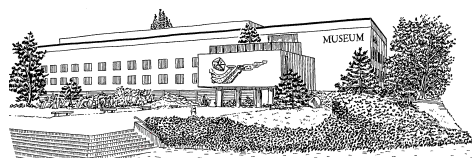


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Biodiversity of the Ediacaran-early Cambrian transition in northwestern Argentina and related areas

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Abstract

The Ediacaran-early Cambrian is a significant time of geological history in terms of biodiversity dynamics. During this time-span a particular soft-bodied fauna developed and disappeared, being replaced by the emergent skeleton-bearing faunas. This very special feature not only gave rise to an abundant fossil record but also triggered the bioturbation of strata, thus generating the “agronomic revolution” – comparable to the revolution produced by mankind upon discovery of the possibilities offered by agriculture. Several outcrops of rocks from that period in northwestern Argentina provide examples spurring a general overview of the major evolutionary trends in the Ediacaran-lower Cambrian seas of the region.

Keywords

Ediacaran, Early Cambrian, Argentina, Gondwana.

INTRODUCTION

The Ediacaran-Early Cambrian times are known as a key period of geological history, during which relevant changes took place in the oceanic environment. These changes involved both the chemistry of the seas and the diversity of the faunas inhabiting them. In terms of time, that period spanned between 575 and 535 Ma.

The amount of oxygen, carbon and other vital elements available in the environment at that time is a matter of discussion with still undefined conclusions. For instance, during the Precambrian/Cambrian transition, a sudden depletion of O¹³ is recorded for the marine domain, whereas phosphorus levels rose to such extents that – at that time – great volumes of phosphatic rocks were deposited worldwide (BRASIER *et al.*, 1994; HALLAM & WIGNALL, 1997; KNOLL *et al.*, 2006; CAMPBELL & SQUIRE, 2010; COHEN *et al.*, 2011).

The terminal Neoproterozoic is characterized, among other features, by the presence of three glacial events known as Sturtian, Marinoan and Gaskiers. When the Gaskiers ended there was a rapid appearance of a soft-bodied fauna identified as the Ediacara Biota (Fig. 1). Its most remarkable expression is found in Ediacara, Australia. However, this fauna may also be observed in different places of North America, Europe, Asia, Africa and South America (FEDONKIN *et al.*, 2007).

An important evolutionary event during the Early Cambrian replaced the soft-bodied fauna with organisms possessing skeletonized carbon-phosphatic structures (biomineralization). This resulted in a revolution of the

biotic structures, generating behaviours different from those of the preceding organisms and thus facilitating their competitiveness (BENGTON, 1994).

The facts causing such a deep transformation at a global level are not altogether clear yet. Numerous hypotheses trying to explain the reason for its origin have been offered, but most are not firmly enough supported to attain adequate scientific certainty. According to MALOOF *et al.* (2010) this event was related to a rapid reorganization of the carbon cycle in presence of strontium, which affected oceanic chemistry.

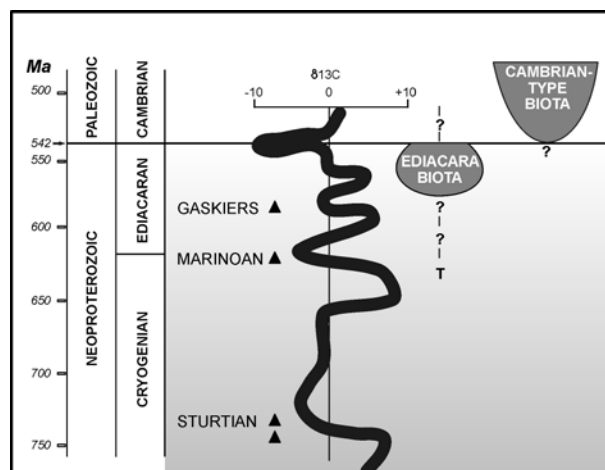


Fig. 1: Relative position of the Ediacara biota in post Gaskiers times and its relation to Cambrian biota. The System boundary displays a negative excursion of δ¹³C.

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This geological period has been known under a number of different names. Firstly, the abundance of soft-bodied organisms led MC MENAMIN (1998) to propose “The Garden of Ediacara”, in reference to an era when life developed on the surface of the sea-bed and, supposedly, in relatively peaceful environments. Towards the end of the Ediacaran period, competition among organisms increased when new organisms with greater capacity to affect the substrate appeared. Then, some of these with mineralized bodies could penetrate and move within the substrate; this concept led SEILACHER & PFLÜGER (1994) to propose the “Agronomic Revolution” by similarity to the change produced by man with the appearance of crops. Finally, the term “Verdun Syndrome” was used to indicate that during that time many organisms needed to “bury” in order to survive, as happened in that French town during the First World War (DZIK, 2007).

Thus, during the Ediacaran-Early Cambrian there were important events marking the global geological history, i.e., the replacement of most of the soft-bodied organisms by others with internal and external skeletonized bodies. At a global level, sequences of Ediacaran age are known in Australia, Newfoundland (Canada), Namibia, Eastern Europe and Siberia (Russia), places where the Neoproterozoic-Phanerozoic transition is fairly well constrained. Fossil data were adjusted with radiometric values that provided the necessary arguments to determine the position of the Ediacaran/Cambrian boundary. The stratotype (GSSP) has been defined in a section at Fortune Head, Newfoundland, Canada, following the IUGS standards (FEDONKIN *et al.*, 2007).

THE EDIACARAN-LOWER CAMBRIAN TRANSITION IN ARGENTINA

A thick sequence of sedimentary rocks assigned to the Ediacaran-Lower Cambrian in Argentina shares—in part—the global conditions mentioned above. These strata in northwestern Argentina are known as the Puncoviscana Formation (*s.l.*). Its magnitude and paleontological content makes it a most significant unit for worldwide correlation with other global reference sections. Other successions in southern South America within this context (Fig. 2) include the youngest rocks of the Sierras Bayas Group in Tandilia (Buenos Aires Province), the El Jagüelito Formation in Río Negro Province, and the beds of similar age exposed in the Malvinas Islands area.

1. Northwestern Argentina: Puncoviscana Formation (*sensu lato*)

During the Ediacaran /Early Cambrian, a large basin was developed along the border of western Gondwana. This was an aulacogen tied to a triple junction point located in southern Bolivia. Facies of this basin are

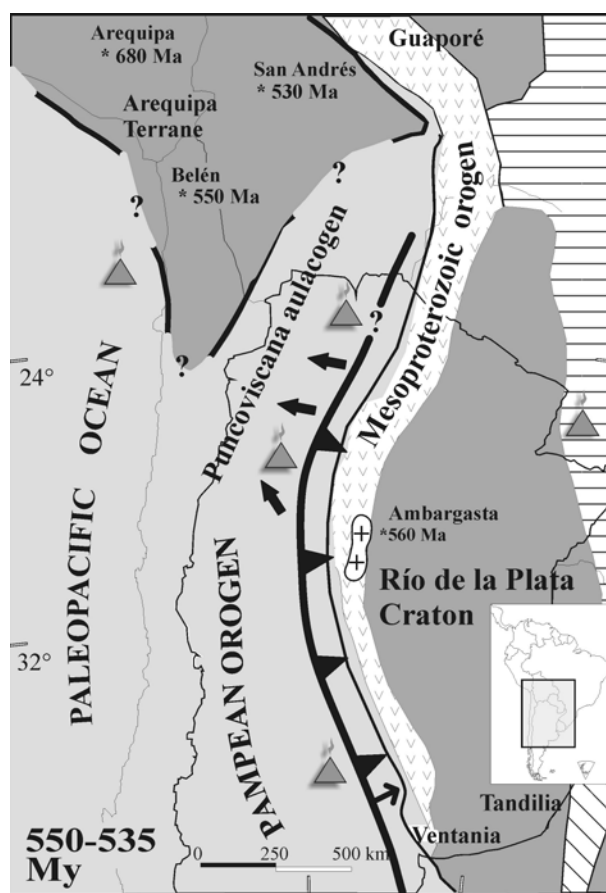


Fig. 2: Palaeogeographic interpretation of the aulacogenic basin of the Puncoviscana Formation *s.l.*

mainly siliciclastic with some limestone and volcanic participation (ACEÑOLAZA, F.G. & ACEÑOLAZA, G., 2005; ACEÑOLAZA, G. & ACEÑOLAZA, F.G., 2009; ACEÑOLAZA, F.G. & TOSELLI, 2009).

The Puncoviscana Formation is strongly deformed and partially affected by a low intensity regional metamorphism. Therefore, its exact thickness could not be determined yet; only an estimate was possible based on local sections not allowing definite conclusions on this issue (JEZEK, 1990).

The sedimentary characteristics of the unit and the presence of a particular suite of trace-fossils, body-fossils, “wrinkle” and algal structures (Pl. I), suggest that the unit was deposited in a wave and tide affected sea platform within the euphotic zone (LÓPEZ DE AZAREVICH *et al.*, 2010a, 2010b).

“Wrinkle-type” and “elephant-skin” structures (Pl. I, figs. 1-4) are frequent in the outcrops mentioned above. These are related to microbial and/or algae mats (BOUOUGRI & PORADA, 2002; SEILACHER & HAGADORN, 2010). It is also known that sunlight penetration in seawater depends on variables related to water transparency and/or turbidity, reaching down to a maximum of about 150 m deep. The deepest light penetration corresponds to the

ultraviolet band; whereas the infrared reaches down to only the first few meters (LALLI & PARSON, 1997). It should be remarked that these microbial and/or algae mats were the basic food for benthic organisms occupying shallow continental shelves and basins (CRIMES, 1974). Such shelves and basins were a favorable site for photosynthetic production by these organisms, taking advantage of solar radiation and availability of atmospheric CO₂. Such conditions favoured the development of the aerobic photosynthetic microbial and algal mats that directly affected the substrates (NOFFKE *et al.*, 2003).

Recent findings of algal structures assigned to Phaeophyceae in the Calchaqui Valley suggest an original coastal intertidal environment (LÓPEZ DE AZAREVICH *et al.*, 2010a, b), supported by sedimentological data.

The material described from the Puncoviscana Formation constitutes an important trace fossil record of Ediacaran-Cambrian age in Argentina. Considering morphological characters and their ethological interpretation, these trace fossils are interpreted as resting (cubichnia), locomotion and grazing (repichnia-pascichnia), feeding (fodinichnia) and dwelling (domichnia) structures (SEILACHER, 1953; BUATOIS *et al.*, 2002).

Cubichnia represents a trace fossil of a stationary activity affecting the sediment surface, mostly leaving shallow impressions. This type – represented by *Ivesheadia* isp. (Pl. III, fig. 10) – is rare in the Puncoviscana Formation.

Repichnia-pascichnia: This set includes those traces caused by displacement of the organisms. This type is common in the Puncoviscana Formation, with outstanding forms such as *Archaeonassa fossulata* FENTON & FENTON (Pl. III, fig. 8), *Cochlichnus anguineus* HITCHCOCK (Pl. II, fig. 4), *Didymaulichnus* isp., *Nereites saltensis* ACEÑOLAZA & DURAND (Pl. II, figs. 2-3), *Neonereites uniserialis* SEILACHER, *N. biserialis* SEILACHER (Pl. III, fig. 3), *Helminthoidichnites tenuis* FITCH (Pl. II, fig. 6), *Helminthopsis abeli* KSIAZKIEWICZ, *Protovirgularia* isp. and *Helminthoraphe* isp. Appendicle traces are represented by *Asaphoidichnus* isp., *Diplichnites* isp., *Dimorphichnus* isp., *Monomorphichnus* isp. and *Tasmanadia cachii* DURAND & ACEÑOLAZA. On the other hand, there is discussion about the origin of other forms such as *Oldhamia* (*O. antiqua* KINAHAN, *O. radiata* FORBES (Pl. III, fig. 7), *O. flabellata* ACEÑOLAZA & DURAND, *O. curvata* LINDHOLM & CASEY (Pl. III, fig. 9), and *O. geniculata* SEILACHER) that represent burrow structures developed on the sediment-biofilm interface.

Domichnia: These represent dwelling structures that reflect the life positions of organisms, such as *Palaeophycus tubularis* HALL, *Treptichnus* cf. *T. aequalternus* SCHLIRF, *Planolites* isp. and *Thalassinoides* isp. (Pl. III, fig. 5).

It must be pointed out that other fossil elements (apart from trace fossils) were assigned to *Aspidella* sp., *Nemiana simplex* (PALIJ) (Pl. I, fig. 5), *Sewkia* sp., *Selkirkia* sp. (Pl. II, fig. 1) and *Vendella larini* GUREEV, also suggesting an Ediacaran age for at least part of the sequence.

The *Oldhamia* ichno-association represents the oldest levels of the Lower Cambrian and its relation to the *Nereites* ichno-association has not been clearly established yet.

2. Tandilia: Cerro Negro Formation

The Ediacaran stratigraphic sequence of the Sierra de Olavarría and Barker region in Tandilia (Buenos Aires Province) is capped by the Cerro Negro Formation, composed of a mainly siliciclastic succession about 170 meters thick, lying unconformably on the Sierras Bayas Group. The sequence is characterized by an alternation of siliciclastic and carbonatic rocks (IÑIGUEZ & ZALBA, 1974; LEANZA & HUGO, 1987; IÑIGUEZ *et al.*, 1989; CINGOLANI & DALLA SALDA, 2000; POIRÉ, 1993).

The base of this unit is represented by 12 m of shales and red marlstones arranged on an irregular karstic surface developed on the limestones of the Loma Negra Formation. These shales and red marlstones show phosphatic levels with gaps bearing fanites and olive grey shales representing two deposit cycles, i.e., a transgression and a regression (LEANZA & HUGO, 1987; BERTOLINO, 1988; BARRIO *et al.*, 1991; ANDREIS *et al.*, 1992). The whole sequence has been recognized as deposited in an intertidal to subtidal coastal environment, deepening towards the second cycle (ANDREIS *et al.*, 1992).

Acritarchs recognized in this unit were identified by GAUCHER *et al.* (2005) as *Leiosphaeridia jacutica*, *L. minutissima* (NAUMOVA), *L. tenuissima* EISENAK, *Lophosphaeridium* sp., *Synsphaeridium* sp., and *Trachysphaeridium* sp., all of which are representative of Ediacaran age.

3. Northern Patagonia: El Jagüelito Formation

The El Jagüelito Formation crops out in the eastern border of the North Patagonian Massif (Sierra Grande; Río Negro Province). It includes a sequence of shales affected by low-grade metamorphism (phyllites). The unit is intruded by Lower Ordovician granites (VARELA *et al.*, 2009) and contains trace fossils and archaeocyathans in carbonatic conglomeratic clasts (GONZÁLEZ *et al.*, 2002, 2011).

Archaeocyathans are an extinct phylum restricted to the Lower Cambrian; they show a wide global distribution. This finding, however, is the first record from South America and is particularly relevant when interpreting the formation of Gondwana during the Ediacaran-Lower Cambrian. The possibility that at least part of the siliciclastic levels with trace fossils may represent the Ediacaran must be carefully considered. GONZÁLEZ *et al.* (2002) already referred to this when they compared the trace-fossils in this unit with those in the Puncoviscana Formation in northwestern Argentina (Pl. III).

Notably, clasts containing the archaeocyatha are up to 20 cm long and – though their origin has not been determined yet – their size and scarce evidence of rolling movement may indicate that they are local. According to GONZÁLEZ *et al.* (2010), seven different archaeocyathan forms may be distinguished and some of them are related to taxa represented in Antarctica and Australia, such as *Erismacoscinus*, *Palmericyathellus* and *Robustocyathus*. Although no fossils suggesting a closer correlation have been found yet, the phyllites of the Valcheta Formation are considered equivalent to the El Jagüelito Formation. They crop out nearby the homonymous town in the northern area of the North Patagonian Massif.

4. Malvinas Islands: Fitz Roy Tillite

In Puerto Purbis, an area in northern Gran Malvina Island, archaeocyathan remains were found in limestone clasts included in the Carboniferous Fitz Roy tillite (STONE & THOMSON, 2005). They were interpreted as originally from Antarctica and carried by the glacial layer covering the region during the Carboniferous. Another possibility is that their origin may have been in areas of the present continental shelf where outcrops of that age may have existed. Both hypotheses unfold the fact that Cambrian limestone clasts are included in Neo-Paleozoic tillites.

REGIONAL RELATION

Uruguay-Brazil-Paraguay

Biostratigraphic studies in Uruguay support a relation between outcrops of the Mina Verdún and Arroyo del Soldado groups with those of the Sierras Bayas Group in Buenos Aires Province (Argentina), based on the presence of the cosmopolitan fossil *Cloudina* (GAUCHER *et al.*, 2009). This Ediacaran form – together with acritarchs, foraminifera and other microfossils – was found in the upper part of the Yermal Formation and in the Polanco limestones (Arroyo del Soldado Group) and El Calabozo Formation (Mina Verdún Group). These levels carry *Cloudina riemkeae* (GERM), *Titanotheca coimbrae* GAUCHER & SPRECHMANN, *Soldadophycus bossii* GAUCHER *et al.*, *Siderophoca* sp. and *Waltheria marburgensis* (GAUCHER & SPRECHMANN) (see GAUCHER, 2000).

Similarly, small seashells identified as *Cloudina luciano* (BEUERLEN & SOMMER) were recorded in the Mato Grosso (Brazil) region, in the base of the Tamengo Formation (Corumbá Group). This fossil, together with the vendobionts *Corumbella werneri* HAHN *et al.* and *Titanotheca coimbrae* GAUCHER & SPRECHMANN, constitutes an Ediacaran reference in the area of Corumbá and Ladario (Mato Grosso, Brazil). Material assigned to the agglutinated foraminifer *Titanotheca* has also been

recognized in these outcrops (BOGGIANI & GAUCHER, 2004; BABCOCK *et al.*, 2005).

A thick siliciclastic sequence of probable Cambrian age (Camarinha Formation) is recognized near Curitiba (Paraná, Brasil). It contains poorly known trace- and body-fossils (CIGUEL *et al.*, 1992).

Finally, *Cloudina luciano* was also identified in carbonatic rocks of the Itapucumí Group in Paraguay (BOGGIANI & GAUCHER, 2004). This occurrence confirms its widespread regional distribution in the South American basins.

Southwest Africa and Antarctica

Regarding intercontinental correlation, the rocks mentioned above are remarkably similar to those in sequences exposed in southwestern South Africa and in Namibia (BLANCO, 2010).

In Namibia, the Ediacaran-Lower Cambrian Nama Group exposes thick sections with the trace fossil *Treptichnus* (guide genus for the base of the Cambrian). Sandy levels are also identified in the Spitskop Formation with *Pteridinium carolinaense* ST JEAN and *Treptichnus narbonnei*. Radiometric data from silicified ash of this unit indicate that sedimentation dates from 543 Ma. Similarly, there are Ediacaran sequences containing *Titanotheca* in the area of Port Nolloth (Holgat Formation); *Cloudina* occurs in the Dabis Formation instead. *Oldhamia geniculata* SEILACHER, *Helminthopsis* and *Treptichnus* were recorded in shales of the Besondereid Formation (Vanrhynsdorp Group) in South Africa (ACEÑOLAZA *et al.*, 2009).

In addition, highly deformed siliciclastic strata lie exposed in the Shackleton Mts. (Antarctica); they are assigned to the Turnpike Bluff Group and contain *Oldhamia* (*O. antiqua* and *O. radiata* FORBES), representing the Lower Cambrian. These trace-fossils are similar to trace-fossils of the Puncoviscana Formation in northwestern Argentina (BUGGISCH, 1989).

CONCLUDING REMARKS

The extent of the Pampean Orogen along the South American border of Gondwana and its relation to the Ross Orogen in Antarctica and the Delamerian in Australia (Fig. 3) have been subject to discussion for a long time. According to data drawn from lithology and fossils (traces and bodies), there is a great identity in the evolution and relation among these three orogenic structures (MILLER & ACEÑOLAZA, 1982; BOGER & MILLER, 2004; ACEÑOLAZA *et al.*, 2002; CAWOOD, 2005; CAWOOD & CRAIG, 2007; VAUGHAN & PANKHURST, 2008).

Dogmatism arising from the application of the Plate Tectonics theory has hindered a coherent revision of events that took place during the Ediacaran-Early

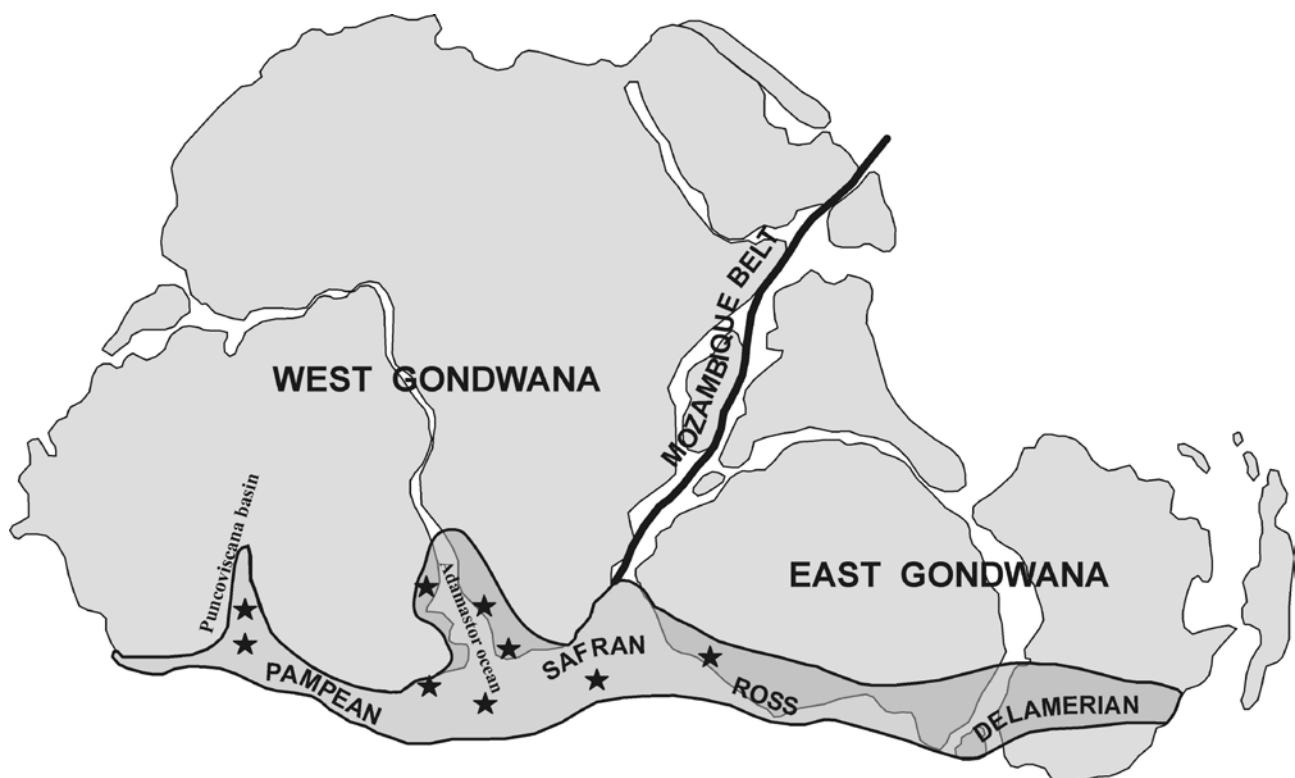


Fig. 3: Paleogeography of the position of the western margin of Gondwana with fossiliferous localities of Ediacaran-Early Cambrian age (black stars) respect to orogenic structures (Pampean, Ross, Delamerian).

Cambrian, along the Gondwanan margin relating South America with Africa, Antarctica and Australia. This added to the diverse interpretations on the origin and faunal migration, leading to an imprecise plate “puzzle” (KEPPIE & BAHLBURG, 1999).

The debate began with the interpretation of the origin of the Precordillera (Cuyania), which for several authors is a microplate derived from Laurentia and inserted in Gondwana by means of an orthogonal or suborthogonal collision (ASTINI *et al.*, 1996; RAMOS, 2004). Another question rose when some authors proposed that the origin of the Puncoviscana basin should be searched in microplates coming from the Kalahari or related to the evolution of the Arequipa-Antofalla craton (RAPELA *et al.*, 2007).

Each of these interpretations modified the proposals of the Gondwanan paleo-Pacific evolution as a typical element of an orogenic structure involving four present-day continents. In this sense, the existence of a common marine platform developed during the Late Proterozoic-Early Paleozoic was suggested (ACEÑOLAZA *et al.*, 2002; FINNEY *et al.*, 2005). This idea holds that outcrops in northwestern Argentina, Buenos Aires Province and Patagonia were all part of the same platform, later joining the African-Antarctic-Australian platform.

This general sketch highlights that complex mechanisms to move tectonic plates of unequal origin are not necessary

if this vast region can be regarded as originally forming part of Gondwana. In this sense, there were movements causing relative drifts of blocks due to transforming faults generated from oblique collisions in the ocean crust against the paleocontinent (para-autochthonous “terrane”), a fact that did not need the participation of different paleocontinents as happened with Laurentia.

South America was not removed from geological and biological events taking place during the Ediacaran-Early Cambrian. If the paleontological record displaying evidence of trace- and body-fossils during this period still has a relatively low impact in the global context, it is because the exploration in this field also does. In addition, many of the sequences are not easily interpreted because of tectonic deformation, metamorphism or relative absence of fossils. Nevertheless, we conclude that the study of such rocks is an issue deserving more attention. It is worth to highlight that trace- and body-fossil associations of this age in South America do have remarkable similarities with those of Africa, Antarctica and Australia. This fact leads us to strengthen the idea that all basins were part of the same Gondwana continent, and weakens the arguments demanding allochthonous non-Gondwanic mobile plates.

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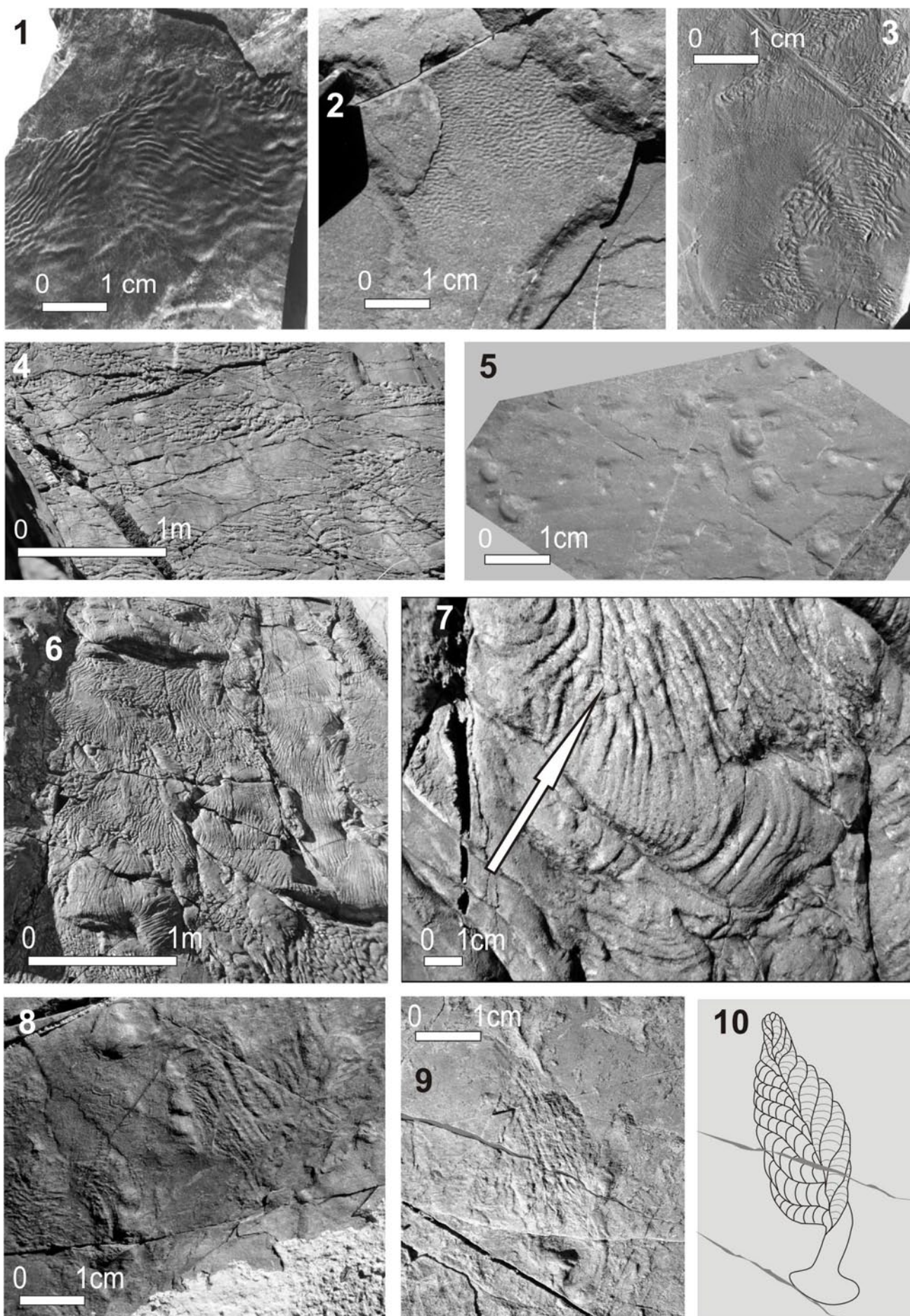
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Plate I

Biogenic structures and fossils of the Puncoviscana Formation *s.l.*

- Figs 1, 2 & 3: Examples of "wrinkle" structures from localities in NW Argentina: 1, Quebrada de Huasamayo, Tilcara, Jujuy; 2, Quebrada del Toro, Salta; 3, Escoipe, Salta.
- Fig. 4: "Elephant skin" structure from Puncoviscana Formation at Palermo, Salta.
- Fig. 5: *Nemiana simplex*, a possible medusoid from Tilcara, Jujuy.
- Fig. 6: Mega-algal structure from Palermo, Salta.
- Fig. 7: Details of dichotomic division and posible aerocistes of algal structure.
- Figs. 8, 9 & 10: Possible "charnid" like structures and interpretation of sample, Palermo, Salta.

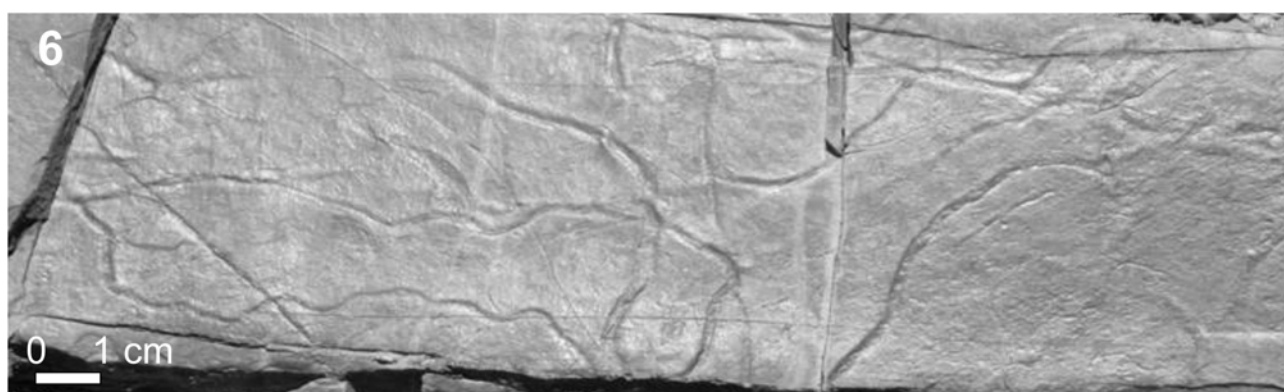
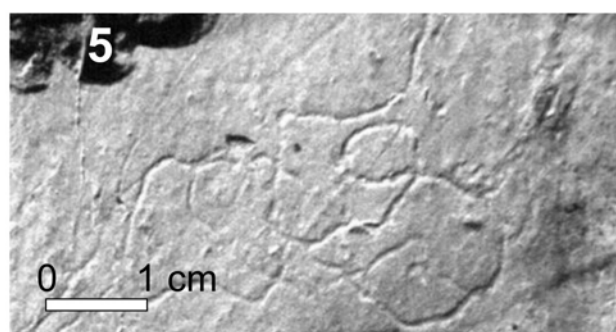
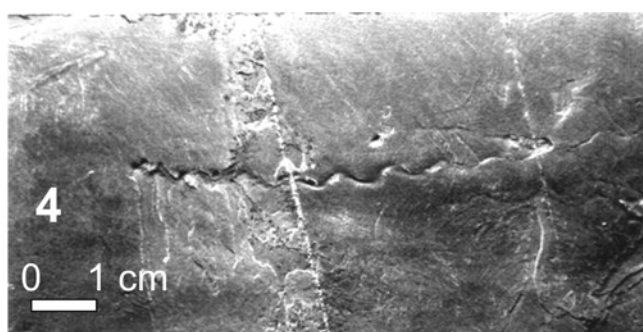
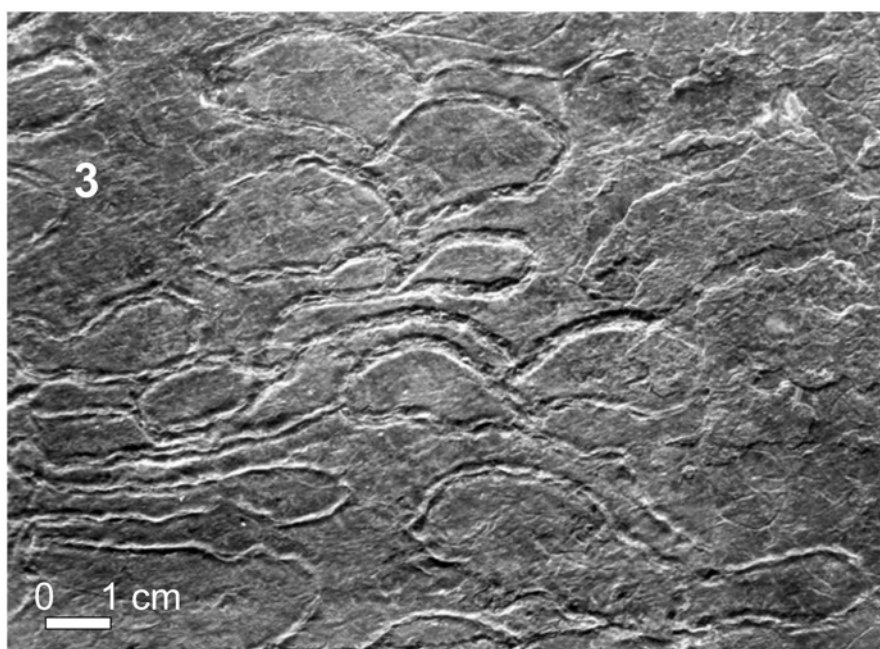
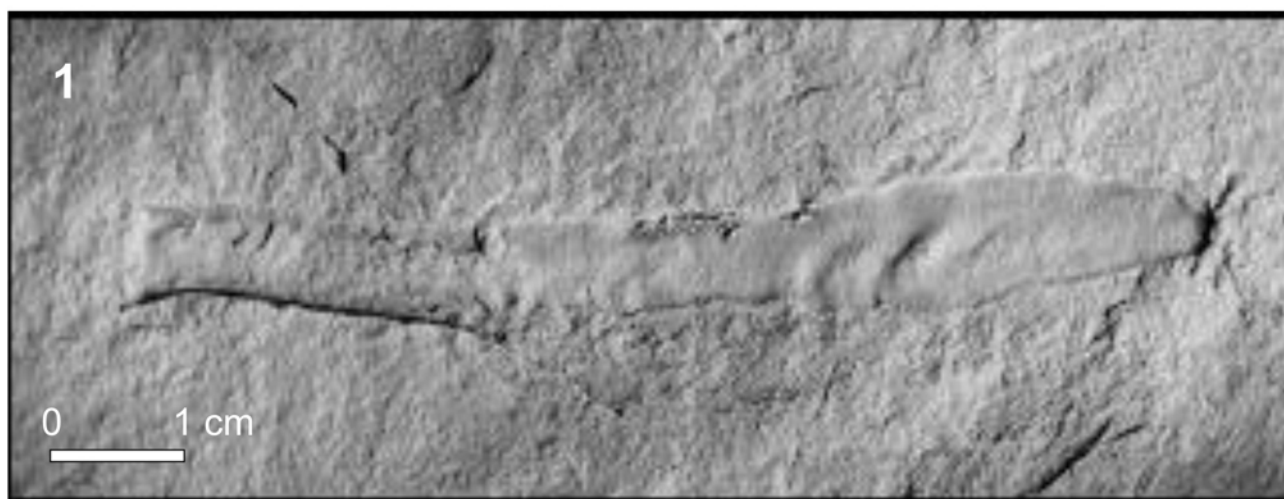


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Plate II

Fossils of the Puncoviscana Formation s.l.:

- Fig. 1: *Selkirkia* sp. from Choromoro, Tucumán.
- Figs. 2 & 3: *Nereites saltensis* from Cachi, Salta (Holotype, 2) and Campo Quijano, Salta (3).
- Fig. 4: Sinusoidal trace assigned to *Cochlichnus anguineus* from San Antonio de los Cobres, Salta.
- Fig. 5: *Gordia marina* of Abra Blanca, Salta.
- Fig. 6: *Helminthoidichnites tenuis* from Tilcara, Jujuy.



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Plate III

Fossils of the Puncoviscana Formation s.l.:

- Fig. 1: *Trichophycus aequalternus* from Choromoro, Tucumán.
- Fig. 2: Bilobulate trace fossil from San Antonio de los Cobres, Salta.
- Fig. 3: *Neonereites* (*N. uniserialis* and *N. biserialis*).
- Fig. 4: *Glokerichnus* isp. from Cachi, Salta.
- Fig. 5: *Thalassinoides* isp. from Cachi, Salta.
- Fig. 6: *Parviscopa* isp.
- Fig. 7: *Oldhamia radiata* from Muñano, Salta.
- Fig. 8: *Archaeonassa fossulata* from San Antonio de los Cobres, Salta.
- Fig. 9: *Oldhamia curvata* from Sierra Ovejera, Catamarca.
- Fig. 10: Body fossil comparable to *Ivesheadia* isp. from Choromoro, Tucumán.

