6	2.1	1.6	2.6	0.8
Sparassocynus derivatus	MACN-PV 17909				2.7	2	3.1	0.9
Hesperocynus dolgopolae	FMNH P 14469	5.2**	2.6	1.5	2.2*		2.7	0.9
Hesperocynus dolgopolae	MLP 86-VII-10-1	6.5			3	1.4	2.8	1.0*
Sparassocynus bahiai	MLP 11-119	11.5	3	1.7	2.6	1.7	2.9	1
Sparassocynus bahiai	MACN 15403	10.2			2.6	1.6	2.6	0.8
Sparassocynus bahiai	MACN 2927	9.3			2.4*	1.8	3	1
'*Sparassocynus*' *heterotopicus*	MNHN-BOL-011896							0.9

continued.

Taxon	Ltrigm1	Wtalm1	Ltalm1	Lm2	Wtrigm2	Ltrigm2	Wtalm2	Ltalm2
Sparassocynus maimarai	1.8	1.9	0.8	3	2.1	2.2	2.2	0.8
Sparassocynus derivatus	2.1	2.1	0.7	3.2	2.1	2.4	2.3	0.8
Sparassocynus derivatus	2.1	2.2	0.8	3.2	2.3	2.4	2.5	0.8
Sparassocynus derivatus	1.7	1.8	0.8	3	2	2.2	2	0.8
Sparassocynus derivatus	1.8	2	0.8	3	2.1	2.2	2.2	0.8
Sparassocynus derivatus	2.2	2.1	0.9	3.4	2.4	2.5	2.3*	0.9
Hesperocynus dolgopolae	1.8	2	0.9	2.9	2.1	2	2.2	0.9
Hesperocynus dolgopolae	1.9	2	0.9				2.1	1.0*
Sparassocynus bahiai	2.1*	2.1	0.8*	3.5	2.3	2.5	2.3	1
Sparassocynus bahiai	2	2.1	0.6	3.3		2.5	2.3	0.8
Sparassocynus bahiai	2.2	1.9	0.8	3.4	2.15	2.4	2.2	1
'*Sparassocynus*' *heterotopicus*				3.2		2.3	1.8	0.9

continued.

Taxon	Lm3	Wtrigm3	Ltrigm3	Wtalm3	Ltalm3	Lm4
Sparassocynus maimarai	3.4	2.2	2.4	2	1	3.5
Sparassocynus derivatus	3.7	2.3	2.7	2.2	1	4.2
Sparassocynus derivatus	3.8	2.6	2.8	2.4	1	4.3
Sparassocynus derivatus	3.4	2.2	2.5	2.2	0.9	4
Sparassocynus derivatus	3.5	2.4	2.4	2.3	1.1	3.9
Sparassocynus derivatus	3.7	2.6	2.7	2.3	1	4.4
Hesperocynus dolgopolae	3.4	2.2	2.3	2.1	1.1	
Hesperocynus dolgopolae	3.6	2.25	2.4	2	1.2	3.8
Sparassocynus bahiai	4	2.5	2.9	2.3	1.1	4.4
Sparassocynus bahiai	3.7	2.5	2.8	2.35	0.9	4.2
Sparassocynus bahiai	4	2.3	2.9	2.1	1.1	4.4
'*Sparassocynus*' *heterotopicus*	3.6	2	2.5	17.5	1.1	3.6
	LM2	WM2	LM3	WM3	LM4	AM4
'*Sparassocynus*' *heterotopicus*	3.25	2.8	3.5	3.2	3.7	3.4

continued.

Taxon	Wtrigm4	Ltrigm4	Wtalm4	Ltalm4	Lm1-3	Lm2-3
Sparassocynus maimarai	2.2	2.5	1.5	1	9	6.4
Sparassocynus derivatus	2.5	3.1	1.5	1.1	9.7	6.9
Sparassocynus derivatus	2.6	3	1.8	1.3	9.8	7
Sparassocynus derivatus	2.2	2.6	1.5	1.4	9	6.4
Sparassocynus derivatus	2.5	2.9	1.7	1	9.2	6.5
Sparassocynus derivatus	2.5	3	1.9	1.4	10.1	7.1
Hesperocynus dolgopolae					9	6.3
Hesperocynus dolgopolae	2	2.8	0.6	1	9	6.2*
Sparassocynus bahiai	2.5	3	1.8	1.4	10.2	7.5
Sparassocynus bahiai	2.5	3	1.7	1.2	9.5	7
Sparassocynus bahiai	2.4	3	1.6	1.4	10	7.4
'*Sparassocynus*' *heterotopicus*	2	2.3	1.5	1.3		6.8

TABLE 2. Mandibular and dental ratios of Sparassocynidae species and '*Sparassocynus*' *heterotopicus* estimated from measurements in Table 1. Upper values are means and lower values are ranges; sample size (*n*) is given in taxon column.

Taxon	Lm1/Ltal	Lm2/Ltal	Lm3/Ltal	Wtrigm4/wtal
Sparassocynus maimarai **sp. nov.** (*n*=1)	3.25	3.75	3.4	1.47
Sparassocynus derivatus (*n*=5)	3.49 (3.13–4)	3.86 (3.75–3.78)	3.63 (3.18–3.8)	1.42 (1.32–1.67)
Sparassocynus bahiai (*n*=3)	3.9 (3.63–4.33)	3.9 (3.4–4.13)	3.8 (3.64–4.11)	1.45 (1.39–1.5)
Hesperocynus dolgopolae (*n*=2)	3.06 (3–3.11)	3.22	3.05 3–3.09)	3.33
Sparassocynus heterotopicus (*n*=1)	–	3.56	3.27	1.33

continued.

Taxon	Lm1/Lm4	Lm1-3	Lm1-3/MH	Lm2-3/MH
Sparassocynus maimarai **sp. nov.** (*n*=1)	0.74	9	1	0.71
Sparassocynus derivatus (*n*=5)	0.67 (0.63–0.7)	9.56 (9–10.1)	0.94 (0.84–1.14)	0.7 (0.59–0.81)
Sparassocynus bahiai (*n*=3)	0.65 (0.62–0.68)	9.9 (9.5–10.2)	0.97 (0.89–1.08)	0.71 (0.65–0.8)
Hesperocynus dolgopolae (*n*=2)	0.74	9 (9–9)	1.44 (1.38–1.5)	1.13 (1.04–1.21)
Sparassocynus heterotopicus (*n*=1)	–	–	–	1.24

Discussion

The assignation of the specimen JUY-P-48 to the Sparassocynidae is based on the presence of the following diagnostic characters of the family (according to Reig & Simpson, 1972; Goin, 1991): (1) high dentary, (2) long symphysis, (3) premolars without diastema, (4) lower molars with high trigonids and low talonids, (5) short and narrow talonids, and (6) metaconid small and partly fused with protoconid.

TABLE 3. Compared mandibular and dental characters diagnostic of Sparassocynid species.

Character	*Hesperocynus dolgopolae*	*Sparassocynus bahiai*
horizontal mandibular ramus (Lm1-3/MH)	shallow	deep
m1-3 talonid relative length (Lm1/Ltal; Lm2/Ltal; Lm3/Ltal)	long	short
relative width of talonid and trigonid of m4 (Wtrigm4/wtal)	narrow m4 talonid	wide m4 talonid
entoconid shape	gracile and labiolingually compressed	gracile and labiolingually compressed
lingual cingulum between para- and metaconid	absent	absent
relative length of m1 and m4 (Lm1/Lm4)	relatively longer m1 with respect to the m4	relatively longer m1 with respect to the m4

continued.

Character	*Sparassocynus derivatus*	*Sparassocynus maimarai* **sp. nov.**
horizontal mandibular ramus (Lm1-3/MH)	deep	deep
m1-3 talonid relative length (Lm1/Ltal; Lm2/Ltal; Lm3/Ltal)	short	short
relative width of talonid and trigonid of m4 (Wtrigm4/wtal)	wide m4 talonid	wide m4 talonid
entoconid shape	gracile and labiolingually compressed	robust and conical
lingual cingulum between para- and metaconid	absent	present
relative length of m1 and m4 (Lm1/Lm4)	relatively longer m1 with respect to the m4	relatively longer m1 with respect to the m4

In the context of the Sparassocynidae specimen JUY-P-48 shared several characters with *Sparassocynus* species. Like them it has a deeper dentary, talonids of m1–3 relatively shorter, and talonid of m4 proportionally wider than that of *Hesperocynus dolgopolae* (Figs. 3 and 5A; Tables 2 and 3). Forasiepi *et al.* (2009) have considered that two characters mentioned previously as diagnostic of the Sparassocynidae (Reig & Simpson, 1972; Goin, 1991) are actually diagnostic of *Sparassocynus*: an extremely reduced metaconid fused with the protoconid and slightly imbricate premolar tooth row. Unfortunately, the first of these traits could not be evaluated in the specimen JUY-P-48. It is hard to establish if the size difference between metaconid and protoconid was similar to that in *S. bahiai* and *S. derivatus* because of worn degree of molars (Figs. 3 A–B and 5A). In relation to the second character, we observed that the imbrication degree of the premolars shows intraspecific variability, at least in one species of this genus; therefore, we considered that this trait is not diagnostic of *Sparassocynus*. All studied specimens of *S. bahiai* have slightly imbricate premolars, but in *S. derivatus* specimens premolars could be not imbricated (e.g., MMP 1379) to slightly imbricated (e.g., MMP 412).

Compared with *S. derivatus* and *S. bahiai*, specimen JUY-P-48 is characterized by its smaller size, the m1 relatively longer with respect to the m4, the proportionally robust and conical entoconids, and the presence of a lingual cingulum extended between para- and metaconid on the m1–3 (Tables 2 and 3). These characters indicate that the new specimen from Maimará locality represents a new species of *Sparassocynus*: *S. maimarai* **sp. nov.**

Didelphoidea indet.

'*Sparassocynus*' *heterotopicus* Villarroel & Marshall, 1983
Fig. 4, Tables 1–2

Holotype. MNHN-BOL-011896, fragment of a left maxilar with M1–3 (Fig. 4A), fragment of a left mandible with m2–4 (Fig. 4B–C), and an edentulous right mandible with roots of c–m4.

Locality and Horizon. Locality of Umala, Department of La Paz, Bolivia. Umala Formation (Montehermosan, early Pliocene *sensu* Marshall *et al*., 1979).

Comparative description. The general morphology of the dentition of *S. heterotopicus* shows characters common to diverse carnivorous didelphoids (Goin & Pardiñas, 1996: 351; Forasiepi *et al*., 2009); among them are the upper molars with long metacristae and small protocones, and lower molars with small talonids and strong paracristids. Upper molars of MNHN-BOL-011896 (Fig. 4A) have a stylar shelf narrower than that of didelphids and as wide as in sparassocynids. The StA is absent on M1 and M3 and reduced on M2. On M1 the StB is the largest stylar cusp (in section it is half of the size of paracone), the StD is smaller than StB and subdivided into two cusps; finally StE is low and poorly developed. On M2 the StB is proportionally larger than on M1 and, as in the M1, StB is larger than StD; this latest is not subdivided and StE is missing. A reduced StB is present on M3. In contrast to the extant compared Didelphidae (*Lutrolina*, *Didelphis*, *Monodelphis, Thylamys,* and *Caluromys*) and the extinct didelphids *Thylatheridium*, *Thylophorops*, and *Hyperdidelphys*, stylar cusps B and D are proportionally smaller. Compared to the Sparassocynidae, particularly *Sparassocynus*, the StB and StD are similarly developed, but MNHN-BOL-011896 differs by having a subdivided StD on M1. Regarding relative sizes between StB and StD on M1–2, MNHN-BOL-011896 is similar to the extinct didelphid *Hyperdidelphis* and sparassocynids in wich StB is larger than StD and differs from the extant compared didelphids, the extinct didelphid *Thylophorops* and *Thylatheridium*, by having a StB smaller than the StD. On M1 the preparacrista is short and points towards the parastylar corner whereas on M3 ends labially at the anterior base of the StB; on M2 the labial end of the preparacrista could not be evaluated because of wear. In the morphology of the preparacrista of M1, MNHN-BOL-011896 differs from all compared taxa in which this crest joins the StB, excepting *Didelphis*, in which the preparacrista contacts the StA. On the other hand, the arrangement of the distal end of the preparacrista in the M3 of Umala specimen is similar to that of the M3 of *Thylophorops, Hyperdidelphis parvula* (Goin & Pardiñas, 1996), and all compared extant didelphids (except *Didelphis*); it also differs from the M3 of sparassocynids and *Thylatheridium* in which this crest joins the StB. The postmetacrista is long, sharp, and oblique as in carnivorous didelphids (e.g., *Lutreolina*), but is slightly shorter than in sparassocynids (a long metacrista is a diagnostic character of the sparassocynids, Reig & Simpson, 1972, Goin, 1991). The metacone is large and the paracone is reduced as in other carnivorous forms (Forasiepi *et al*., 2009); despite both cusps are closer to each other than in didelphids, they are not fused as in sparassocynids (Reig & Simpson, 1972; Goin, 1991). The paracone is less reduced than the metacone compared to sparassocynids and didelphids. There is no evidence of para- and metaconule on M1–2, but on the M3 a small paraconule is present at the base of the paracone and the end of the preprotocrista. The protocone on M1–3 has a small occlusal surface in relation to the total molar occlusal surface; in this proportion, protocones are smaller than those of didelphids and larger than in sparassocynids. Furthermore protocones in *S. heterotopicus* are eccentric, similarly to those in sparassocynids and some didelphids (e.g., *Thylophorops* and *Hyperdidelphys*). The ectoflexus is poorly developed in the M1–2 and strongest in the M3, as occurs, for example, in the sparassocynids and most didelphids (Voss & Jansa, 2009).

The mandible of MNHN-BOL-011896 is broken in front of the m2 and has lost most of the coronoid and angular processes, as well as a portion of the condylar process. The horizontal ramus is shallow (see Table 2) and bears a strong labial scar for the masseteric muscle on its posterolateral surface; the masseteric fossa appears to have been deep as in *Lutreolina*. The articular condyle is transversely elongated and the angular processes acute and strongly inflected as is common among didelphids (Voss & Jansa, 2009). Lower dentition of MNHN-BOL-011896 is partially preserved (Fig. 4B–C). The metaconid, part of the protoconid of m2, and the metaconid of m4 are lost, so the morphology of the trigonid cusps (high and relative size) can be better described from those whole cusps of m3. Similarly to some didelphids (e.g., *Thylatheridium*), the trigonid of the m3 is higher than the talonid, but not as tall as it is in sparassocynids. The paraconid is a robust cusp (as in m2 and m4), similar to the metaconid in height, but quite larger in section. The metaconid is a small cusp located close to the protoconid resembling sparassocynids and, in less extent, *Lutreolina* among didelphids. A strong paracristid is developed along the protoconid and paraconid cusps; it is not straight (e.g., *Monodelphis*, *Thylamys*, and *Didelphis*) but forms an obtuse angle between the proximal (premetacristid) and distal (postparacristid) portions as occurs, for example, in sparassocynids, *Thylatheridium* and *Lutreolina*. The anterobasal cingulum of m2–4 is narrow and it extends posteriorly up to the anterior wall of the protoconid. The talonids of m2–4 are very shallow and have a smaller

occlusal surface than trigonids; on m2–3 talonids are short and narrow like in the sparassocynids (Figs. 2, 4B and 5A; Table 2). In all molars the hypoconid projects slightly, not exceeding the labial wall of the protoconid. In the m2 both cusps are equally projected but in the m3 the hypoconid is placed more lingually than the protoconid, thus the talonid is narrower in the m3 than in the m2. In the m4 the hypoconid is a small cusp positioned behind the posterior wall of the protoconid. The cristid obliqua is slightly oblique on m2, and antero-posteriorly oriented on m3–4. The entoconid is a poorly differentiated cusp on m2–3 (better seen on m2), and absent on m4. The hypoconulid is smaller than the entoconid and positioned behind this cusp on m2–3. The talonid of m4 is relatively wider than in Sparassocynidae species and several didelphids such as *Thylatheridium* and *Monodelphis*. In contrast with these taxa, *S. heterotopicus* lacks a cingulum along the labial wall of the talonid bellow the hypoconid; in this regard, the talonid of m4 of *S. heterotopicus* is similar to that in *Lutreolina* and *Didelphis*.

Discussion

In its dental and mandibular morphology *Sparassocynus heterotopicus* exhibits a combination of characters of diverse didelphoids, as well as unique characters. Similarly to the compared didelphids, and in contrast to sparassocynids (see diagnostic characters above), *S. hetrotopicus* have a shallow mandible and lower molars with high trigonids and low talonids. Certain traits as the presence of a preparacrista on M3 ending at the anterior base of the StB and the absence of a labial cingulum on talonid of m4 are shared by *S. heterotopicus* and some didelphids. Alternatively, some characters such as reduced stylar cusps, reduced metaconids, and short and narrow talonids relate *S. heterotopicus* to the sparassocynids. A large paracone is a trait unique of *S. heterotopicus* and some other characters, all of them on upper molars, have a morphology intermediate between didelphids and sparassocynids: the lenght of the metacrista on M3, proximity among para- and metacone, and size of protocones.

From this comparative study of the morphology of *S. heterotopicus*, it could be concluded that there is no ground for an unambiguous familiar assignation. To date, there is no published phylogeny including extant and extinct didelphoids (but see advances in Beck *et al.*, 2012) that allow exploring the phylogenetic relationships of *S. heterotopicus*. In relation to this, the taxonomic value of some dental characters, possibly convergent among carnivorous didelphoids, should be taken carefully because they could support erroneous taxonomic assignations (Goin & Pardiñas, 1996). In view of the taxonomic uncertainty expressed above, we propose to consider *Sparasocynus heterotopicus* a Didelphoidea *indet*., and left this species in open nomenclature as '*Sparassocynus*' *heterotopicus*.

Final remarks and conclusions

The origin and earliest evolutionary history of didelphids and the close related sparassocynids (Goin, 1991, 1995) are still poorly known. Even though the clade including extant didelphids is thought to originate in the Eocene or early Oligocene (see Jansa *et al*., 2014: Table 2), didelphoids are unknown yet from Paleogene fossil assemblages (Forasiepi *et al*., 2009); to date, the earliest record of this superfamily comes from the early Miocene of southern South America (Goin *et al*., 2007). The didelphoids are well documented from the late Miocene with the appearance of Sparassocynidae and some Didelphidae (e.g., *Hyperdidelphys*, *Thylatheridium*, and *Thylamys*; Goin *et al*., 2000). *Sparassocynus maimarai* **sp. nov.** is the oldest record of the genus, which suggests that the two main lineages of Sparassocynidae (i.e., *Sparassocynus* and *Hesperocynus*) were already differentiated by the late Miocene. The end of the Miocene is viewed as the period when didelphids began to invade South American dry-forest habitats concurring with the geographic expansion of xeric-adapted plants (Jansa *et al*., 2014). The climatic-environmental change to more arid conditions from the late Miocene in southern South America (Ortiz-Jaureguizar & Cladera, 2006) could explain the diversification of the sparassocynids. Reig & Simpson (1972) pointed out that some cranial structures of *Sparassocynus* (e.g., large hypo- and epitympanic sinuses) could be interpreted as open habitat adaptations; additionally, faunal associations where the first sparassocynids were recorded are indicative of open paleoenvironments (Goin *et al*., 2000). Particularly, sedimentary deposits of the Maimará Formation would have been developed in an ephemeral fluvial system under arid and semi-arid conditions (Galli *et al*., 2012).

As a result of the present study '*Sparassocynus*' *heterotopicus* is considered a Didelphoidea *indet*. instead of a

Sparassocynidae; thereby, the distribution of sparassocynids that previously included the Pliocene of Bolivia is now restricted, most certainly, to the late Miocene and Pliocene of central and NW of Argentina. *Sparassocynus maimarai* **sp. nov.** is one of the few mammals recovered from the Maimará Formation under precise stratigraphic control, which is fundamental for possible biostratigraphic correlations between Maimará Formation and the remaining late Miocene-Pliocene stratigraphic units of NWA. We expect that the joint study of the new species, the remaining fossil mammals recovered in the Maimará Formation, and their geological context will improve the knowledge of the paleobiogeographic and paleoenvironmental setting where mammal faunas of NWA evolved towards the end of the Neogene.

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