

First record of *Podichnus* in orthide brachiopods from the Lower Ordovician (Tremadocian) of NW Argentina and its relation to the early use of an ethological strategy



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ABSTRACT

Well preserved etchings from the pedicle attachment of brachiopods occur on orthide brachiopod shells from Lower Ordovician (Tremadocian) of NW Argentina. Under the name *Podichnus conicus* isp. n. this trace fossil is interpreted as a fixichnia produced by the attachment of brachiopod pedicles upon hard substrates. The trace is characterized by an irregular and asymmetrical cluster of circular pits. Each individual pit has a typical conical shape and presents the external mean diameter/length ratio close to 1. The occurrence of *P. conicus* isp. n. in the Tremadocian is the oldest record of this ichnogenus, and points to orthide brachiopods as *Podichnus* producers for the first time. The presence of this structure provides new information regarding colonization of biogenic hard substrates during the Early Ordovician and an adaptive strategy of its use by orthide brachiopods.

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1. Introduction

Modern and ancient marine environments feature abundant substrates that are sufficiently firm and consolidated to be encrusted and bored. These hard substrates range from coarse sand grains to vast expanses of lithified seabed, and include skeletons of living and dead organisms as well as rock clasts (Taylor and Wilson, 2003). It is commonly known that brachiopods acted as hosts for many encrusters and borers (e.g. Kessling et al., 1980; Zumwalt and Delaca, 1980; Alexander and Scharpf, 1990; Barnes and Clarke, 1995; Cuffey et al., 1995; Bitner, 1996; Fagerstrom, 1996; Taddei Ruggiero et al., 2006; Rodrigues et al., 2008; Taddei Ruggiero and Raia, 2010) and this was particularly true in the Palaeozoic when brachiopods were a major component of the marine fossil record.

During the Ordovician, a major evolutionary adaptive radiation occurred among marine invertebrates known as “The Great Ordovician Biodiversification Event” (Webby et al., 2004; Harper, 2006). This general increase in diversity was linked not only to a taxonomic radiation but also to new life modes and behaviours by benthic marine invertebrates, which also is reflected in the ichnodiversity of trace fossils

(Mángano and Droser, 2004). Wilson and Palmer (2006) coined the term for this increase in the diversity and abundance of borings as “The Ordovician Bioerosion Revolution”. According to these authors, the number of borings per unit of hard substrate area increased considerably through this period. So far, nine different macroboring ichnogenera are known to appear during Late Ordovician (Pickerill, 1976; Mayoral et al., 1994; Wilson, 2007) represented by *Trypanites* Mägdefrau, 1932, *Palaeosabella* Clarke, 1921, *Gastrochaenolites* Leymerie, 1842, *Petroxestes* Wilson and Palmer, 1988, *Cicatricula* Palmer and Palmer, 1977, *Vermiforichnus* Cameron, 1969, *Pinaceocladichnus* Mayoral, 1988, *Sanctum* Erickson and Bouchard, 2003, and *Oichnus* Bromley, 1981.

Most articulate brachiopods live attached to hard substrates. In this context, Bromley and Surlyk (1973) described how some of these organisms penetrate into carbonate substrates using either anchoring papillae or rootlets that extend from the attachment surface of the pedicle. They named these typical brachiopod-pedicle etching traces *Podichnus*. These etchings, which resemble groups of finger-shaped traces, represent the anchoring or fixation by brachiopods to a substrate by means of a soft body part and such traces are assigned to the ethological class fixichnia (Gibert et al., 2004). According to Bromley and Asgaard (1993), the *Podichnus* ichnogenus belongs to the *Gnathichnus* ichnofacies constituted mainly by epigenic and shallow-tier structures. The ichnofacies is characterized by hard substrates such as shells and lithoclasts.

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The presence of *Podichnus* on material of Ordovician age represents not only an important source of new information regarding colonization of hard substrates during the Ordovician Bioerosion Revolution but also shows an adaptive strategy for its use. The aims of the present study are twofold: 1) to report the first evidence of *Podichnus* from the Lower Ordovician orthide brachiopods and, also produced by orthides, and to characterize, describe and interpret formally these structures as a new Ordovician *Podichnus* ichnospecies, and 2) to give some information about the new strategy adopted by brachiopods to colonize biogenic substrates during the Early Ordovician.

2. Geographic and geological setting

Specimens were collected from the Saladillo Formation, Santa Victoria Group, exposed along the track to the Parcha locality, between Angosto de Lampazar and Abra de Sococha, close to Quebrada del Toro in the Argentine Cordillera Oriental (Salta Province, Northwest Argentina, Fig. 1).

The Saladillo Formation consists of shaly mudstones with intercalated thin sandstone beds at its base (Fig. 2). The fossils are preserved in argillite nodules, up to 40 cm in diameter, encased within calcareous cement, and the nodules are most abundant in the upper half of the unit (Harper et al., 2004; Villas et al., 2009). The fossiliferous nodules contain very abundant disarticulated, calcitic brachiopod shells, together with other scarce fossil components such as trilobites and orthoconic cephalopods. The nodules were collected about 100 m above the base of the Saladillo Formation (see Fig. 2).

According to Villas et al. (2009) the fossiliferous horizon of the Saladillo Formation is probably referable to the lower part of the *Paltodus deltifer* Biozone. Regarding the graptolite biozonation, it occurs within a 70 m thick interval barren of graptolites, between the *Bryograptus* Biozone and the *Kiaerograptus* Biozone (Ortega and Albanesi, 2002, 2003). The levels could be correlated with the early late Tremadocian *Peltocare* regressive event (sensu Erdtmann (1986)).

The Saladillo Formation has been interpreted as being deposited during a transgressive phase in middle to distal platform environments (Moya, 1988). The brachiopod accumulation yielding *Podichnus*

coincides with the lens-like bioclastic Type A accumulations described by Aceñolaza and Nieva (2001) from the same formation. These authors also interpreted the accumulations as para-autochthonous, resulting from tempestitic events and ulterior diagenetic processes of carbonate enrichment. The original emplacement of the studied brachiopod association can thus be interpreted as belonging to an upper offshore sedimentary regime with fine-grained unconsolidated substrates, above the storm-weather wave base.

3. Material and methods

One hundred and seventy nine disarticulated valves belonging to *Notorthisina muscosa* Villas and Herrera (in Villas et al. (2009)), *Nanorthis bifurcata* (Harrington, 1937) redescribed by Villas et al. (2009), and *Lipanorthis santalaurae* Benedetto (in Benedetto and Carrasco (2002)) were collected from the Saladillo Formation after nodules were slightly etched with diluted acetic acid. The two former species are impunctate orthidines and the later one is a punctate dalmanellidine, which is the oldest known punctate brachiopod (Harper et al., 2004). Shells of all the three species show pedicle etching traces with variable abundances.

The studied brachiopod shells are well preserved as both internal and external moulds, promoted by burial in very fine-grain sediment. Our study resulted in the recognition of an etching trace described herein, which was observed on exteriors of dorsal and ventral valves belonging to those brachiopods (Fig. 3). No remains of encrusting organisms were recorded, although ramified boring traces on brachiopod shell interiors, similar to those of ctenostomate bryozoans, occasionally can be seen.

To perform this study, each brachiopod valve was divided into seven areas to partition the distribution of trace fossils according to Alexander (1994) (Fig. 4). The bioerosion structures within these areas were counted and measured. All the specimens studied and illustrated herein are housed in the Museo de Paleontología de la Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina under repository numbers CORD-PZ 30403-1, 30403-2, 30421, 30425a-2, 30431a-1, 30434a-1, 30434b2-6, 30436a-13 and 30436b-12.

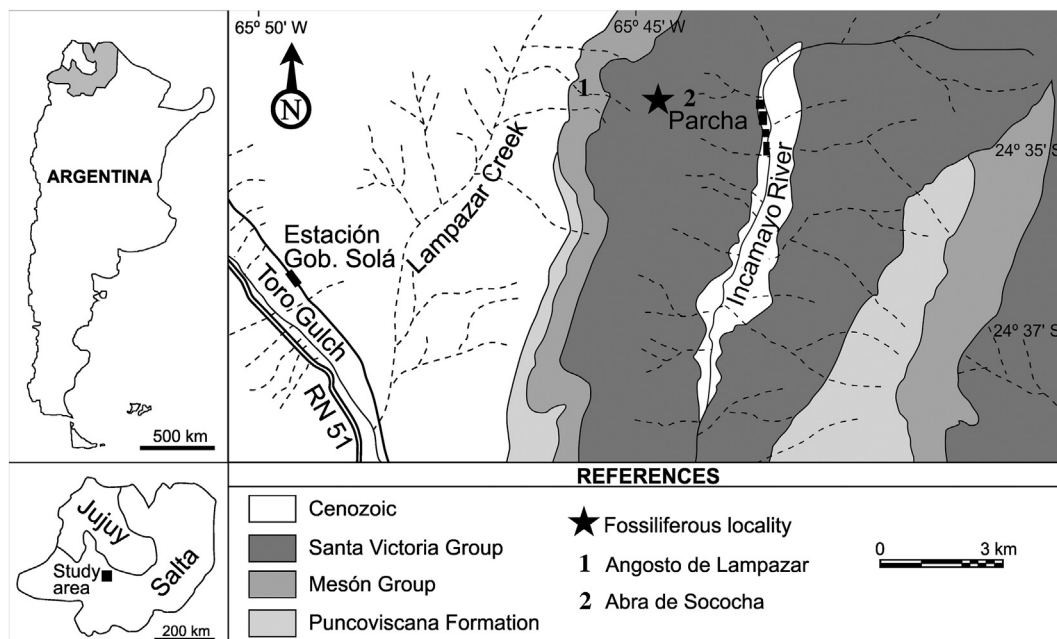


Fig. 1. Geographic and geologic maps showing the location of the studied outcrop close to Parcha in the Argentine Cordillera Oriental (Salta Province, Northwest Argentina) (after Harper et al., 2004).

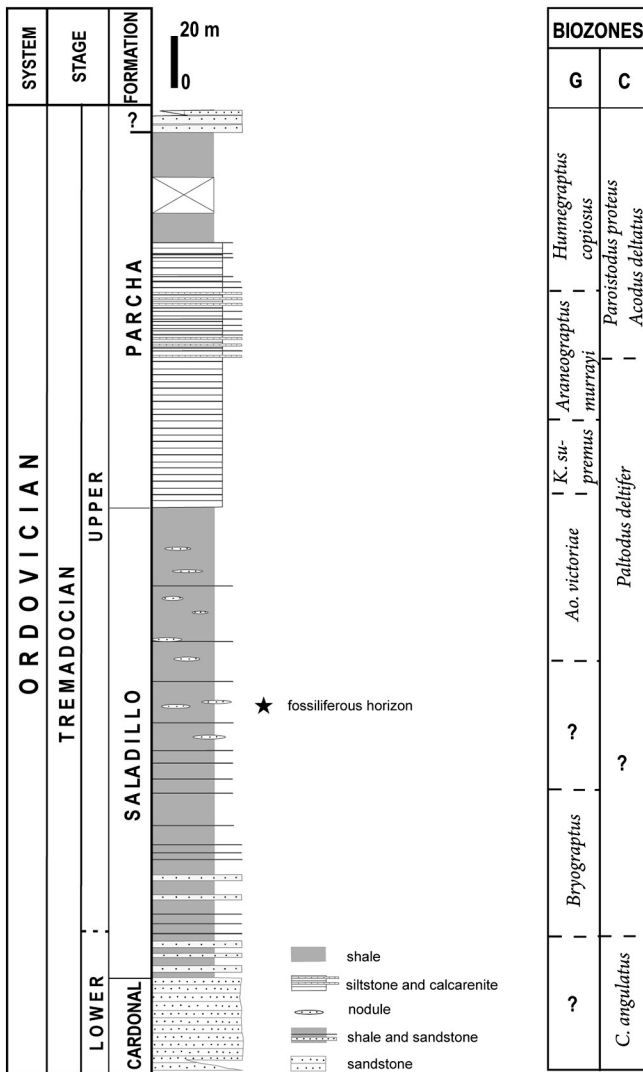


Fig. 2. Stratigraphic profile for the Saladillo Formation (Salta Province, Northwest Argentina) indicating the location of the fossiliferous horizon (after Villas et al., 2009).

4. Results

4.1. Taphonomic analysis

The brachiopod assemblage from the studied outcrop consists of disarticulated shells. Only a few valves are fragmented. Generally, brachiopod valves lack a preferred orientation and went through very slight size sorting. Only the smallest valves, below 4 mm wide are

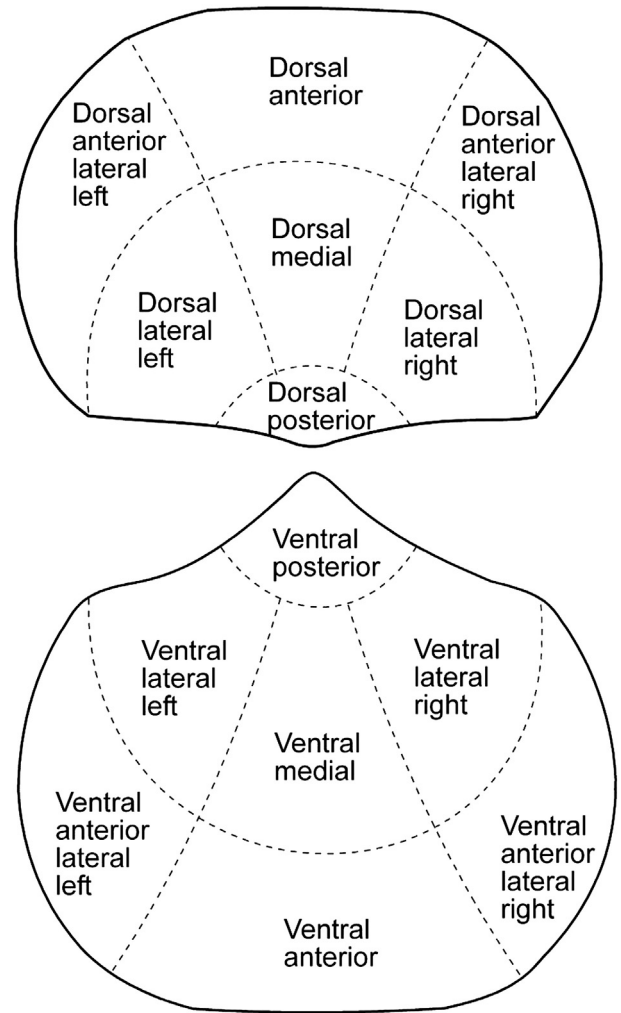


Fig. 4. Schematic division of brachiopods valves according to Alexander (1994).

absent. All the other valve sizes, between 4 and 15 mm wide, are well represented in the three recorded brachiopod species: *Notorthisia musculosa*, *Nanorthis bifurcata*, and *Lipanorthis santalaurae*. The valves have been sorted by shape, with dorsal valves more abundant than ventral in all the three species. The ratios of ventral to dorsal valves being 0.64 in *N. musculosa*, 0.75 in *N. bifurcata* and 0.86 in *L. santalaurae*. In summary, following the taphonomic criteria by Pickerill and Brenchley (1979), the disarticulation of the shells, the slight size sorting of the valves, the lack of preferred orientation and fragmentation, as well as the ratio of ventral to dorsal valves, approaching unity both in *N. bifurcata* and *L. santalaurae*, and well above 0.5 in *N. musculosa*, indicate

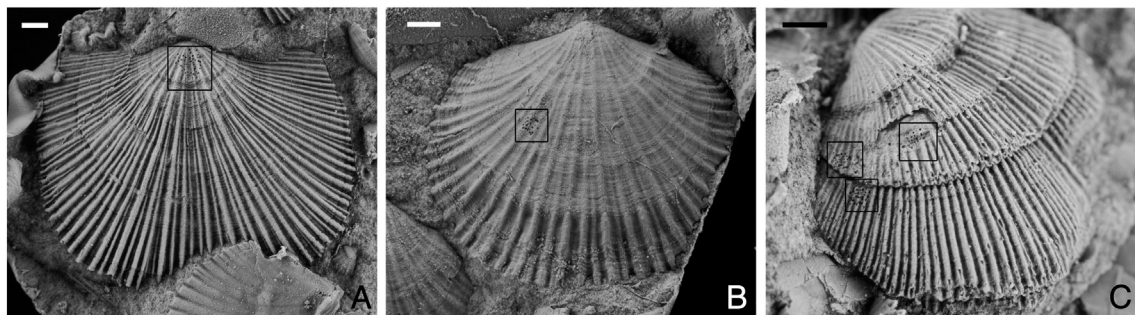


Fig. 3. A–C. Valves of the three brachiopod species recorded in the assemblage hosting *Podichnus conicus* isp. n. (scale bars = 1 mm). A) Latex cast of exterior of dorsal valve of *Nanorthis bifurcata*, CORD-PZ 30436b-12. B) Latex cast of exterior of ventral valve of *Notorthisia musculosa*, CORD-PZ 30434-6. C) Latex cast of exterior of dorsal valve of *Lipanorthis santalaurae* in lateral view, CORD-PZ 30431a-1.

that the assemblage has been disturbed but that the degree of disturbance was limited. Thus, although some transport and winnowing have occurred it does not seem to have been sufficiently extensive to modify substantially the original association.

According to the above criteria, the three recorded species are considered to have been part of the same community with abundances not too different from those recorded in the fossil assemblage. *Notorthisina musculosa* and *Nanorthis bifurcata*, with 44% and 42%, respectively, of the total shell numbers, are the most abundant species. *Lipanolthis santalaurae*, with only 14% of the total shell number, represents a minority species. These percentages have been calculated using the numbers of the most abundant valve of each species, which represents a total of 102 different possible shells from a total of 179 studied valves.

Only one of the three species occurs elsewhere in the succession. It is *Lipanolthis santalaurae* that occurs besides *Nanorthis calderensis calderensis* Benedetto, 2007 in nodules about 40 m below the studied horizon. Nevertheless the grain size of these lower nodules is not so fine as that of the nodules from the higher horizons, and no evidence of etching traces on the shells has been observed. *L. santalaurae* is also known from its type locality in the Floresta Formation of the same Argentine Cordillera Oriental, Jujuy Province (Benedetto and Carrasco, 2002). Although no description of etching traces on these shells or those of accompanying brachiopods from La Floresta Formation has been made, it could be dependant on a rock grain size too coarse for their preservation.

4.2. Distribution of pedicle etching traces

Pedicle traces were found on three brachiopods species (*Lipanolthis santalaurae*, *Notorthisina musculosa* and *Nanorthis bifurcata*) (Fig. 5A–C). Among the 179 studied specimens, only 9 of the 66 recovered valve external moulds (13%) are affected with bioerosion. The bioerosion is always present on the valve exteriors. In all the three brachiopod species pedicle-etching traces are present in both the dorsal and ventral valves of relatively large sizes, indicating adult growth stages of the hosts. None of these traces on the valve exteriors are deep enough to completely penetrate the sell. No response has been observed by the host brachiopods to increase internally the shell thickness of the areas suffering bioerosion.

It seems there is an apparent symmetrical pattern in both valves related with the distribution of traces on *Lipanolthis* and *Notorthisina*

species (Fig. 5A–B). A total of 30 *Podichnus* specimens were found and distributed over four valves of *Lipanolthis santalaurae*, three valves of *Notorthisina musculosa* and two valves of *Nanorthis bifurcata*.

The dorsal valve of *Lipanolthis santalaurae* hosts the higher number of *Podichnus* with 13 traces (Fig. 5A), while its ventral valves host a total of 10 traces. The other two brachiopod species host a similar number of *Podichnus*. The dorsal and ventral valves of *Notorthisina musculosa* host three and one *Podichnus* specimens, respectively (Fig. 5B). The dorsal and ventral valves of *Nanorthis bifurcata* host one and two *Podichnus* specimens each (Fig. 5C).

The area occupied by clusters in *Lipanolthis santalaurae* is 304 mm² (Table 1). On the dorsal valves the percentage of occupancy is ca. 9% and the maximum number of *Podichnus* is present on the dorsal medial and dorsal lateral right areas (Fig. 5A). On the ventral valves the percentage of occupancy is 5.0% (Table 2) and the maximum number of *Podichnus* is present on the lateral right and anterior areas (Fig. 5A).

In *Notorthisina musculosa* the cluster area extends up to 331 mm² (Table 1), representing 1.0% of occupancy on the dorsal valves and 0.3% on the ventral (Table 2). The maximum number of *Podichnus* on the dorsal valves is present on the lateral left area and, in the ventral valve, on the medial and lateral left areas (Fig. 5B).

Finally, in *Nanorthis bifurcata*, the cluster area is the largest, reaching 723 mm² (Table 1), but constituting only 0.9% of occupancy on the dorsal valve and 0.8% on the ventral valve (Table 2). On the dorsal valve the maximum number of *Podichnus* is present on the posterior area and, on the ventral valve on the medial area (Fig. 5C).

5. Systematic palaeoichnology (by A. Santos and E. Mayoral)

Ichnogenus *Podichnus* Bromley and Surlyk, 1973

Type ichnospecies *Podichnus centrifugalis* Bromley and Surlyk, 1973

Other ichnospecies *Podichnus obliquus* Robinson and Lee, 2008; *Podichnus perpendicularis* Robinson and Lee, 2008; *Podichnus donovani* Breton, 2011.

Podichnus conicus isp. n.

Etymology From the Greek *κωνικός* (conical shape).

Locus typicus Quebrada del Toro (Salta Province, NW Argentina).

Stratum typicum Argilite nodules in shaly mudstones. Saladillo Formation. Early Ordovician in age.

Holotype On the external mould of a dorsal valve of *Lipanolthis santalaurae* CORD-PZ 30421/1. (Fig. 6A–B).

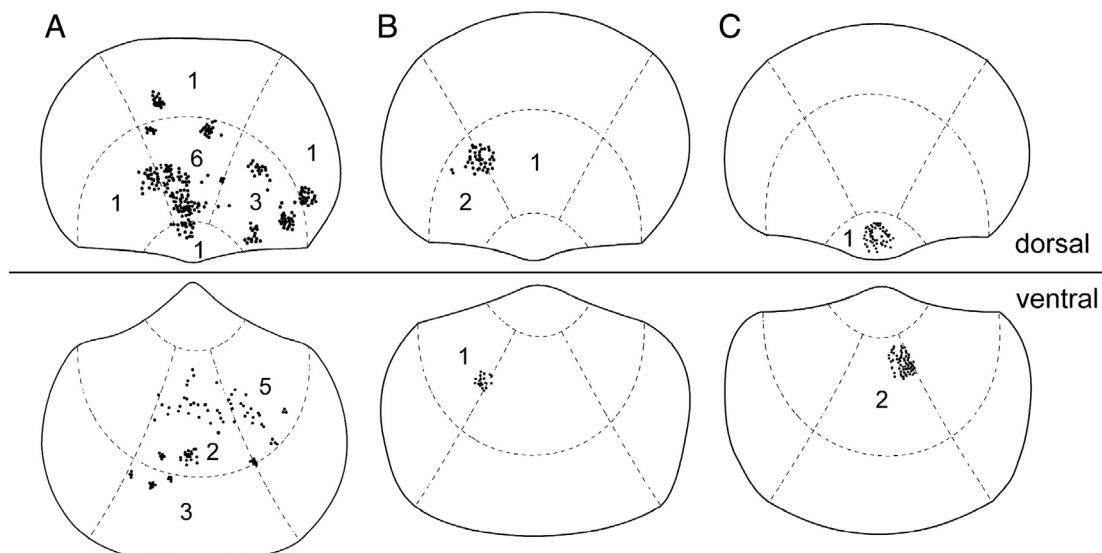


Fig. 5. Frequency and spatial distribution of brachiopod pedicle etching traces in each sector of *Lipanolthis santalaurae* (A), *Notorthisina musculosa* (B) and *Nanorthis bifurcata*.

Table 1
Measurements of *Podichnus conicus* isp. n.

Taxa	Diameter (µm)			Area (mm ²)			Mean diameter (µm)	Scattered area (mm ²)
	Peripheral pits			Central pits				
<i>Lipanorthis santalaurae</i> (N° measured pits: 322)	Min. 43	Max. 56	Mean 49	Min. 28	Max. 37	Mean 33	304	32
<i>Notorthisina muscolosa</i> (N° measured pits: 83)	55			36			331	44
<i>Nanorthis bifurcata</i> (N° measured pits: 100)	54			43			723	68

Paratypes CORD-PZ-30421/2 (Fig. 6C) (on the external mould of a dorsal valve of *Lipanorthis santalaurae*); CORD-PZ-30425a/1 (Fig. 6D) (on the external mould of a ventral valve of *L. santalaurae*); CORD-PZ-30403/1 (Fig. 6E, F) (on the external mould of a ventral valve of *Nanorthis bifurcata*); CORD-PZ 30436b/12 (Fig. 7A) (on the external mould of a dorsal valve of *N. bifurcata*), CORD-PZ 30403/2 (Fig. 7B) (on a fragment of the external mould of a dorsal valve of *Notorthisina muscolosa*).

Diagnosis An irregular and asymmetrical cluster of variable outline constituted by circular to subcircular pits in calcareous shells of brachiopods. The pits at the centre of the group are smaller than peripherals. Internal moulds of the small pits are short and rounded, while the large are typically conical or subcylindrical, having the external mean diameter/length ratio close to 1.

Description Group of circular to subcircular pits constituting irregular clusters of variable outline, more or less compact or disposed in an isolated or scattered pattern (Figs. 6–7, 9; Table 1). Clusters are normally asymmetrical and when they are well defined, central and peripheral pits are distinguished. The pits at the centre of the group are smaller with a diameter from 28 µm (in *Lipanorthis santalaurae*, Table 1) to 43 µm (in *Nanorthis bifurcata*, Table 1). The more peripheral pits are larger, ranging from 43 µm to 56 µm (in *Lipanorthis santalaurae*, Table 1). Pits are perpendicular to the substrate, the central pits usually are closely spaced (Figs. 6B, 7B), while the peripheral pits are further apart and occasionally entering the surface at a slightly oblique angle (Fig. 6C–D). When the pits appear scattered, the diameter varies between 18 µm and 68 µm (Table 1). The number of pits could vary between 15 and 58. The cluster area varies from 304 mm² on *L. santalaurae*, 331 mm² on *Notorthisina muscolosa* and 723 mm² on *N. bifurcata*. The shell surface between the pits is undisturbed.

External natural moulds or latex casts reveal the typical profile of these pits. The central pits are short and with rounded edges. On the other hand, peripheral pits show an internal or distal diameter approximately 40% smaller than the external diameter, which value is practically similar to the length of the hole. This external diameter/length ratio (1.01) results in a conical shape (Figs. 6B–E; 8; Table 3), only slightly cylindrical in some isolated, large pits.

Remarks The morphologic analysis of the etching structures preserved revealed the presence of a new ichnospecies belonging to *Podichnus*. The bioerosive structures correspond to those left by the etching activity of brachiopod pedicles and, from an ethological point of view, are included in Fixichnia as they resulted from the anchoring or fixation of sessile epibionts by means of a soft body part (Gibert et al., 2004).

Table 2
Percentage of emplacement of *Podichnus conicus* isp. n. in relation to the total valve area of brachiopods. A. *Lipanorthis santalaurae*. B. *Notorthisina muscolosa*. C. *Nanorthis bifurcata*.

Taxon	Valve	Total valve area (mm ²)	Mean area occupied by <i>Podichnus</i> (mm ²)	% emplacement
A	Dorsal	48.81	0.29	8.9
	Ventral	49.62	0.31	5.0
B	Dorsal	74.27	0.75	1.0
	Ventral	57.97	0.19	0.3
C	Dorsal	87.04	0.69	0.9
	Ventral	83.45	0.70	0.8

Podichnus conicus isp. n. differs from other known *Podichnus* ichnospecies (*Podichnus centrifugalis* Bromley and Surlyk, 1973, *Podichnus obliquus* Robinson and Lee, 2008, *Podichnus perpendicularis* Robinson and Lee, 2008 and *Podichnus donovani* Breton, 2011), basically by presenting an asymmetrical cluster with short, rounded and small central pits together with large and typically conical peripheral pits with an external mean diameter/length ratio close to 1. *Podichnus silesiacus* proposed by Malkowski (1975) is considered here a junior synonym of the ichnospecies *P. centrifugalis* in agreement with Michalík (1977), because it closely resembles the type species of the ichnogenus.

Podichnus conicus isp. n. diverges from *Podichnus centrifugalis* and *Podichnus obliquus*, in that both show a centrifugal pattern where peripheral pits enter the substrate obliquely or centrifugally. In the case of *P. centrifugalis* the shell surface within the outline of the trace is mostly removed. Relative to *Podichnus perpendicularis*, the new ichnospecies lacks the typical curved furrows and the shell surface within the outline of the trace is not removed.

The other known ichnospecies, *Podichnus donovani* is very different and much more complex. This ichnospecies is characterized by a subcircular group of cylindrical pits, penetrating obliquely in the substratum after a subhorizontal direction. These are transversely striated and centrifugally and radially arranged. Additionally, all groups are surrounded by a peripheral crown, made of one row of irregular plates separated by tiny radial grooves. These characteristics are completely absent in *Podichnus conicus* isp. n.

Stratigraphic range Early Ordovician

6. Discussion

6.1. How far back does *Podichnus* record extend?

The typical brachiopod pedicle etching trace referred to *Podichnus* was first described by Bromley and Surlyk (1973) from Cretaceous and modern material. By this time, one ichnospecies was erected and named *Podichnus centrifugalis* Bromley and Surlyk, 1973. Since then, the study of diverse materials from different ages and localities expanded the stratigraphic range of *Podichnus*, which was in fact much more widespread than previously thought. To date, several occurrences of this trace fossil were recorded from recent (Bromley and Surlyk, 1973) to the Silurian (Bundschuh, 2000).

All recent and fossil records of *Podichnus* are considered to have been produced by species of the extant brachiopod orders Terebratulida and Rhynchonellida. This is the case not only for the post early Jurassic

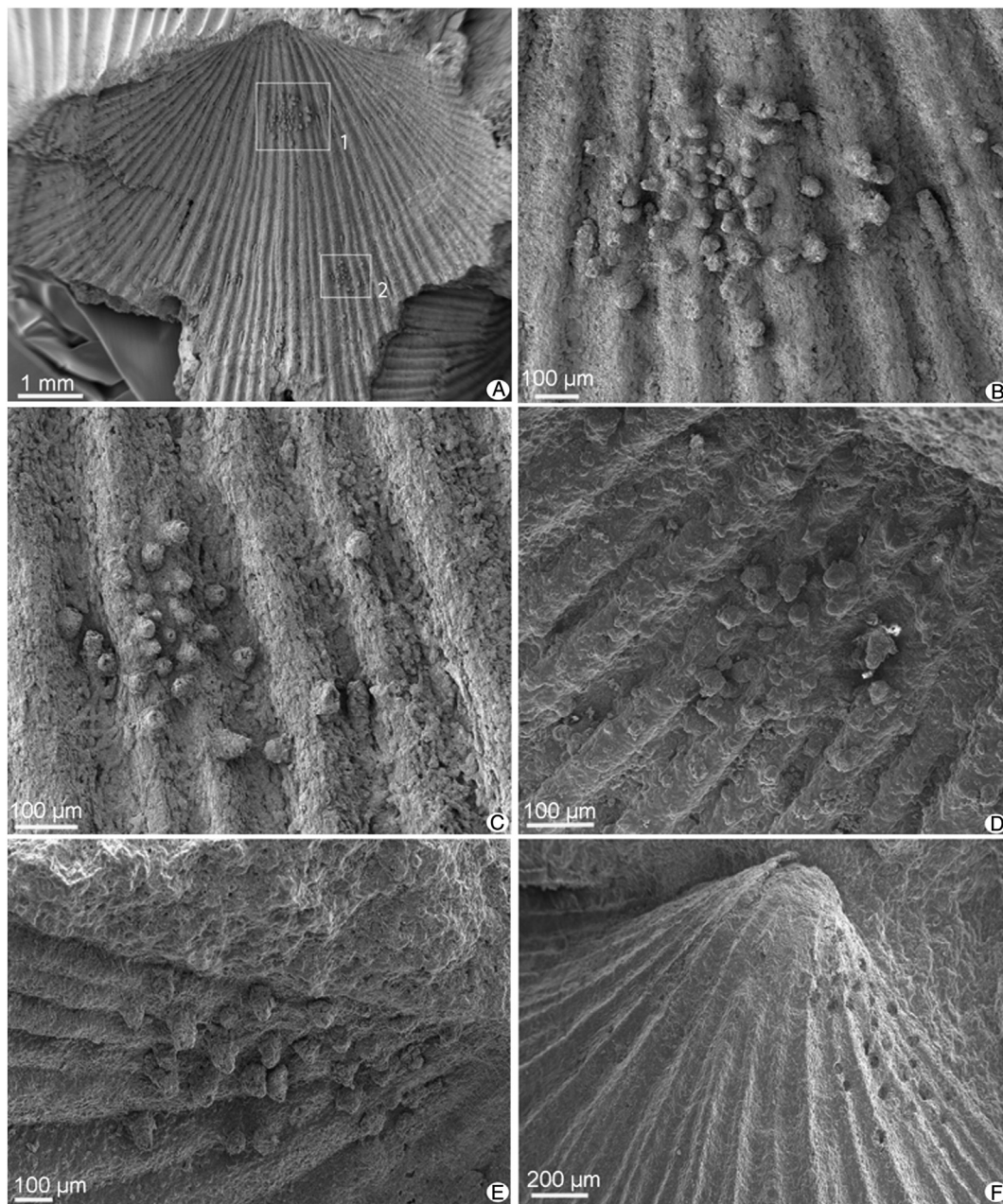


Fig. 6. A–D. *Podichnus conicus* isp. n. A) General view of the specimen CORD-PZ-30421, the external mould of a dorsal valve of *Lipanorthis santalaurae*, showing the holotype (square 1) and one paratype (square 2). B) Close-up view of the holotype (CORD-PZ-30421/1). C) Idem for the paratype (CORD-PZ-30421/2). D) Pit casts of one asymmetrical cluster on the external mould of a ventral valve of *Lipanorthis santalaurae* (Paratype CORD-PZ-30425a-2). E–F) Pit casts on the external mould of a ventral valve of *Notorthisina muscolosa* (Paratype CORD-PZ-30403-1) showing the characteristic conical shape (E) and its latex cast (F) exhibiting a scattered pattern.

times, in which only those two rhynchonelliformean orders survived, but also for previous times, including the late Palaeozoic, when other rhynchonelliformean brachiopod orders were at their maximum peak of diversity (Williams and Carlson, 2007: Fig. 1900). This is the case for the Devonian (Vogel et al., 1987), Carboniferous, and Permian *Podichnus* records (Alexander, 1994), in which leiorhynchids (order Rhynchonellida) are considered to have produced the etching traces. No boring abilities have been described until now for any of the other pedunculate rhynchonelliformean brachiopod orders known from the Palaeozoic: Orthotetida, Billingsellida, Protorthida, Orthida, Pentamerida, Strophomenida, Spiriferida, Spiriferinida, Atrypida or Athyridida. Among them, only the first five orders are known from the Lower Ordovician (Williams and Carlson, 2007) and only the order Orthida has been recorded from the Lower Ordovician rocks of NW Argentina (Benedetto, 2003). On the basis of this occurrence, the

stratigraphic range of *Podichnus* now extends from the Early Ordovician (Tremadocian) to the Recent. Besides extending the stratigraphic range of the ichnogenus, this finding demonstrates that the ability of brachiopod pedicles to dissolve carbonate substrates was early developed by a primitive group: the order Orthida.

6.2. Trace-maker interpretation

This study on Early Ordovician brachiopod faunas provides evidence for the acquisition of new features (morphologic changes such as the type of pedicle) that define a new behaviour by brachiopods. It must be stressed that in this kind of soft-sediment environment the presence of stable hard substrates was a key limiting factor for epifaunal organisms. In this context, during the expansive episode of faunal diversification in the Early part of the Ordovician Period, shells of living or dead

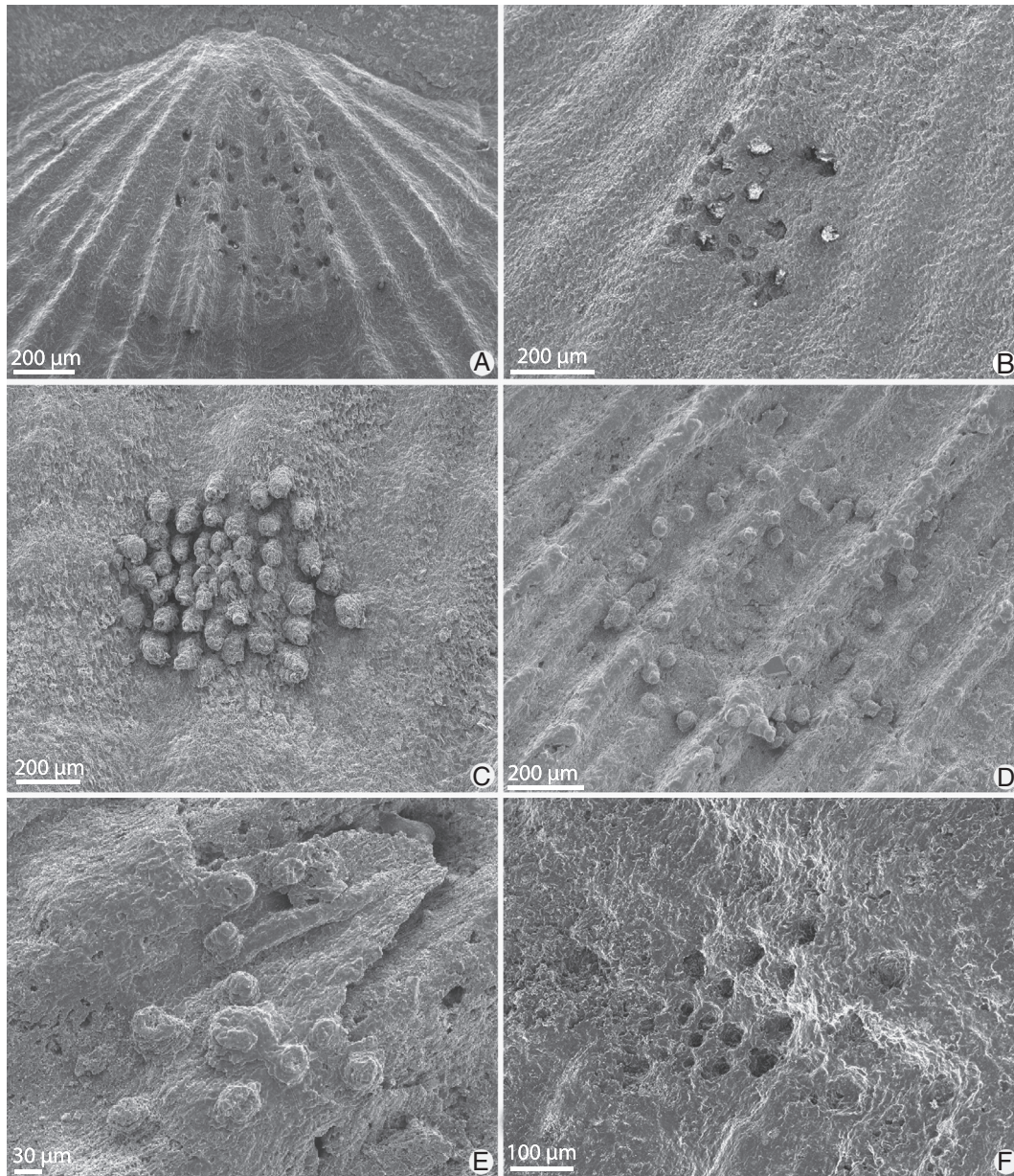


Fig. 7. A–F. *Podichnus conicus* isp. n. A) Cluster of pits irregularly arranged seen on the latex cast of a dorsal exterior of *Nanorthis bifurcata* (Paratype CORD-PZ-30436b-12). B) Cluster of pits closely spaced seen on the latex cast of a dorsal exterior of *Notorthisina musculosa* (Paratype CORD-PZ-30403-2). C) Pit casts in an asymmetrical cluster on the external mould of a ventral valve of *N. musculosa* (CORD-PZ-30434-b2-6). D) Pit casts in a small, asymmetrical cluster on the external mould of a ventral valve of *Lipanorthis santalaurae* (CORD-PZ-30425a-2/1). E) Pit casts in a large spaced cluster on the same external mould than E (CORD-PZ-30425a-2/2). F) Isolated and irregular, scattered pattern on the same external mould than E and F (CORD-PZ-30425a-2/4).

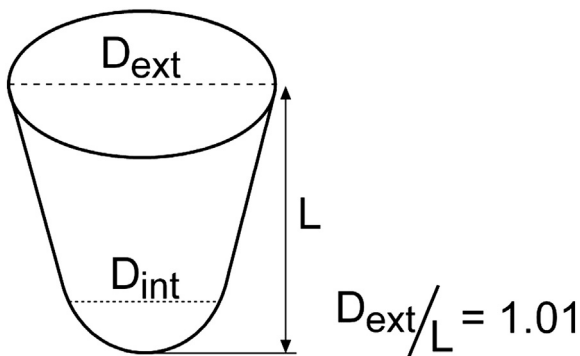


Fig. 8. Idealized sketch for *Podichnus conicus* isp. n. showing the characteristic conical shape derived from the external mean diameter/length ratio.

organisms have appeared to serve as potential and stable hard substrates for bioeroders and epibiont colonization. The shells, themselves, functioned as important benthic islands on which several biological groups found a stable place for settlement (e.g. [Zusckin and Pervesler, 1996](#); [Taylor and Wilson, 2003](#)) in an adverse environment.

Although any of the three pedunculated orthide species of the studied community could have been the producer of the described pedicle etching traces, several evidences points to *Lipanorthis santalaurae* as the trace-maker. According to the taphonomical results and palaeo-environmental interpretations, it seems that *L. santalaurae* was able to thrive on fine grain soft substrates directly attached to other brachiopod shells, conspecific or not, by its functional pedicle ([Fig. 10](#)).

Being the original brachiopod association not substantially modified as determined by the taphonomic analysis, the low number of bioeroded valves with *Podichnus* (13% of the total 66 studied exterior

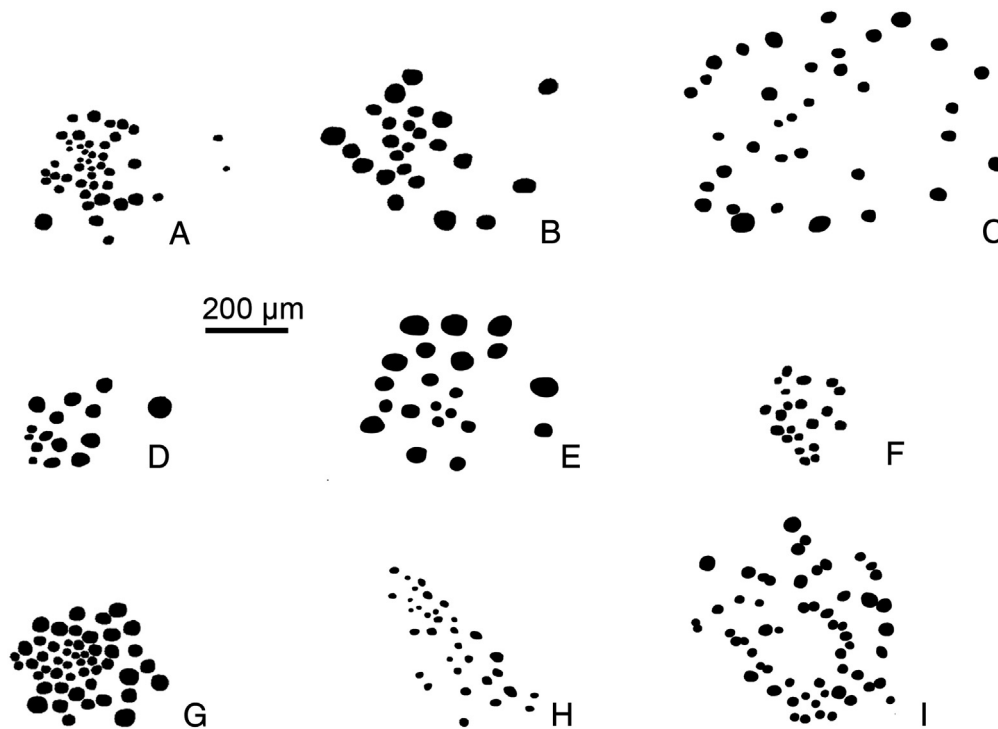


Fig. 9. Plan view of *Podichnus conicus* isp. n. A–E) On *Lipanorthis santalaurae*. F–H) On *Notorthisina musculosa*. I) On *Nanorthis bifurcata*. A general asymmetrical cluster pattern is typical with small central holes and larger peripheral ones. Some scattered patterns are frequent also (8C, 8F, 8H).

valves) points to a producer that should be a minor part of the association. *Notorthisina musculosa* and *Nanorthis bifurcata*, representing 44% and 42% respectively of the brachiopod association, can be rejected as the trace-maker, because they would have perforated a higher number of shells than those recorded. However, the collected valves of *Lipanorthis santalaurae*, which represent about only the 14% of the preserved shells, displays several features pointing to it as the best candidate to be the trace producer. These shells are those with the highest incidence of bioerosion within the association, not only in relative number of bioeroded valves (at 50% of its studied exterior valves) but also in density of etching traces on the same valve (Figs. 3; 5). This could be explained by a preference of the producer larvae to attach to conspecific specimens forming clusters. This is a strategy also known from other carbonate boring brachiopods (e.g. Vogel et al., 1987; Alexander, 1994). Such a strategy would not only allow them to thrive on soft substrates but would also be an advantage during

reproduction, favouring the early fecundation of female gametes immediately after being released by the exhalant currents of parent brachiopods.

The trace producer larvae settled also on other species of brachiopod shells different than *Lipanorthis santalaurae* within the community, although much more seldom. There are evidences of this only in 7% of the *Notorthisina musculosa* and in the 11% of the *Nanorthis bifurcata* exterior valves. This rarer colonization might have been the way of the trace producer to enter into a new environment characterized by soft substrates inhospitable to them, but to which other brachiopod species like *N. musculosa* and *N. bifurcata* would be able to attach by means of specialized pedicles or as epizoa on soft-bodied benthic animals. The *L. santalaurae* larvae would have settled not only on living brachiopod shells, occasionally several of them close to their host shell commissure, but also on disarticulated valves of dead brachiopods lying with their convex side up (Fig. 10). The latter also would have provided a

Table 3
Measurements of the external and internal diameter and length of casts of *Podichnus conicus* isp. n. on *Nanorthis bifurcata*. The internal diameter is approx. 40% smaller than the external and the length of the pit is equal to the external diameter showing the characteristic conical shape.

	External diameter (D.ext)	Internal diameter (D.int)	Length (L)	D.ext/L
	71.5	16.0	66.8	1.07
	74.2	44.8	87.4	0.84
	50.2	25.5	81.0	0.62
	75.7	24.8	77.3	0.97
	67.9	26.4	93.1	0.73
	85.0	35.1	94.1	0.9
	66.2	29.3	70.3	0.94
	65.2	23.6	74.5	0.87
	76.2	19.4	59.3	1.28
	46.1	29.1	50.5	0.91
	55.9	33.2	71.2	0.78
	75.0	25.0	62.5	1.20
	72.8	19.4	60.0	1.21
	64.2	20.6	54.3	1.18
	75.4	28.6	43.6	1.73
Mean value	68.1	26.7	69.7	1.01

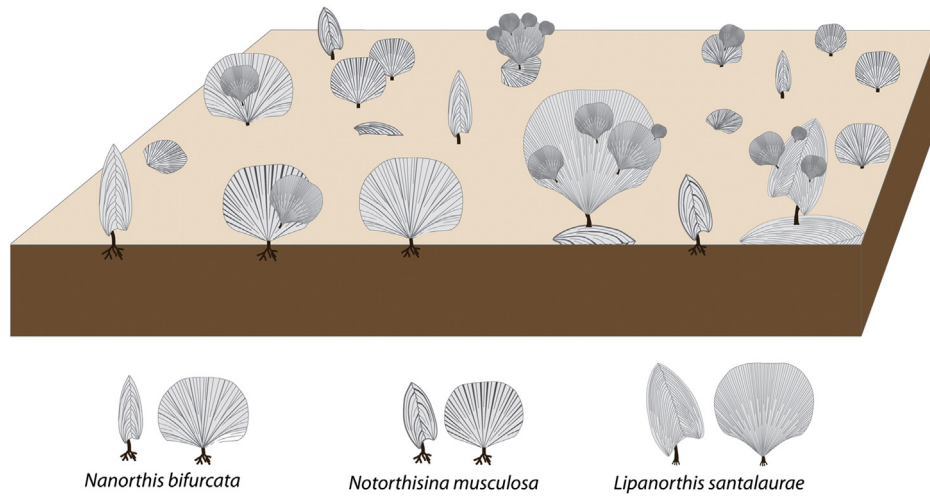


Fig. 10. Sketch diagram showing the hypothetical reconstruction of *Lipanorthis santalaurae*, *Notorthisina muscolosa* and *Nanorthis bifurcata* mode of life, discussed on the text, according to *Podichnus* distribution.

prominent place on the substrate at a distance from the soft bottom that probably enhanced stability and filter-feeding. These factors would explain the frequency of etching traces on the median convex areas of many studied valves and a total absence on the concave interior valves. Following Bromley and Surlyk (1973, p. 362) and Bromley (2008, p. 230), the irregularity and asymmetry of some *Podichnus* traces, common in the new ichnospecies, can be interpreted as a response of the producer to a steeply sloping substrate. This would be the case if the producer attached not to disarticulated valves but to living brachiopods, placed vertically on top of a stalk-like pedicle, the usual orientation considered for orthides (Harper and Moran, 1997; Sánchez et al., 2003).

None of the three brachiopod species in the studied association have a shell shape that, in case of failure of its pedicle attachment, allowed them to thrive on soft substrates as free recumbent epifauna. It seems highly improbable, as well, that an extremely specialized carbonate boring pedicle, as belonging to the trace-maker, was also able to attach directly to a soft siliciclastic substrate. Variations in the pedicle shape of a same brachiopod species are known (Ekman, 1896; Schumann, 1969; Surlyk, 1972; Bromley, 2008) but, as far as we know, no brachiopod pedicle has been described with such versatility.

6.3. Brachiopod pedicles and pedicle traces

The occurrence of pedunculate brachiopods in fine grained sedimentary strata has long presented a dilemma to palaeoecologists (Harper and Pickerill, 1996). However, a variety of life modes evolved. Some atrophied their pedicles and pursued a recumbent life strategy resting on the mud, while others with a brush-like pedicle or thread-like pedicle are anchored within a soft substrate or attached to other shells or soft bodied organisms forming clusters, and others use their branching pedicle to anchor to shifting sands (Richardson, 1997).

Nevertheless, most orthide brachiopods with their biconvex shells and wide functional pedicle openings are systematically interpreted as living attached to the substrate and rising above it by a stalk-like pedicle (Harper and Moran, 1997). Many of them thrived on unconsolidated, coarse to fine-grain substrates. This is the case for the high and mid-latitude platforms surrounding Gondwana, which during the Early and Middle Ordovician were dominated by orthide brachiopods, as found in the Central Andean Basin, Avalonia or Ibero-Armorica. Until now no record of pedicle attachment scars is known from these areas. On the basis of the Argentine *Podichnus* finding, however, it may be expected that other orthide taxa were able to anchor on carbonate biosubstrates, and dissolve them but have gone undetected so far. In this context, the main mode of life allowing orthide brachiopods to thrive on soft

substrates must have been a branching pedicle, similar to that of the Australian recent brachiopod *Parakinetica stewardi* Richardson, 1987. This type of pedicle allows the brachiopod, not only to anchor on shifting bryozoan sands, but also to move upward or downward depending of the input of sand or shifting substrate (Richardson, 1997). Some of these branching pedicles might have been developed by the species co-occurring with the producer of the new *Podichnus*, allowing it to initiate the colonization of soft substrates.

Moreover, the size, the cross-section, the arrangement of the pits and the presence of undisturbed areas between them in the surface shells studied are similar to those described for *Podichnus obliquus*, a trace made by short massive pedicles, distally divided in rootlets and characteristic of brachiopods belonging to the suborder Terebratulidina (Robinson and Lee, 2008). It also could indicate that the attachment scars of the new *Podichnus* may have been made by pedicle rootlets (Bromley and Surlyk, 1973). Until now, that type of trace has been recognized only in brachiopods belonging to suborder Terebratulidina ranging from the Middle Triassic to the Recent. Robinson and Lee (2008) suggested that rhynchonellids could have been able to make *P. obliquus*, as well. The possible producer of the new *Podichnus* from the Early Ordovician studied here belongs to the order Orthida and suborder Dalmanellidina. In this context, it is clear that the ability to bore carbonate substrates with pedicles distally divided in rootlets was not an exclusive feature belonging to two of the surviving brachiopod orders, Terebratulida and Rhynchonellida, but probably also developed already by the Early Ordovician by one of the most primitive orders, the Orthida. This seems to be probable based on the work of Sutton et al. (2005) where a 3-D reconstruction of the Silurian orthid *Bethia* is made, and in which a robust ridged pedicle with distal rootlets is recorded.

The work by Sandy (1996) recorded the oldest direct evidence of peduncular attachment of articulate brachiopods to crinoid stems from the Upper Ordovician of Ohio (U.S.A.). Nevertheless, no evidence of brachiopod pedicle-attachment scars was found on the crinoid ossicles. Yet, the trace fossils studied, herein, connect for the first time such scars with the adaptation of orthid brachiopods to a new way of life (anchoring) on biogenic hard substrates which would led to the development and subsequent changes of the tiering structure during Early Ordovician times. This would led to those groups expanding and colonizing into new or previously underused ecological niches dominated by loose carbonate or siliciclastic sands. In this context, it is possible for the first time to trace the early use of Fixichnia ethologic class (anchoring or fixing bioerosion structures produced by sclerobionts, according to Gibert et al. (2004) as an ethological strategy employed by brachiopods.

The species *Lipanorthis santalaurae* which is the most probable producer of this trace seems to develop a preference to colonize the topographic high points on other brachiopod shells (alive or dead) probably for more efficient filter-feeding in prevailing currents. In this sense, it is possible to assume that this brachiopod species evolved filling the niche as epizoan secondary tierers (sensu Bottjer and Ausich, 1986) during Early Ordovician times. This corroborates the work of Frisk and Harper (2013), who suggest that the condition of the seabed influences certain species in the arrangement of communities.

7. Conclusions

During the early part of the Ordovician Period an expansive episode of faunal diversification occurred. This is demonstrated in material from the Saladillo Formation (NW part of Argentina) as conspicuous bioerosion structures produced by brachiopods. The structures provide evidence of a new ecological niche related to a behavioural evolution/ecological adaptation by brachiopods during this episode. The presence of *Podichnus* presumably produced by *Lipanorthis santalaurae* heralds an ancient marine hard substrate community. The main conclusions of this study can be summarized as follows:

- 1) *Podichnus conicus* isp. n. constitutes a new ichnospecies, as described from an Early Ordovician (Tremadocian) brachiopod community in Northwest Argentina and, produced by orthid species. It is distinguished by an irregular and asymmetrical cluster of circular pits. Each individual pit conforms to a typical conical shape, being the external mean diameter/length ratio close to 1.
- 2) With *Podichnus conicus* isp. n., the record of *Podichnus* extends back to the Early Ordovician (Tremadocian), which represents the oldest record of this ichnogenus.
- 3) Ordovician orthid-brachiopod etchings represent the earliest known attempts of a fixichnia strategy for brachiopods, and provide evidence for more complex hardground trophic structures than were previously thought to exist during the Early Ordovician for this group of organisms. It is the first instance that brachiopods from the Order Orthida are identified as *Podichnus* producers.
- 4) The occurrence of *Podichnus* in brachiopod shells from the Saladillo Formation represents not only an important source of new information regarding colonization of biogenic hard substrates during the Ordovician Bioerosion Revolution and an adaptive strategy of its use, but also may provide indirect evidence regarding the soft-part morphology of the pedicle belonging to *Lipanorthis santalaurae*.
- 5) As direct evidence of organism–substrate interaction, the presence of *Podichnus* may be used to interpret the life style and probable habitat of fossil species like *Lipanorthis santalaurae*. In this context, *L. santalaurae* were attached to other living specimens of the same species or, more rarely, to other species by its functional pedicle.

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