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The worm *Palaeoscolex* from the Cambrian of NW Argentina: extending the biogeography of Cambrian priapulids to South America

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The worm *Palaeoscolex* from the Cambrian of NW Argentina: extending the biogeography of Cambrian priapulids to South America

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Over one hundred years of palaeontological research in northwestern Argentina has provided extensive knowledge of Andean lower Palaeozoic fossil assemblages, with trilobites, graptolites, brachiopods and echinoderms being among the most prominent groups. This record is enriched by the recent discovery of soft-bodied worms in Cambrian outcrops of northwestern Argentina. *Palaeoscolex* sp. cf. *P. ratcliffei* from the Furongian Lampazar Formation in Jujuy is described, considerably expanding the biogeographical range of this genus and filling the distributional gap, between the well-known early–middle Cambrian occurrences of *Palaeoscolex* and those of its Ordovician species.

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Key words: soft-bodied biota, priapulids, Palaeoscolecida, Furongian, Argentina.

STUDIES of Argentinean lower Palaeozoic fossil assemblages have been based primarily on sclerotized and mineralized remains; few have dealt with soft-bodied organisms. Non-mineralized organisms are assumed to have existed in Argentina's Palaeozoic seas, even though few are preserved in this region. Palaeoecological evaluations of the biota largely overlook the range of soft-bodied elements, which were probably very important in lower Palaeozoic trophic chains. Perception of these 'ghost taxa' has increased via the description of ichno-assemblages, which record the activities of a varied and abundant soft-bodied fauna, while the latter provides data critical for phylogenetic evaluation and autecological appraisal.

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Soft-bodied fossils constitute an exceptional source of information on past life particularly with respect to functional morphology, life habits and biodiversity than more common skeletal fossils. The deposits containing these special fossils, known as *Konservat-Lagerstätten*, are very scarce, and among the best-known suites of early Palaeozoic age are the Cambrian assemblages of the Burgess Shale in Canada, Chengjiang and Kaili in China, and Sirius Passet in Greenland. Studies carried out at these localities show that organisms lacking a mineralized skeleton constitute over 80% of the assemblages (Conway Morris 1986, Zhao *et al*. 2009). Soft-bodied vermiform organisms, such as those described herein, are important constituents of the faunas that arose between 540 and 520 million years ago, during the Cambrian 'explosion'. In the latest complete surveys of the Chengjiang biota (Steiner *et al*. 2005), about

9% of the genera correspond to priapulids, whereas in the younger Burgess Shale, they constitute about 4% of the total diversity (Caron & Jackson 2008). Many components of these groups suffered an important setback during the Ordovician, as was the case for the palaeoscolecids.

The palaeontological literature of northwestern Argentina includes several other putative soft-bodied fossils, but these have mostly been reinterpreted as trace fossils, sedimentary structures associated with microbial mats, or are still regarded as *incertae sedis*. An example of the first case is that of a medusoid ('*Brooksella*') from the Casa Colorada Formation at the Quebrada de Humahuaca in Jujuy Province (Moya *et al*. 1986), which was synonymized with the ichnofossil *Gyrophyllites*. Similarly, forms assigned to *Squamodictyon* and *Protopalaeodictyon* are now interpreted to be structures associated with microbial mats (Aceñolaza & Aceñolaza 2001, 2003, 2005, 2007). The presence of subcircular bodies with a central knob (Durand & Aceñolaza 1990, and references therein), had been assigned to *Tiernavia*, *Sekwia* and *Beltanelliformis*, with some of them recently synonymized with *Beltanelloides* (Aceñolaza *et al*. 2005). A fossil from the Puncoviscana Formation at Choromoro in Tucumán Province, originally assigned by Aceñolaza (2004) to *Sphenothallus*? sp., has been reassigned to the priapulid worm *Selkirkia* sp. (Aceñolaza & Aceñolaza 2007, fig. 3.5). An additional soft-bodied organism recently described by Vaccari *et al*. (2004), consists of a single specimen of a new euthycarcinoid arthropod, *Apankura machu*, collected from a pebble in the Huasamayo River in Tilcara, Jujuy Province. This unique specimen is interpreted to come from shales of the Casa Colorada Formation, which is partially equivalent to the Lampazar Formation and crops out extensively in the area of Tilcara (Jujuy). The presence of soft-bodied arthropods, together with the worm described here, suggests that further research in northwest Argentina may reveal a greater diversity of Cambrian forms, apparently unrivalled in South America.

Geological setting and provenance of material

The material examined here derives from a unit in the Neoproterozoic–lower Palaeozoic succession of northwestern Argentina, the Furongian Lampazar Formation. The Lampazar Formation in the Sierra de Cajas, Jujuy Province (Fig. 1), has produced two specimens of the worm *Palaeoscolex* sp. cf. *P. ratcliffei*.

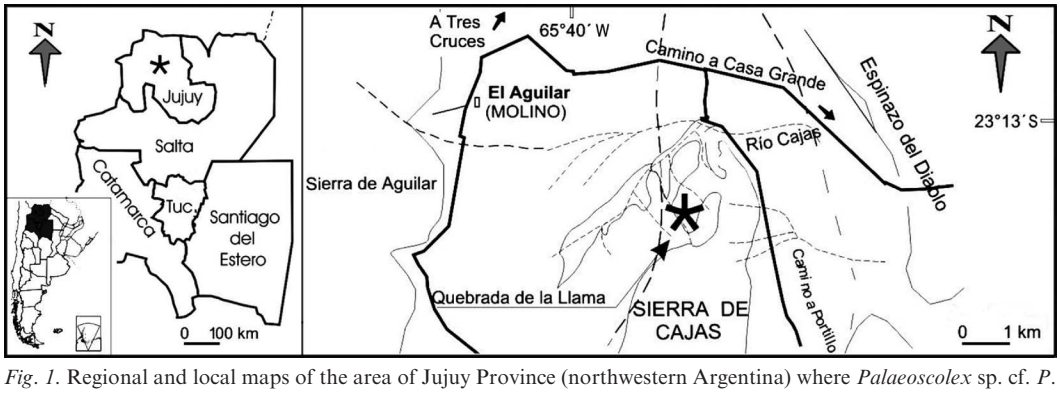

Fig. 1. Regional and local maps of the area of Jujuy Province (northwestern Argentina) where *Palaeoscolex* sp. cf. *P. ratcliffei* was collected.

The Lampazar Formation (Harrington 1957) was originally described near the locality of Ingeniero Maury (Salta Province), and consists of grey to green, banded mudstones and sandstones with a total thickness of almost 100 m (Harrington 1957, Tortello & Rao 2000). Additional exposures of this formation have since been recognized to the north (Fig. 1), in the Sierra de Cajas (Jujuy Province), where it is 178 m thick (Fig. 2) and conformably overlies the sandstones and quartzites of the Padrioc Formation and underlies the quartz-rich sandstones of the Cardonal Formation. The Lampazar Formation contains a rich fossil record consisting of trilobites and other arthropods, conodonts, brachiopods, echinoderms, ichnofossils (Aceñolaza 1968, Benedetto 1977, Rao 1999 and references therein), and the two specimens of the worm *Palaeoscolex* sp. cf. *P. ratcliffei* described here (Figs 3A–D).

The *Palaeoscolex* specimens come from the pelitic and sandy levels in the upper part of the unit on the western slope of the Sierra de Cajas (Fig. 1). Although the material is fragmentary, the preserved morphological details allow an approximate taxonomic assignment. A detailed study of sedimentary facies within the Lampazar Formation was carried out by Tortello & Esteban (2003), who recognized seven lithofacies ranging from laminated black and dark grey shales in the lower part (facies 1 and 2) to laminated green shales (facies 3) with intercalated siltstones and sandstones (facies 4–7) in the middle and upper parts. This facies pattern points to a predominantly outer platform environment transitioning to an inner platform, within a general shallowing-upward trend. The sporadic record of tempestites suggests random oxygenation events, which would have enabled the establishment of opportunistic faunas. A wide range of trilobites corresponding to the *Parabolina (N.) frequens argentina* Zone (*Pseudorhaptagnostus–Gymnagnostus* Biozone) and the presence of *Iapetognathus* (Conodonta) in the overlying Cardonal Formation (Rao 1999) point to a Furongian (upper Cambrian) age for the Lampazar Formation (Tortello & Esteban 2003).

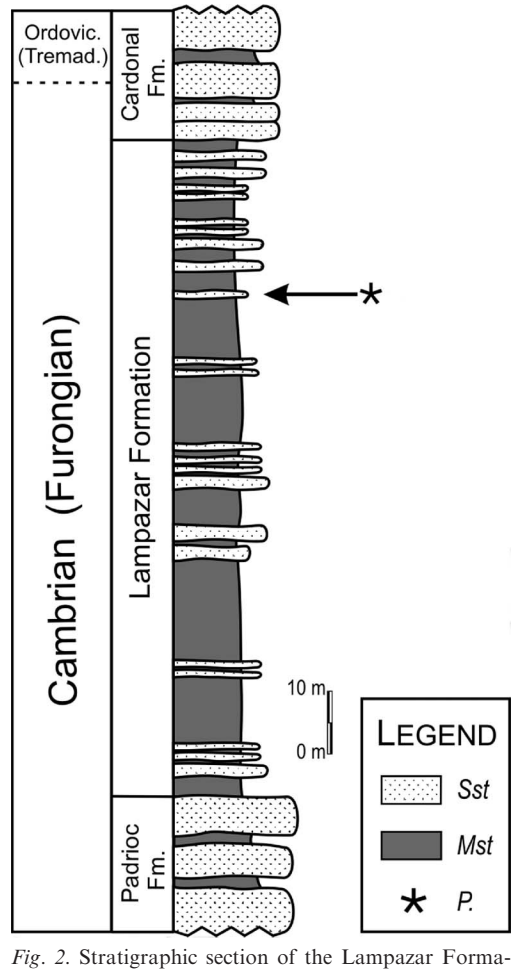

Fig. 2. Stratigraphic section of the Lampazar Formation indicating the level at which *Palaeoscolex* sp. cf. *P. ratcliffei* was collected (asterisk). Abbreviations: *Sst*, Sandstone; *Mst*, Mudstone; *P.*, *Palaeoscolex* sp. cf. *P. ratcliffei*.

Systematic palaeontology

These fossils are housed in the collections of the Facultad de Ciencias Naturales e Instituto Miguel Lillo (Universidad Nacional de Tucumán), under the prefix PIL (Paleontología Invertebrados Lillo).

Phylum PRIAPULIDA Delage & Hérouard, 1897
Class PALAEOSCOLECIDA Conway Morris & Robison, 1986
Family PALAEOSCOLECIDAE Whittard, 1953

Palaeoscolex Whittard, 1953

Type species. *Palaeoscolex piscatorum* Whittard, 1953.

Other species. *Palaeoscolex ratcliffei* Robison, 1969; *P. antiquus* Glaessner, 1979; *P. sinensis* Hou & Sun, 1988; '*Palaeoscolex' tenensis* Kraft & Mergl, 1989; *P. huainanensis* Lin, 1995; *P. lubovae* Ivantsov & Wrona, 2004; *P. spinosus* Ivantsov & Wrona, 2004.

Distribution. Early Cambrian–Early Ordovician; England, USA, Australia, China, Czech Republic, Russia, Spain, Argentina.

Palaeoscolex sp. cf. **P. ratcliffei** Robison, 1969 (Fig. 3A–D)

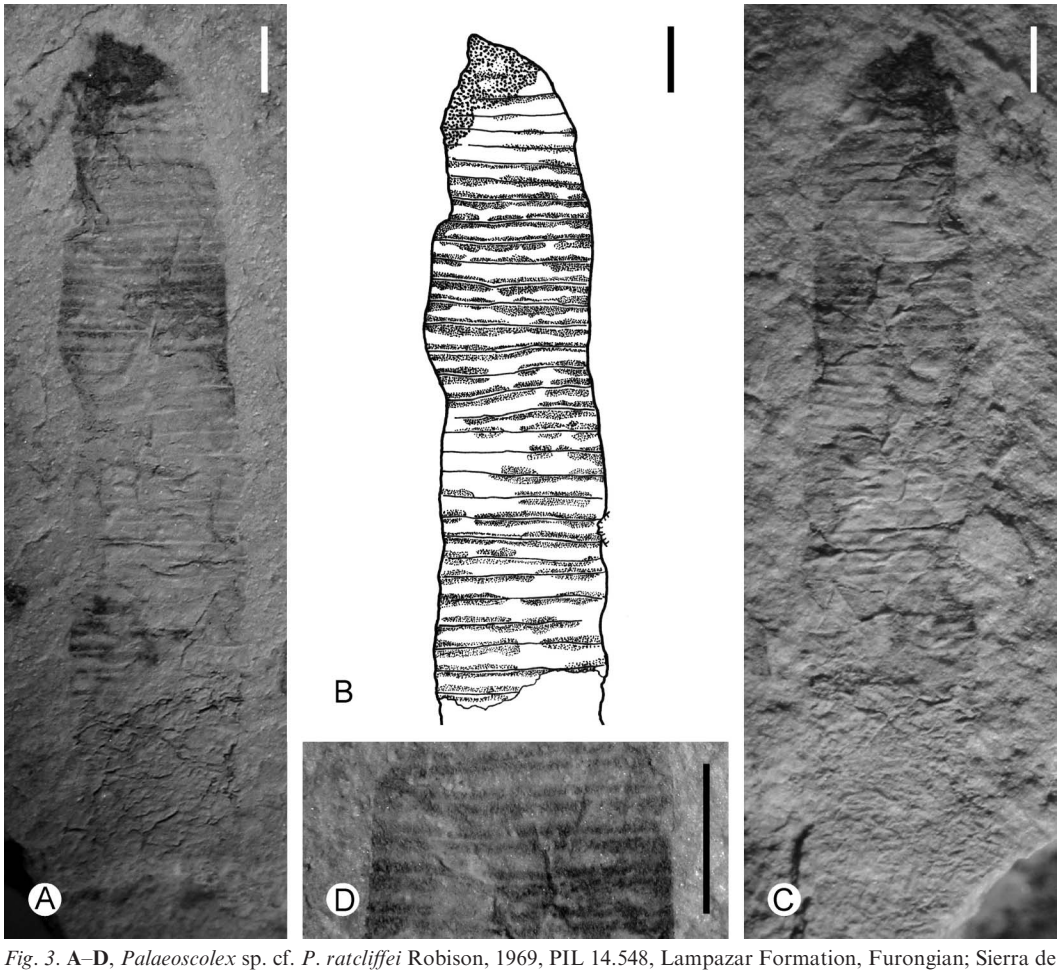

Fig. 3. **A**–**D**, *Palaeoscolex* sp. cf. *P. ratcliffei* Robison, 1969, PIL 14.548, Lampazar Formation, Furongian; Sierra de Cajas (Jujuy, Argentina). **A**, part; **B**, *camera lucida* drawing; **C**, counterpart. **D**, detail of segments eight through eleven of the part. Scale bars: **A**–**C** = 1 mm; **D** = 0.5 mm.

1969 *Palaeoscolex ratcliffei* Robison, pp. 1171–1172, pl. 138, figs 1–2.
1986 *Palaeoscolex* cf. *P. ratcliffei* Robison; Conway Morris & Robison, pp. 16–18, fig. 8.
1995 *Palaeoscolex* cf. *P. ratcliffei* Robison; Gámez Vintáned, pp. 211–212, pl. 1.
1997 *Palaeoscolex* cf. *P. ratcliffei* Robison; García-Bellido Capdevila, pp. 37–38, fig. 11, pl. 5, figs 1–3.
2005 *Palaeoscolex* cf. *P. ratcliffei* Robison; García-Bellido & Aceñolaza, pp. 470–471, pl. 1, figs 3–4.

Studied material. Two incomplete fragments with part and counterpart. One with relatively good contrast (PIL 14.548), the other considerably weathered (PIL 14.549).

Description. The rock seems to have split along the plane of compression, revealing a fossil slightly darker than the surrounding matrix (Fig. 3A, C–D), with a total preserved length of 18 mm. The edges of the body are parallel to each other along most of the body length, with a compressed width of 2.4 mm (original diameter before compaction estimated to be 1.5 mm), tapering in the distal 3 mm to a pointed tip. Along three-quarters of the length of the body, parallel grooves delineate the body annulations, which are unrecognizable in the area closer to the break in the rock, possibly due to weathering. The total number of preserved annulations is 30 — possibly 31 (if the faint pattern in the darker area of the body tip is included), with a width of *ca* 0.24 mm, thus producing an average of about 4 rings per mm. Each ring has two transverse lines of sclerite pits, located beside the grooves, leaving an unornamented central band in the ring (stippled areas of Fig. 3B). There are some longitudinal and oblique folds and wrinkles, possibly due to the compaction process that took place after burial during early diagenesis. There are no clear criteria to define whether the preserved termination is the oral or anal end of the body. The second specimen is fragmentary but similar in size to the first, and the poor quality of preservation does not allow counting of its rings, nor recognition of sclerites.

Discussion. The observed characters of these incomplete specimens only allow comparison with true *Palaeoscolex ratcliffei*. This species was first discovered in the middle Cambrian Spence Shale of Utah (USA), with three specimens from the middle Cambrian Murero Formation (Zaragoza, Spain) later being assigned to it under open nomenclature. Lengths of complete specimens of this species range between 32 mm (see Gámez Vintáned 1995, pl. 1, figs 1, 2) and 125 mm in the type specimen (Robison 1969, figs 1, 2). The maximum width of the Argentinean specimen does not differ greatly from the 2.6 mm compressed width of the small Murero specimen. The small dimensions of these two fossils, compared with conspecific specimens, suggest that they may represent juveniles. On the other hand, the Argentinean *Palaeoscolex* resembles, in outline and annulation, an indeterminate worm from the Burgess Shale of British Columbia (Canada), but which is even smaller in size, being 3 mm long (broken) and 0.6 mm wide (García-Bellido Capdevila 2000, fig. 4). The state of preservation of the specimen described here does not allow detailed characterization of the sclerite ornamentation or their size range and shape (which may be circular to oval, or even polygonal), all of which are important diagnostic characters for palaeoscolecids. However, the pattern consisting of two uniserial bands of sclerite pits separated by an unornamented band on each ring (see Conway Morris & Robison 1986, fig. 9), together with the number of annulations per millimetre, similar to the American holotype with 3–4 rings per mm, places this specimen closest to *P. ratcliffei*. The

available values for other species in the genus are: *P. antiquus*, 0.7–2 rings/mm; *P. sinensis*, 5 rings/mm; *P. piscatorum*, 8–10 rings/mm; *P. huainanensis*, 6–8 rings/mm. The sclerite pattern in these and other species is considerably more complex than that of *P. ratcliffei*.

Palaeoscolecids were a widespread group of extinct marine vermiform organisms, millimetric to decimetric in size, widely assigned to the Priapulida (e.g. Wills 1998, Lehnert & Kraft 2006), with some very convincing arguments presented towards this assignment by Harvey *et al*. (2010) based on a cladistic analysis of 34 taxa and 95 characters. Some authors broaden this assignment to stem-group Cycloneuralians (Conway Morris & Peel 2010). The first palaeoscolecid was described from the Upper Ordovician of Kentucky more than 130 years ago (*Protoscolex* Ulrich, 1878), while the next genus assigned to the group, *Palaeoscolex* Whittard, 1953, came from the Tremadocian of the British Isles. However, all later described species of this genus, including *Palaeoscolex ratcliffei*, have been reported from the Cambrian, with the specimen reported herein filling the chronological gap between the older and younger *Palaeoscolex*. The genus is now known from most Cambrian continents (Avalonia, Baltica, Laurentia, Siberia, South China) and around the perigondwanan margin, the majority of them in tropical or temperate waters, with the Argentinean occurrence being the highest in latitude. This implies, that priapulid worms were more eurythermic, and capable, already in the Cambrian, of inhabiting the boreal and cold temperate waters they have been pushed to occupy today (see Conway Morris 1977).

Summary and conclusions

The early Palaeozoic seas covering the South American Andean margin contained a highly varied marine biota, which included not only biomineralized metazoans, but also soft-bodied and lightly sclerotized organisms. Although the former tend to dominate the fossil record, it becomes increasingly necessary to document all faunal elements in order to achieve the broadest possible palaeoecological reconstructions of these basins.

This publication elaborates on the preliminary work by García-Bellido & Aceñolaza (2005) on an interesting fossil discovery from the Cambrian strata of the Jujuy Province. *Palaeoscolex* sp. cf. *P. ratcliffei* occurs in the Furongian Lampazar Formation exposed in the upper sector of the Quebrada de la Llama, on the western slope of the Sierra de Cajas (Jujuy). Known soft-bodied fossil diversity from this region is increasing with the discovery of this priapulid together with *Selkirkia* sp. (Aceñolaza & Aceñolaza 2007) and the euthycarcinoid arthropod *Apankura machu* (Vaccari *et al*. 2004). This is to be expected based on extrapolation from other *Konservat-Lagerstätten*, where these types of worms constitute the second or third most diverse group (usually behind arthropods and sponges), and in a few cases are even the most abundant. Sponges have now been described in the Cambro-Ordovician transitional levels of the Orcomato Formation in the Subandean Ranges of northwest Argentina, lacking earlier records in sub-andean South America (Beresi *et al*. 2006).

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