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First record of *Indalecia* (Mammalia, Litopterna?, Indaleciidae) in the Río Loro Formation (early Paleogene, Tucumán Province, Argentina)

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Recibido: 22 de marzo 2023 - **Aceptado:** 4 de septiembre 2023 - **Publicado:** 27 de septiembre 2023

Para citar este artículo: Luis Sebastián Saade, Daniel Alfredo García-López, María Judith Babot, Pablo Joaquín Alonso-Muruaga, & Guido Ezequiel Alonso (2023). First record of *Indalecia* (Mammalia, Litopterna?, Indaleciidae) in the Río loro Formation (early Paleogene, Tucumán Province, Argentina). *Publicación Electrónica de la Asociación Paleontológica Argentina* 23(2): 134–145.

Link a este artículo: http://dx.doi.org/10.5710/PEAPA.04.09.2023.459

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ISSN 2469-0228

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ARTÍCULO Año 2023 - 23(2): 134–145 PeAPA Publicación Electrónica ASOCIACIÓN PALEONTOLÓGICA ARGENTINA

FIRST RECORD OF *INDALECIA* (MAMMALIA, LITOPTERNA?, INDALECIIDAE) IN THE RÍO LORO FORMATION (EARLY PALEOGENE, TUCUMÁN PROVINCE, ARGENTINA)

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Abstract. The Río Loro Formation (early Paleogene, Tucumán Province, northwestern Argentina) has yielded several endemic vertebrates, including turtles, crocodiles, and mammals. The age of this unit is currently under discussion given the lack of absolute chronological data, although recent works favored a middle Paleocene–early Eocene age. In this contribution, we present a left maxillary fragment (PVL 5901), preserving part of the M1 and the M2. A first analysis indicates a close relationship with *Indalecia* (Litopterna?, Indaleciidae), a genus previously recorded for the Lower Lumbrera Formation (?Ypresian; Salta Province, northwestern Argentina). Given that the Indaleciidae and the representatives of Amilnedwardsidae and Notonychopidae were considered related in the context of the order Notopterna, a comparison was made between PVL 5901 and these taxa, confirming its resemblance with *Indalecia*. However, PVL 5901 differs from *Indalecia grandensis* (type and only species of the genus) by the presence of a cuspule on the base of the ectoflexus, the absence of a small fossette mesial to the distolabial fossette, and a conspicuous entoflexus. Hence, we refer PVL 5901 to *Indalecia* sp. This is the first common faunal element between the Río Loro and Lower Lumbrera formations. Nevertheless, the marked taxonomic discrepancies between the Río Loro vertebrate assemblage and other early Paleogene units contrast with this single common record, and a partial temporal correspondence between the Río Loro and Lower Lumbrera formations is not supported here. Instead, this record indicates a more extended temporal and geographical distribution for the genus *Indalecia* in northwestern Argentina.

Key words. Río Loro Formation. Lower Lumbrera Formation. Notopterna. Biostratigraphy. Northwestern Argentina.

Resumen. PRIMER REGISTRO DE *INDALECIA* (MAMMALIA, LITOPTERNA?, INDALECIIDAE) EN LA FORMACIÓN RÍO LORO (PALEÓGENO TEMPRANO, PROVINCIA DE TUCUMÁN, ARGENTINA). La Formación Río Loro (Paleógeno temprano, provincia de Tucumán, noroeste argentino) ha brindado diversos vertebrados endémicos, incluyendo tortugas, cocodrilos y mamíferos. La edad de esta unidad está actualmente en debate, dada la falta de dataciones absolutas. Aun así, trabajos recientes propusieron una edad paleocena media–eocena temprana. En esta contribución, presentamos un fragmento maxilar izquierdo (PVL 5901) con parte del M1 y el M2. Un primer análisis indica una relación cercana con *Indalecia* (Litopterna?, Indaleciidae), género previamente registrado en la Formación Lumbrera Inferior (?Ypresiense; provincia de Salta, noroeste argentino). Dado que los Indaleciidae y los representantes de Amilnedwardsidae y Notonychopidae fueron considerados relacionados en el contexto del orden Notopterna, se realizaron comparaciones entre PVL 5901 y estos taxones, confirmándose la similitud con *Indalecia*. Sin embargo, PVL 5901 difiere de *Indalecia grandensis* (especie tipo y única del género) por la presencia de una cúspula sobre la base del ectoflexo, la ausencia de una pequeña foseta mesial a la foseta distolabial y un entoflexo conspicuo. Así, referimos el espécimen PVL 5901 a *Indalecia* sp. Este es el primer elemento faunístico común entre las formaciones Río Loro y Lumbrera Inferior. Sin embargo, las marcadas discrepancias taxonómicas entre la asociación de vertebrados de Río Loro y otras unidades del Paleógeno temprano contrastan con este único registro en común, por lo que no se respalda una correspondencia temporal entre las formaciones Río Loro y Lumbrera Inferior. Por el contrario, este registro indica una distribución geográfica y temporal más extensa para este género en el noroeste argentino.

Palabras clave. Formación Río Loro. Formación Lumbrera Inferior. Notopterna. Bioestratigrafía. Noroeste argentino.

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Paleontological evidence from the Paleogene Río Loro Formation of NWA is difficult to integrate with respect to other coeval stratigraphic units of the region, such as the Mealla, Maíz Gordo, and Lower Lumbrera formations. Remarkably, and in spite of the increased amount of paleontological information obtained in recent decades for the Río Loro Formation, the uncertain phylogenetic position of most records (*e.g.*, *Lorosuchus* Pol & Powell, 2011, *Satshatemnus* Soria, 1989a, *Eoastrapostylops* Soria & Powell, 1981), precludes an accurate characterization of its fossil vertebrate fauna.

Since the first vertebrate remains finding conducted by Powell & Palma (1981), numerous fossil specimens have been documented, illustrating an intriguing and abundant vertebrate fauna composed by crocodiles, turtles, and—mainly—by mammals (Powell & Palma, 1981; Soria, 1989a, 1989b, 1989c; Pol & Powell, 2011; Powell & Ortiz, 2014; Babot *et al.*, 2017; Gelfo *et al.*, 2020). Nevertheless, although several contributions improved the paleontological knowledge of the Río Loro Formation, the lack of absolute temporal data reinforces the necessity of refining the relative age of the fossil-bearing levels. Previous studies including comparisons with other Paleogene faunal assemblages supported an age between the early Paleocene and early Eocene (Powell & Palma, 1981; Soria & Powell, 1981; Ortiz-Jaureguizar, 1996; Pascual & Ortiz-Jaureguizar, 2007; Woodburne *et al.*, 2014; Kramarz *et al.*, 2017). Moreover, a recent contribution favored a Paleocene age (*i.e.*, the pre-Itaboraian SALMA part of the proposed age range for the Río Loro Formation; see discussion at Gelfo *et al.*, 2020). These efforts have faced the problem of the singular and endemic nature of the fauna of the Río Loro Formation, which limits its taxonomic and phylogenetic assessment and temporal correlations with other Paleogene vertebrate assemblages. Deeper revisions and integrative studies are required, both for already described taxa (*e.g.*, *Eoastrapostylops*, *Satshatemnus*) and for new unpublished materials.

Among these, Powell (2006) mentioned the presence of an indaleciid mammal (Litopterna?) in the Río Loro Formation levels (Powell, 2006; Powell & Ortiz, 2014; Gelfo *et al.*, 2020) but a more precise assignment of this material was not undertaken. In this contribution, besides establishing its genus assignment, we discuss its taxonomic context and some biostratigraphic issues related to the early Paleogene communities of NWA.

Location and stratigraphic setting

The Río Loro Formation (Bossi, 1969) crops out in several localities distributed to the north of the city of San Miguel de Tucumán in Tucumán Province (NWA). These strata unconformably overlie Precambriam–Cambrian metamorphic rocks of the Medina Formation as well as Cretaceous sandstones and conglomerates of the El Cadillal Formation, and are, in turn, overlain by Eocene mudstone beds of the Río Nío Formation and Miocene greenish to yellowish mudstone and marl deposits of the Río Salí Formation (Bossi *et al.*, 1998; Georgieff *et al.*, 2014). In the study area, the unit rests over the El Cadillal Formation and is covered by the Río Salí Formation (Fig. 1).

The Río Loro Formation is represented by a siliciclastic continental succession, mainly composed of light greyish to pinkish very coarse- to medium-grained sandstones interbedded with reddish to brownish mudstones and sandy-mudstones containing rhizoliths and calcretes. Environmentally, these deposits are interpreted as accumulated in a fluvial system, characterized by sandy moderate- to high-sinuosity channels with well-developed muddy to sandy floodplains preserving paleosoils (Powell & Palma, 1981; Bossi *et al.*, 1998; Alonso-Muruaga *et al.*, 2022). Fossil-bearing intervals, particularly with skeletal remains, are typically related to floodplain deposits; although locally, bioturbation structures produced by plants and invertebrates are present in sandy channel beds (Alonso-Muruaga *et al.*, 2022).

MATERIALS AND METHODS

The specimen here studied (PVL 5901) is held in the PVL, Facultad de Ciencias Naturales and Instituto Miguel Lillo (Universidad Nacional de Tucumán, Argentina). In order to reach a solid systematic background, PVL 5901 was compared not only with the holotype of the species *Indalecia grandensis* Bond & Vucetich, 1983 (PVL 4186), but also with other taxa closely related to the genus *Indalecia* Bond & Vucetich, 1983 (*e.g.*, *Notonychops* Soria, 1989c, *Adiantoides* Simpson & Minoprio, 1949, *Amilnedwardsia* Ameghino, 1901). Most of these comparisons were made directly on

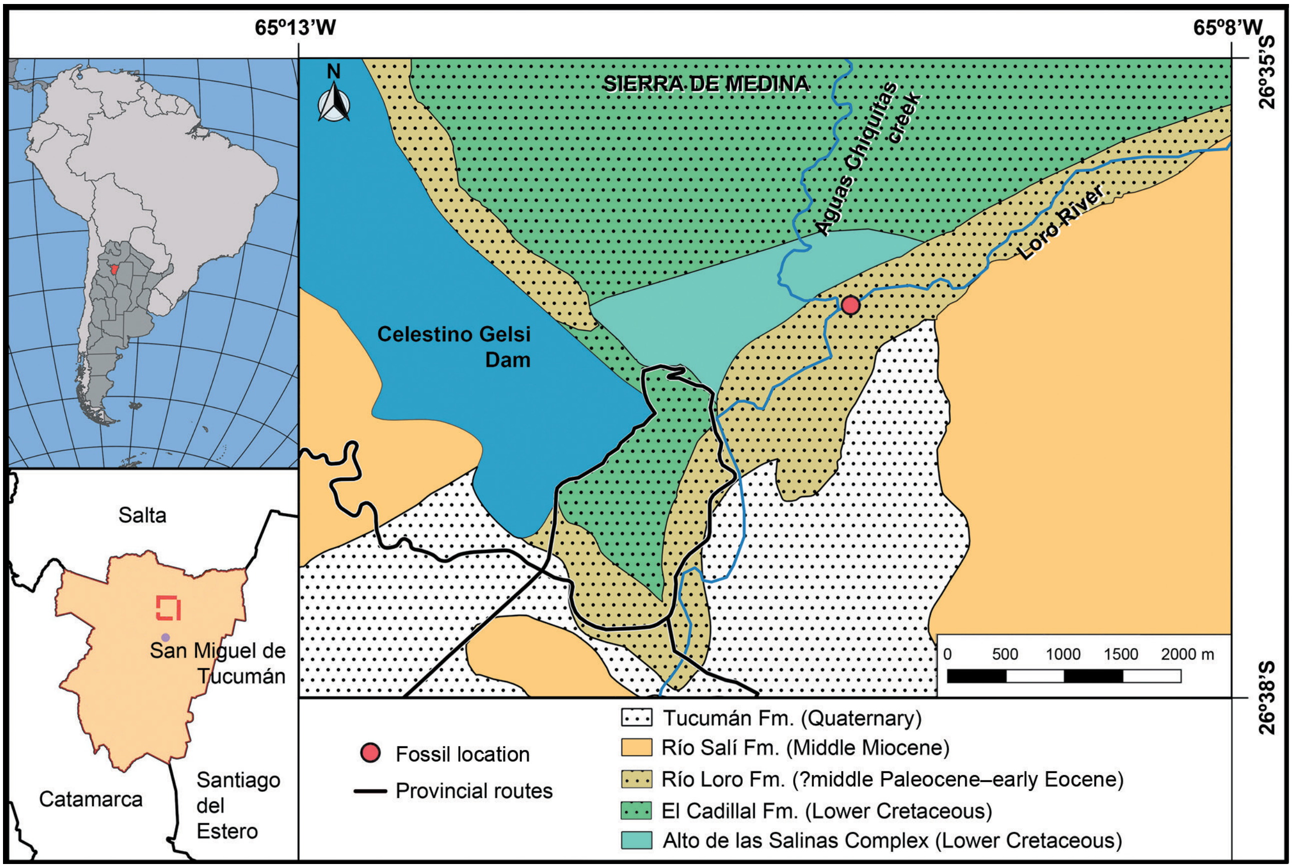

Figure 1. Map showing the geological context and location of the specimen **PVL 5901**.

the materials (*Notonychops*, *Amilnedwardsia*), but other were based on bibliographic sources (*e.g.*, Simpson & Minoprio, 1949; Cifelli & Soria, 1983; Soria, 1989a, 1989b; Bonaparte & Morales, 1997). Dental nomenclature follows Hershkovitz (1971) and Smith & Dodson (2003), and more specific surveys performed on South American ungulate groups (*e.g.*, Gelfo, 2006; García-López & Powell, 2011; Castro *et al.*, 2021).

Institutional acronyms. AMNH, American Museum of Natural History, New York, USA; **MACN-A,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"-Colección Ameghino, Ciudad Autónoma de Buenos Aires, Argentina; **MCNAM-PV,** Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano"-Colección de Paleovertebrados, Mendoza, Argentina; **PVL,** Colección Paleontología de Vertebrados Lillo, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; **UNPSJB-Pv,** Universidad Nacional de la Patagonia San Juan Bosco-Colección de Paleontología de Vertebrados, Repositorio Científico y Didáctico Dr. Eduardo Musacchio, Comodoro Rivadavia, Argentina.

Other abbreviations. M, upper molar; **NWA,** northwestern Argentina; **SALMA,** South American Land Mammal Age.

SYSTEMATIC PALEONTOLOGY

Order Litopterna? Ameghino, 1889
Family Indaleciidae Bond & Vucetich, 1983

Genus ***Indalecia*** Bond & Vucetich, 1983

Type species. *Indalecia grandensis* Bond & Vucetich, 1983. Early Eocene, Lower Lumbrera Formation (?Ypresian; Fernicola *et al.*, 2021; del Papa *et al.*, 2022). Pampa Grande, Salta Province, Argentina.

Indalecia **sp.**
Figure 2.1–2.4

Referred specimen. PVL 5901, left maxillary fragment with distal part of M1 and complete M2.

Stratigraphic and geographic occurrence. Confluence between the Aguas Chiquitas Creek and the Loro River, northeast of the Celestino Gelsi Dam, Tucumán Province (Fig. 1); 26° 36′ 26.1″ S; 65° 10′ 27.6″ W. Río Loro Formation, ?middle Paleocene–early Eocene (Gelfo *et al.*, 2020).

Description. The specimen represents an adult individual. This is evident given the wear degree of the teeth, which is similar to that of the holotype of *Indalecia grandensis* (PVL 4186). Both molars preserved in the specimen PVL 5901 are brachydont. The distal part of the M1 was preserved, bearing half of the distolabial fossette, most of the central fossa, the metastyle, and the labial end of the postcingulum (Fig. 2.1–2.2). These structures are basically indistinguishable from those observed in the M2 (see below). The main difference is related to the central fossa, which is considerably shallower than that of the M2.

The M2 shows a subtrapezoidal occlusal outline and moderate wear (Fig. 2; measurements are given in Tab. 1). This molar preserves the stylar cusps (parastyle and metastyle), the paracone, metacone, protocone, and hypocone. Although affected by wear, we also distinguish the presence of the paraconule and metaconule. The trigon basin is wide. The central fossa is well developed, it is located at the center of the basin, and is obliquely arranged. The mesiolabial and distolabial fossettes are conspicuous and subcircular in outline, and show a relatively wide and

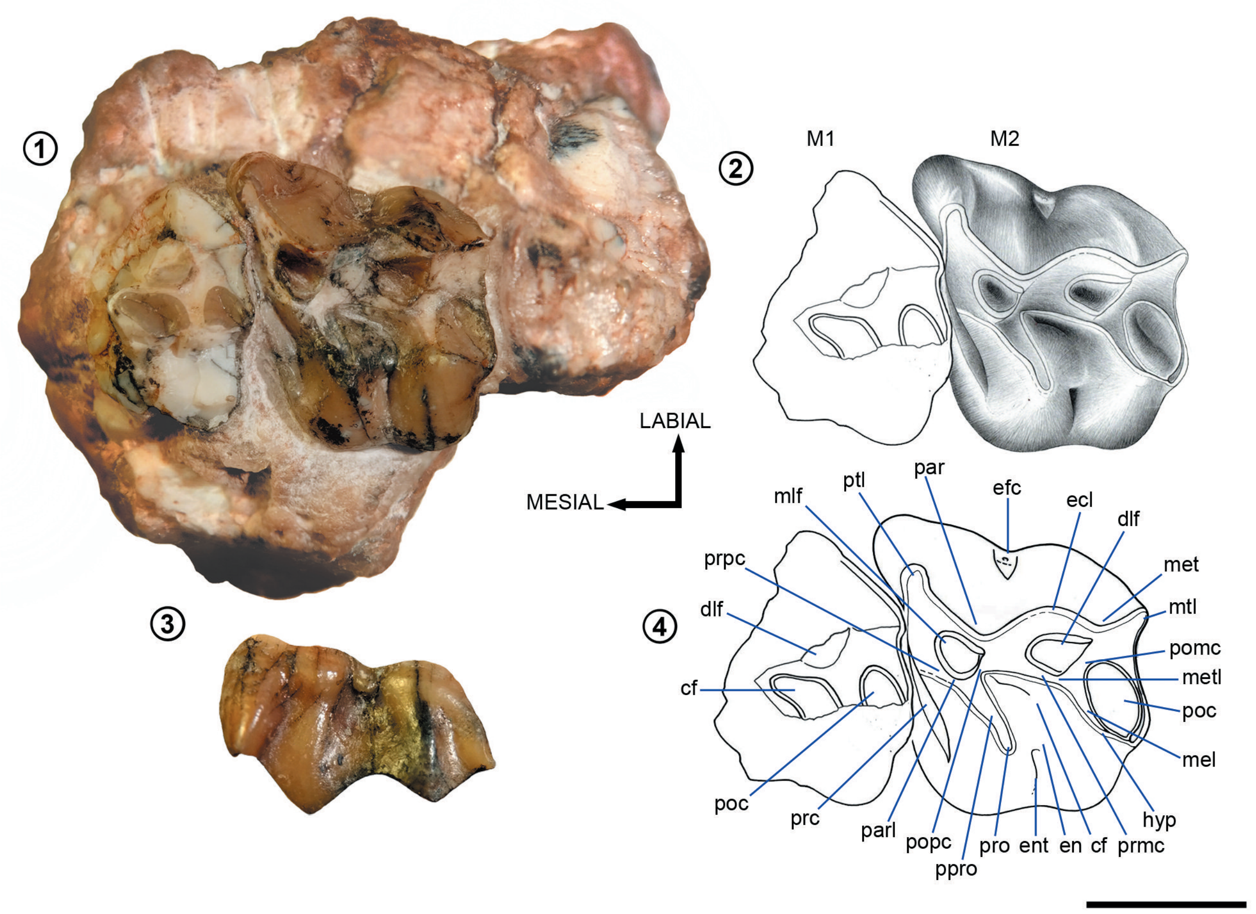

Figure 2. ***Indalecia*** **sp., PVL 5901. 1,** Left maxillary fragment with partially preserved M1 and complete M2 in occlusal view; **2,** Drawing showing teeth details; **3,** M2 in labial view; **4,** Drawing of dental features mentioned in the text. Abbreviations: **cf**, central fossa; **dlf,** distolabial fossette; **ecl,** ectoloph; **efc,** ectoflexus cuspule; **en,** entocrista; **ent,** entoflexus; **hyp,** hypocone; **mel,** metaloph; **met,** metacone; **metl,** metaconule; **mlf,** mesiolabial fossette; **mtl,** metastyle; **par,** paracone; **parl,** paraconule; **poc,** postcingulum; **pomc,** postmetaconular crista; **popc,** postparaconular crista; **ppro,** preprotocrista; **prc,** precingulum; **prmc,** premetaconular crista; **pro,** protocone; **prpc,** preparaconular crista; **ptl,** parastyle. Scale bar= 5 mm.

bowl-like bottom. These fossettes, subequal to each other, are aligned on a mesiodistal axis. The lingual edge of the mesiolabial fossette is formed by the paraconule, which presents a well-developed preparaconular crista (connected to the parastyle), a wide postparaconular crista (forming the distal edge of the fossette), and a straight preprotocrista connecting the paraconule and protocone. Both the preprotocrista and the preparaconular crista are integrated into a protoloph. Distally, there is a narrow and straight dentine bridge between the central fossa and the distolabial fossette. This bridge is formed mainly by the premetaconular crista. The metaconule is also connected to the metacone by means of the postmetaconular crista (forming the distal wall of the distolabial fossette) and to the hypocone by means of a straight and short crista. The connection between this crista and the postmetaconular crista builds up the metaloph (hence, this loph is curved mesially, toward the metaconule). The paracone and metacone are subequal, the former being slightly higher and located more lingually than the latter. The parastyle is large, labially elongated, and imbricated with the distolabial region of the M1 (*i.e.*, the metastyle). The labial column of the metacone is more labially projected than that of the paracone, although considerably less developed than the parastylar column. The ectoloph is sinuous. There is a shallow and wide ectoflexus which bears a small cuspule at its base (Fig. 2.1–2.2). The metastyle is smaller and lower than the parastyle; however, it is well defined by a column on the labial wall of the ectoloph. The protocone and hypocone are about the same size in occlusal view, although the hypocone is higher and shows a more rounded apex. The lingual wall of the tooth bears a moderately-marked sulcus, running from the base of the crown to a poorly-developed entocrista (short and low) connecting the protocone and hypocone. The distal wall of the tooth is roughly straight and shows a proportionally wide postcingulum. The precingulum is narrow; it is also lower and more labiolingually extended than the postcingulum.

Comparisons and comments on the taxonomic assignment. Comparisons were made with taxa closely related to the genus *Indalecia* considering the context of the Notopterna (see Discussion below) and hence, the families Amilnedwarsidae, Indaleciidae, and Notonychopidae. Among the Amilnedwardsidae, the type and only specimen of *Ernestohaeckelia aculeata* Ameghino, 1901 is currently lost (Mones, 1986; Soria, 1989a); hence, comparisons with this taxon cannot be undertaken. Soria (1989a) mentioned a series of characters treated in the original description of Ameghino (1901) which apparently rises some doubts on the familiar context of this species. Considering this, no further observations can be made. On the other hand, the species *Rutimeyeria conulifera* Ameghino, 1901 is only known by a M3 and hence, cannot be directly compared with the specimen PVL 5901.

The species of the genus *Amilnedwardsia*, *A. brevicula* Ameghino, 1901 and *A. acutidens* Ameghino, 1901 show a more bunodont condition of the molars and lack a metaloph. Moreover, besides its smaller size (Tab. 1), *A. brevicula* differs from PVL 5901 in several features. The holotype of *A. brevicula* (MACN-A 10578; Fig. 3.1) shows a narrow cingulum extended almost on the entire labial wall. In *Indalecia*

TABLE 1. Dental measurements (in mm) of the M2 in specimens of Amilnedwardsidae, Notonychopidae, and Indaleciidae.

		Length	Width
Amilnedwardsia brevicula	MACN-A 10578* (right)	4.50	6.30
Notonychops powelli	PVL 4298 (left)	7.02	9.97
Adiantoides leali	MCNAM-PV 3004 (left)	5.05	8.00
Indalecia grandensis	PVL 4186 (left)	6.27	7.43
Indalecia sp.	PVL 5901 (left)	6.63	7.36

* Identified as M1 or M2.

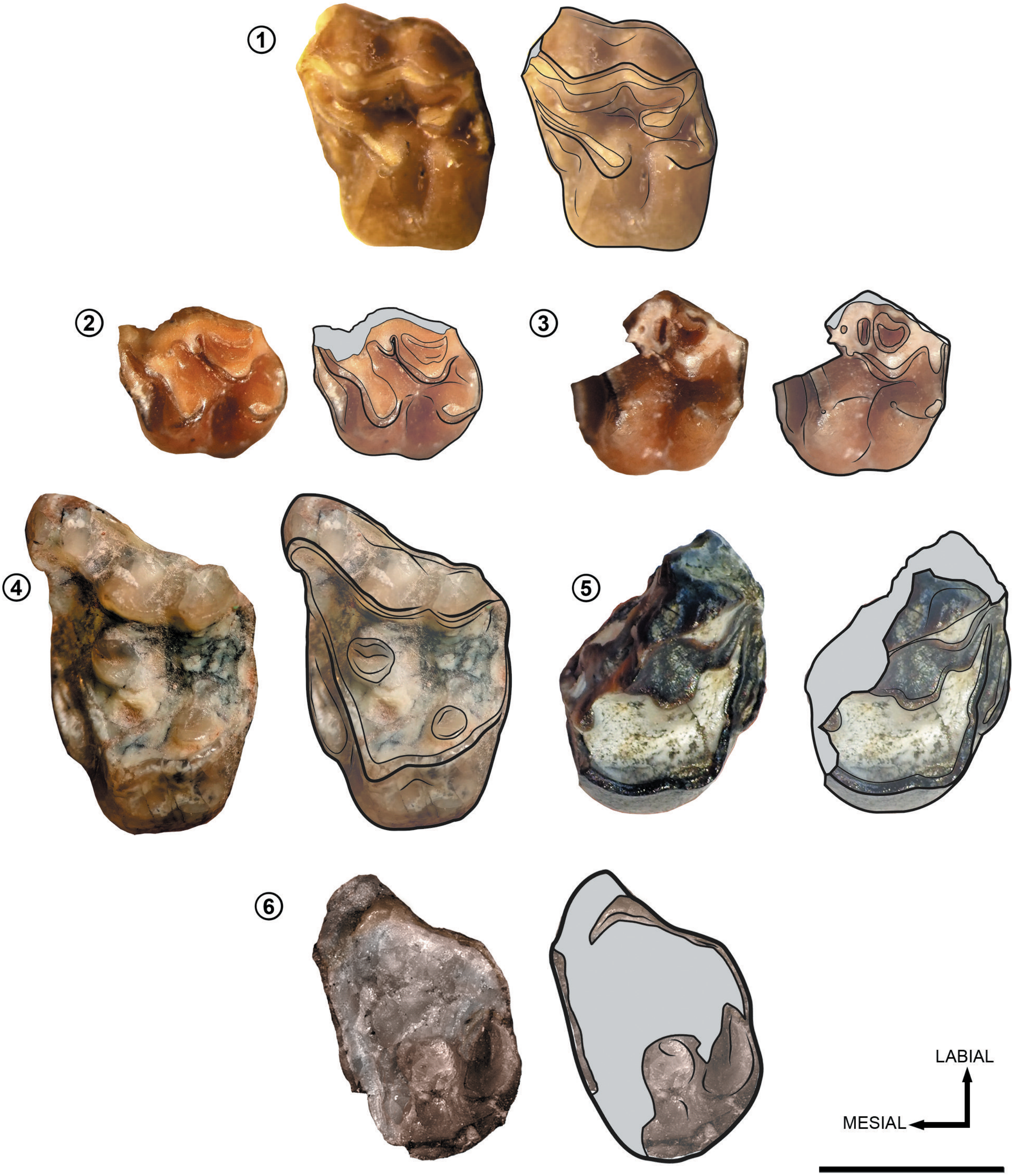

Figure 3. Upper molar morphology in Amilnedwardsidae, Notonychopidae, and Indaleciidae (occlusal view). **1,** ***Amilnedwardsia brevicula*****, MACN-A 10578** (holotype), right M1 or M2 (reflected); **2,** ***Amilnedwardsia acutidens*****, MACN-A 10731b** (paralectotype), left M1 or M2; **3,** ***Amilnedwardsia acutidens*****, MACN-A 10731c** (paralectotype), left M1 or M2; **4,** ***Notonychops powelli*****, PVL 4298** (holotype), left M2; **5,** ***Requisia vidmari*****, UNPSJB-Pv 947**, left M1?; **6,** ***Adiantoides leali*****, MCNAM-PV 3004** (holotype), left M2. Grey areas indicate worn or broken occlusal surfaces; scale bar= 5 mm.

sp., there are faint horizontal enamel folds on the basal surface of the paracone and metacone, with a small cuspule developed on the ectoflexus area (versus a short cingulum in *I. grandensis*; see below). The paracone column is more developed in *A. brevicula* than in *Indalecia* sp. In occlusal view, the mesiolabial and distolabial fossettes are absent in *A. brevicula*, mainly given the lack of postparaconular and premetaconular cristae, respectively. The metaconule also differs from PVL 5901 by its bunoid morphology (isolated from the surrounding structures except by the presence of a narrow postmetaconular crista) and mesiodistal elongation. *Amilnedwardsia brevicula* also shows a trigon basin not developed as a central fossa and a narrower postcingulum than in PVL 5901.

Amilnedwardsia acutidens (paralectotypes MACN-A 10731b and MACN-A 10731c) shows a distolabial fossette (Fig. 3.2–3.3). However, this structure is very different from that of *Indalecia* sp., being kidney-shaped, shallow, and showing a narrow bottom. Mesially to the distolabial fossete, there is at least one crista pointing toward the trigon basin, which encloses a small fossette in the specimen MACN-A 10731c (Fig. 3.3). This condition is similar to that of the holotype of *Indalecia grandensis* but differs from the specimen PVL 5901 (*Indalecia* sp.), which apparently lacks cristae and accessory fossettes or these were faint and early obliterated by wear.

The family Notonychopidae is currently integrated by two species: *Notonychops powelli* Soria, 1989c and *Requisia vidmari* Bonaparte & Morales, 1997. The former species is known by a single specimen (PVL 4298) with heavily worn teeth (Fig. 3.4); however, several differences are evident regarding the specimen PVL 5901. The molars are larger in *N. powelli* (Tab. 1). These teeth are also transversally developed and show a strong parastyle. The metastyle is also more extended labially that in PVL 5901, resulting in a clearly concave external outline for the molars. The labial wall also shows a well-defined cingulum, mesiodistally continuous (similar to that of *Amilnedwardsia brevicula*), and a paracone column more conspicuous than in PVL 5901. The presence of mesiolabial and distolabial fossettes is difficult to evaluate, given the heavy wear. There is a small enamel plate, barely concave, located between the paracone and paraconule. Considering this plate as the remaining bottom of the mesiolabial fossette, it is narrower than in PVL 5901. There is no evidence of the distolabial fossette. The paraconule seems to be less conspicuous in *N. powelli* and there is no evidence of a well-developed metaconule. Protocone and hypocone are well connected (wide and straight entocrista) and the entoflexus is barely defined. There is a wide enamel plate labial to the hypocone and the metacone seems to connect to the protocone, without the development of a clear metaloph. The precingulum bears a defined protostyle and the postcingulum is narrower than in the specimen PVL 5901.

As for *Requisia vidmari*, Bonaparte & Morales (1997) described an isolated and incomplete molar that they referred as a “probable M1” (UNPSJB-Pv 947; Fig. 3.5). This tooth shows several of the same differences pointed out between *Notonychops* and the specimen PVL 5901, such as the lesser development of the entoflexus and stronger connection of protocone and hypocone (note that the authors do not recognize the presence of the latter cusp and mention it as “protocone”), and narrower postcingulum (which the authors refer as “hypoloph”). It also shows a shallow trigon basin (not forming a discrete central fossa). There is also a bunoid metaconule bearing a narrow postmetaconular crista, resembling the condition in *Amilnedwardsia brevicula*, and disconnected from the hypocone (metaloph absent), representing clear differences regarding PVL 5901.

Finally, the Indaleciidae are represented by the genus *Adiantoides* (*A. leali* Simpson & Minoprio, 1949 and *A. magnus* Cifelli & Soria, 1983) and the species *Indalecia grandensis*. The species *A. magnus* is only known by mandibular remains (holotype AMNH 28888) and could not be compared for this study. The upper dentition of *A. leali* is worn and the occlusal surface is mostly broken in the holotype (MCNAM-PV 3004; Fig. 3.6). However, some features of *A. leali* are distinctive regarding the specimen PVL 5901: the molars are smaller (Tab. 1) and transversely developed, paracone and metacone columns are apparently less developed, and protocone and hypocone are more closely located. On the other hand, there are some common features between *A. leali* and PVL 5901, such as the presence of a central fossa and a developed metaloph reaching the hypocone.

The specimen PVL 5901 and the holotype of *Indalecia grandensis* (PVL 4186; Fig. 4) share several characters: the development of parastyle, paracone, and metacone labial columns, well-defined central fossa, conspicuous mesiolabial and distolabial fossettes (given the presence of postparaconular and premetaconular cristae, respectively), the separation and similar size of protocone and hypocone, and the presence of a conspicuous metaloph determine a strong resemblance between those specimens (Fig. 4). On the other side, PVL 5901 and PVL 4186 display some differences. First, there is a small cuspule located on the base of the ectoflexus which is absent in PVL 4186 (in this case, there is a short cingulum in that location). Second, PVL 4186 presents a very small fossette, located mesially to the distolabial fossette, probably evidencing the development of small cristae as in *Amilnedwardsia acutidens* (MACN-A 10731c; Fig. 3.3). This small fossette is absent in PVL 5901, which shows a simple premetaconular crista running mesiolabially. Third, PVL 5901 bears a conspicuous entoflexus, less developed in the holotype of *I. grandensis*.

In summary, the specimen PVL 5901 is clearly different from most of the species included in the families Amilnedwardsidae, Notonychopidae, and Indaleciidae. In relation to *Indalecia grandensis*, PVL 5901 shares several features but some differences also emerge between these forms. Considering that PVL 5901 is hitherto known by a single and incomplete specimen, to our understanding insufficient to propose the presence of a new taxonomic entity, we maintain a cautious approach and refer the studied material as *Indalecia* sp.

DISCUSSION

Comments on the taxonomic context of *Indalecia*

The holotype of *Indalecia grandensis* comes from the Lower Lumbrera Formation (?Ypresian; see del Papa *et al.*, 2022) exposed at the locality of Pampa Grande, Salta Province, Argentina. Bond & Vucetich (1983) included *Indalecia* within the order Litopterna, given the close relationship stated by those authors with *Adiantoides leali* (considered as undoubtedly part of that order). Originally,

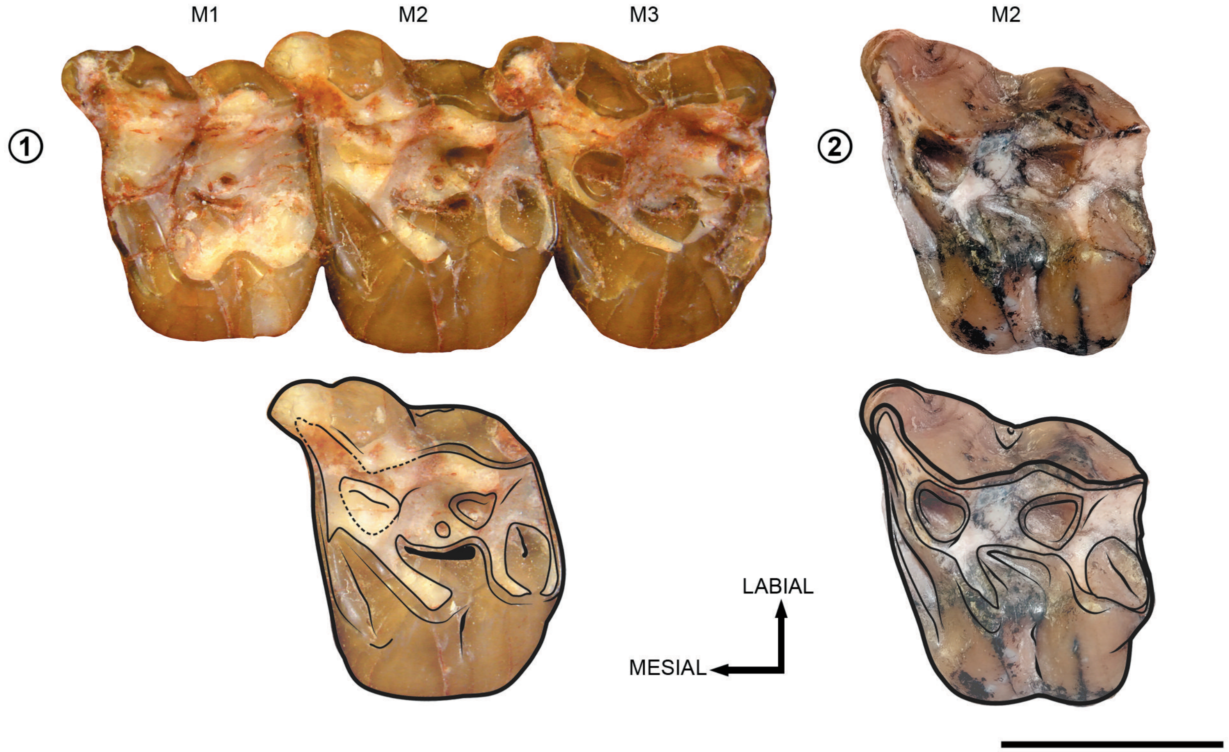

Figure 4. Upper molar morphology in the genus *Indalecia*. **1,** ***Indalecia grandensis***, **PVL 4186** (holotype), detail of M1–3 in occlusal view and scheme of morphological details for the M2; **2,** ***Indalecia*** sp., **PVL 5901**, detail of M2 in occlusal view and scheme of morphological details. Scale bar= 5 mm.

Bond & Vucetich (1983) also included *I. grandensis* within its own subfamily (Indaleciinae) within the litoptern family Adianthidae; however, later Soria (1984, 1989b) raised the Indaleciinae to the family level (*i.e.*, Indaleciidae) and included the group within a new South American ungulate order, the Notopterna. Soria (1989b, 1989c) established that the Notopterna encompassed taxa previously considered as basal Litopterna (Amilnedwardsidae and Indaleciidae) plus *Notonychops powelli* (Notonychopidae) from the Río Loro Formation.

The definition of the order Notopterna rests mainly on dental characters (although other traits related to body size and petrosal were also considered) and has not been extensively tested cladistically. Some contributions have included some of the taxa mentioned by Soria (1989b, 1989c) as Notopterna in phylogenetic analyses, but assuming those taxa as part of other clades and without providing any statement on the validity of the order Notopterna. Cifelli (1993) included *Indalecia* and *Adiantoides* in a phylogeny of “archaic South American ungulates”, treating both genera *a priori* as Litopterna. Gelfo *et al.* (2008) included *Indalecia*, *Adiantoides*, and *Notonychops* in a phylogenetic hypothesis of Xenungulata but specifically indicating those genera as Litopterna. McGrath *et al.* (2020) included *Adiantoides leali* as a representative of Indaleciidae in their study on the proterotheriids and macraucheniids from Pampa Castillo (Chile), which results indicated that Indaleciidae were nested within Proterotheriidae and were, therefore, part of Litopterna. Once again, these authors, although tacitly implicated by their results, do not make any direct statement on the validity of the order Notopterna.

The only contribution that discusses the validity of Notopterna is the work of Bonaparte & Morales (1997). These authors described a basal ungulate (*Requisia vidmari*) as a Notonychopidae, which in turn they considered *a priori* as part of the Litopterna. They performed a phylogenetic analysis including a combination of litoptern taxa and those considered as notopterns by Soria (1989b, 1989c). Their results did not recover Notopterna as a natural group, and the authors (Bonaparte & Morales, 1997, p. 272) specifically stated that “*la utilización del suborden Notopterna para las familias Indaleciidae y Notonychopidae no queda justificada*” (the use of the suborder Notopterna for the families Indaleciidae and Notonychopidae is not justified) (note the use of subordinal instead of ordinal rank, being this probably a typo error).

Other systematic surveys and taxonomic lists have treated the indaleciids alternatively as Litopterna and Notopterna, even in recent years (Vucetich *et al.*, 2007; Woodburne *et al.*, 2014; Gelfo *et al.*, 2016; Croft *et al.*, 2020). Hence, although most of the contributions support indaleciids as Litopterna, the relationships of these forms must be phylogenetically assessed, taking into consideration not only dental but also cranial characters, in a relatively wide taxonomical spectrum.

In this complex systematic context, it should also be considered that some recent phylogenies have failed to recover Litopterna as a monophyletic group (Billet, 2010; Billet *et al.*, 2015). Hence, given this set of issues, in this contribution we choose to maintain the conservative position of Indaleciidae within Litopterna, but with reserves about the future of such assignation.

Relevance of the record

Until now, the absence of absolute dating for the Río Loro Formation precluded direct temporal correlation with other mid-latitude Paleogene assemblages (*e.g.*, Mealla, Maíz Gordo, and Lower Lumbrera formations, Itaboraí fauna, etc.; Babot *et al.*, 2017). This uncertainty is increased by the endemic nature of the fossil mammals that compose the Río Loro fauna, with no documented taxa (until this contribution) shared with other associations from the South American Paleogene (Gelfo *et al.*, 2020).

In this context, any common record of a taxonomic entity, even at a generic level, should be carefully addressed. With the specimen documented here, the genus *Indalecia* is present both in the Río Loro and the Lower Lumbrera formations. This fact deserves some comments in a biostratigraphic context, given the age considered for both units and the faunal differences between them.

The Lower Lumbrera Formation was referred to the middle Eocene (Vacan subage of the Casamayoran SALMA; del Papa *et al.*, 2010, 2013, 2017; Powell *et al.*, 2011) but recently proposed as old as early Eocene (?Ypresian, ?Itaboraian SALMA; Fernicola *et al.*, 2021; del Papa *et al.*, 2022). The temporal context of the Río Loro Formation is more uncertain (see review in Babot *et al.*, 2017); recently, Gelfo *et al.* (2020) proposed a probable span between the middle Paleocene and the early Eocene (although favoring a pre-Itaboraian span) based on the mammalian composition of the fauna, which suggests that the Río Loro Formation is older than the Lower Lumbrera Formation. This idea may also be supported by the singular nature of the Río Loro assemblage, as the South American land mammal faunas represented mainly isolated entities until the Itaboraian SALMA (Woodburne *et al.*, 2014).

The differences between both faunal assemblages are remarkable, even when large clades are considered. Metatherians and xenarthrans, for example, are common elements for the Lower Lumbrera Formation (Powell *et al.*, 2011; Herrera *et al.*, 2016; Babot *et al.*, 2017) but are absent in the Río Loro fauna. In turn, Xenungulata, represented by the species *Rodcania kakan* Gelfo *et al.*, 2020, constitute a notable element of the Río Loro assemblage. This clade has not been yet documented for any other unit in NWA. Another significant element of the Río Loro fauna is *Eoastrapostylops riolorense* Soria & Powell, 1981, a putative Astrapotheria following Kramarz *et al.* (2017). This taxon and other clearly related specimens are among the most common remains in the Río Loro Formation, but are absent in the Lower Lumbrera Formation. If we consider Astrapotheria *sensu lato*, the Lower Lumbrera Formation yielded only one species so far, *Albertogaudrya carahuasensis* Carbajal *et al.*, 1977 (originally referred with some doubts) which is classified among the Astrapotheriidae and, henceforth, more derived than *Eoastrapostylops*, even in the sense in which Soria & Powell (1981) and Soria (1987, 1988) considered the order.

The order Notoungulata is also profusely recorded in the Lower Lumbrera Formation. There, it shows a number of taxa that represents a good sample of the Paleogene diversity within that group: *Boreastylops lumbrerensis* Vucetich, 1980 (Notostylopidae), *Colbertia lumbrerense* Bond, 1981 ('Oldfieldthomasiidae'), two species of the genus *Pampahippus* Bond & López, 1993 ('Notohippidae') and two species of the genus *Pampatemnus* Vucetich & Bond, 1982 ('Isotemnidae'), among others. In the case of the Río Loro Formation, the species *Satshatemnus bonapartei* Soria, 1989a was described as a basal notoungulate. This was based on a very fragmentary material, lacking most of its dental features. However, the finding of new specimens indisputably assignable to the same taxon led to the separation of *S. bonapartei* from Notoungulata (although a close phylogenetic position to the possible stock of sister taxa for that order should not be yet discarded; see García-López *et al.*, 2022).

The record of *Indalecia* sp. for the Río Loro Formation represents the first common element at a generic level with any other Paleogene unit. Being the Lower Lumbrera Formation now considered as a possibly Itaboraian assemblage, this may be considered as a proxy for the temporal context of the Río Loro assemblage. Nevertheless, although representing a remarkable datum, this common record contrasts with the clear differences in alpha taxonomy exposed above and this fact leads us to maintain a similar perspective to that of Gelfo *et al.* (2020), considering the Río Loro levels as pre-Itaboraian in age and hence, much probably older than the classic fossil-bearing levels of the Lower Lumbrera Formation. In this scenario, *Indalecia* sp. of the Río Loro Formation represents the first appearance datum for the genus and for the Indaleciidae.

As the Indaleciidae and other potentially related clades (*i.e.*, Amilnedwardsidae, Notonychopidae) have been the focus of limited studies in the last years, this record of *Indalecia* in the Río Loro Formation opens the possibility for a deeper analysis focused on the affinities of these lineages.

CONCLUSIONS

The specimen PVL 5901 is here referred to the genus *Indalecia* (Indaleciidae, Litopterna?). We were unable to reach a specific allocation given the scarcity of the material. Although this may have potential biostratigraphic relevance considering that is the first common mammal genus between the Río Loro Formation and the Lower Lumbrera Formation and, in fact, of any other Paleogene fossil-bearing unit, the marked faunal discrepancies observed contrast with this single record, and a partial temporal correspondence or temporal closeness between those bearing levels is not supported here.

Even so, taking into account the more solid temporal frame known for the Lower Lumbrera Formation (although not based on absolute chronological data; see Fernicola *et al.*, 2021; del Papa *et al.*, 2022), this record should be weighted in future works dealing with the age of the Río Loro Formation and the biogeographical context of this singular fossil assemblage.

ACKNOWLEDGEMENTS

We thank P. Ortiz (PVL) for access to collections under his care. We are indebted to M. Casas, G. Bravo, and L. Sosa for their assistance during fieldwork. We also thank M. Luna and A. De Sosa Tomas (UNPSJB), J. Escobar (MACN), G. López (MLP), E. Cerdeño (IANIGLA), and G. Campos (MCNAM) for sending us photographic material. Enrique Guanuco made the drawings of the specimen PVL 5901. This work was funded by Universidad Nacional de Tucumán (PIUNT G626), Agencia de Promoción Científica y Tecnológica (PICT 2020-03651), Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 700; PIP 778), and Fundación Miguel Lillo (CUP G-0035-1).

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doi: 10.5710/PEAPA.04.09.2023.459

Recibido: 22 de marzo 2023
Aceptado: 4 de septiembre 2023
Publicado: 27 de septiembre 2023

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