



***Meandrovaleichnus huenickeni* ichnogen. et ichnosp. nov. from the Bajo de Véliz Formation (Upper Carboniferous–Permian), Argentina: a new case of worm-type burrowing**

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ABSTRACT

A new ichnofossil, *Meandrovaleichnus huenickeni* ichnogen. et ichnosp. nov., is described from the fluvio-lacustrine deposits of the Bajo de Véliz Formation (Upper Carboniferous–Permian). The trace fossil consists of meanders (epichnial) with regular constrictions of variable width along the course. It is interpreted as a locomotion trace (repichnion) due to peristaltic burrowing of a worm, probably an annelid.

Keywords: Ichnology, Upper Paleozoic, Argentina, *Meandrovaleichnus huenickeni*, repichnia.

RESUMEN

Un nuevo icnofósil, *Meandrovaleichnus huenickeni* ichnogen. et ichnosp. nov., es descrito en los depósitos fluvio-lacustres de la Formación Bajo de Véliz (Carbonífero Superior–Pérmico). La traza fósil consiste en meandros (epichnia) con constricciones regulares de ancho variable a lo largo de la pista. Es interpretada como una traza de locomoción (repichnion) producto de la excavación peristáltica de un gusano, probablemente anélido.

Palabras clave: Icnología, Paleozoico Superior, Argentina, *Meandrovaleichnus huenickeni*, repichnia.

1. INTRODUCTION

Understanding the palaeobiological factors influencing trace fossils is one of the main goals of ichnology, particularly as regards recognizing the tracemaker, the mode of construction, and its ethology (Seilacher, 2007; Gibert & Ekdale, 2010). Possible locomotion and burrowing modes for invertebrates includes peristalsis, which is especially interesting as it has been adopted by diverse groups over the course of time. In the specific case of organisms with a vermiform body plan, this mechanism can be inferred through the ichnological record, although clear peristalsis indicators are commonly absent (Buatois & Mángano, 2011), which circumstance makes the present report of particular interest. The material analysed in this study is from the Bajo de Véliz Formation (Upper Carboniferous–Permian), in the province of San Luis, Argentina. This unit is world-renowned for its fossil content, including an abundant record of Gondwana flora and a significant record of insects and arachnids, all of which indicate a fluvio-lacustrine setting for the formation. The aim of this paper is to describe *Meandrovaleichnus huenickeni* ichnogen. et ichnosp. nov., interpreted as peristaltic burrowing of a worm-like organism (probably an annelid) based on its morphological and construction characteristics.

2. GEOLOGICAL AND STRATIGRAPHIC SETTING

The Gondwana site of Bajo de Véliz lies in the northwestern sector of the Sierra Grande de San Luis, about 25 km west of the Santa Rosa locality. It occupies a narrow graben about 12 km long oriented south to north and occupied by the Cautana Creek (Fig. 1). The section is located at 32°18'41" S – 65°24'48" (Fig. 2).

The Upper Carboniferous–Permian sedimentary deposits are surrounded by igneous and metamorphic rocks ranging from the Upper Precambrian to the Carboniferous. The Bajo de Véliz Formation, named after the locality, was defined by Flores (1969) and then studied in greater detail by Hünicken & Pensa (1972), who estimated a geological column that is 168 m thick. It is represented by a siliciclastic sequence primarily comprising greenish-grey sandstones and lutites (Fig. 3).

Hünicken & Pensa (1981) and Hünicken *et al.* (1981) recognize three members based on their lithological features. They are, from bottom to top: Cautana, Pallero and Lomas members. The 102 m-thick Cautana Member starts with a basal polymictic conglomerate that grades upwards to fine-grained sandstones intercalated with greenish-grey siltstones, capped by arkosic sandstones and banks of greenish siltstones.

The next member above, the Pallero Member (Hünicken & Pensa, 1972) consists of 53 m of well-stratified fine-grained sandstones and greenish limolites containing abundant fossil remains, marlekor structures (flat concretions) and local dropstones. This member has provided well-preserved fossil plants, such as *Gangamopteris obovata*, *Glossopteris* sp. and *Samaropsis kurtzi*, palynomorphs, such as *Clogranisporites patelliformis* and *Acantotriletes filiformis*, insects, and arachnids. In fact, this unit is famous for having yielded the renowned *Megarachne servinei* Hünicken, 1979, a bizarre eurypterid, similar to rare forms known from Carboniferous rocks of Scotland and South Africa (after Selden *et al.*, 2005; Selden & Penney, 2010). The trace fossil described herein is found in these levels. Overall, its sedimentology and flora associations indicate a mixed, fluvio-lacustrine setting (Hünicken *et al.*, 1981).

The sequence is crowned by medium to coarse-grained yellowish to dark-greenish sandstones defined by Hünicken & Pensa (1972) as the Lomas Member. The entire sedimentary complex is located within a graben that is cut in basement phyllites of the San Luis Formation (Prozzi & Ramos, 1988).

3. SYSTEMATIC ICHNOLOGY

The criteria for description and interpretation follows Bromley (1981) and Bertling *et al.* (2006).

Ichnogenus *Meandrovaleichnus* ichnogen. nov.

Derivatio nominis. Latin, *meander*, meandering; *ovale*, ovals; *ichnos*, trace.

Type ichnospecies. *Meandrovaleichnus huenickeni* ichnosp. nov.

Diagnosis. Meandering to straight horizontal, epichnial structure, with non meniscate active fill, without walls. It is semi-circular in cross-section, with regularly spaced constrictions, perpendicular to the direction of the trace course, which can be visible as variably sized asymmetric ovals in plan view.

Ichnospecies *Meandrovaleichnus huenickeni* ichnosp. nov.

Derivatio nominis. Named after Dr. Mario Hünicken, who discovered the material described herein.

Type material. One specimen, the holotype: PIL 15.769. A slab (Fig. 4), from the Bajo de Véliz Formation

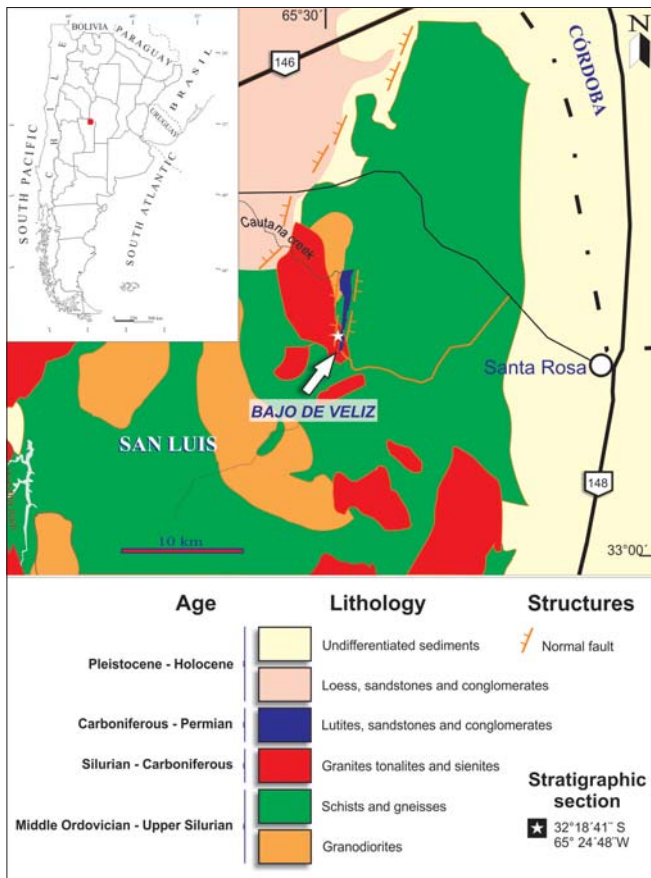


Figure 1. Simplified geological map of the study area (after Sato *et al.*, 2003 and Hünicken *et al.*, 1981). The arrow points to the Bajo de Véliz locality.

(Upper Carboniferous–Permian), northern part of the San Luis Province, Argentina. Deposited in the Paleontología Invertebrados Lillo collection (prefix PIL).

Diagnosis. As for the ichnogenus.

Description. The trace fossil is preserved as a negative epirelief on the surface of a finely laminated grey lutite (Fig. 4a). It is a continuous structure, primarily parallel to the bedding or slightly inclined. The margins are sharp. The orientation in plan view ranges from straight to highly meandering. In cross-section, it is semi-circular to slightly semi-ovoid. There are complete self-crossings that produce nodes (Figs 4b–c) that can cross-cut pre-existing trajectories (Fig. 4c). It ranges in width from 0.4 to 1 cm. The trace fossil displays regularly distributed gradual constrictions and swellings, forming small, interconnected ‘ovals’ in plan view (Figs 4a–f). The constrictions are of varying size in different parts of the section. Most constrictions are asymmetric, suggesting the organism’s direction of movement (see ‘Trace construction’ section in DISCUSSION). True branchings do not occur, although over-crossings are common, which produce false branching

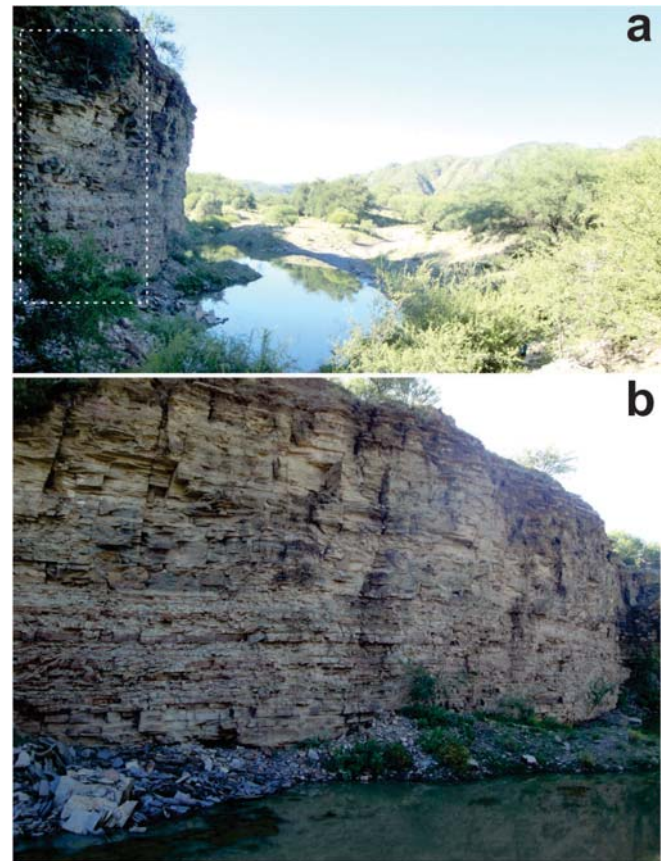


Figure 2. Outcrop photographs of the Pallero Member section. a) Panoramic view. b) Detailed succession.

(Fig. 4e). There are also successive secondary branching (*sensu* D’Alessandro & Bromley, 1987) that suggest the reworking of a previous structure due to a re-entry of the tracemaker (Figs 4d, f). The fill is massive, red from haematite, distinguishing it from the host rock.

Remarks. *Meandervaleichnus huenickeni* bears a certain morphological similarity to some examples preserved as negative epireliefs (epichnial depressions) of *Ptychoplasma* Fenton and Fenton, 1937, particularly with *P. vagans* (Książkiewicz, 1977). *Ptychoplasma* has been extensively revised by Uchman *et al.* (2011) and attributed to the locomotion of bivalves with a wedge-shaped foot. The main morphological features of *M. huenickeni* that resemble *P. vagans* are: I) orientation in plan view, straight to meandering or looping; II) the proportion of the width to the length; III) constrictions and swellings along the course, forming oval mounds in plan view; IV) similar distances between mounds in respect to the width and length; and V) sharp margins. However, *P. vagans* differs in that its hypichnial mounds are notably steep in cross-section. *M. huenickeni* is semi-circular in cross-section. In addition, it can be differentiated from *P. excelsum* Fenton and

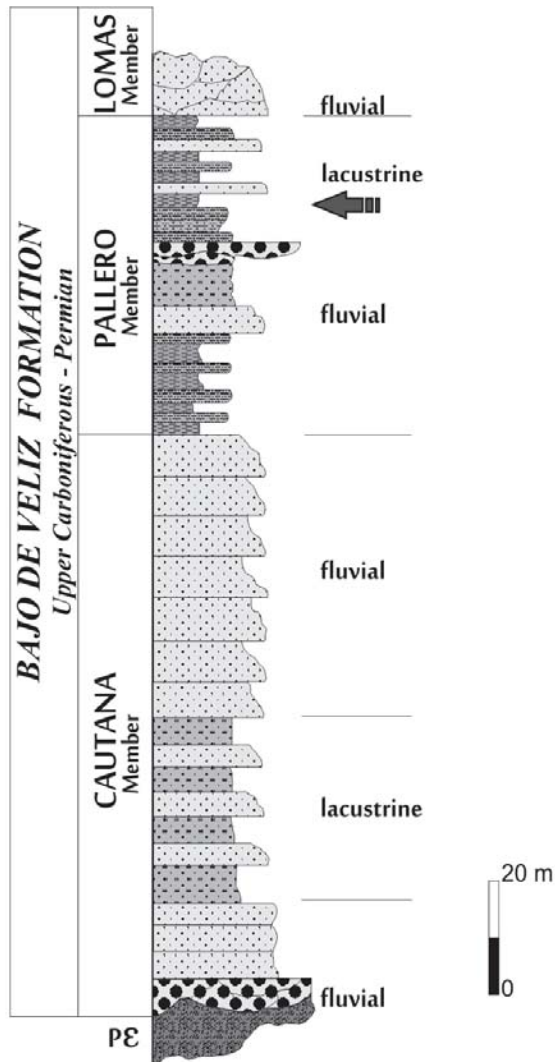


Figure 3. Integral stratigraphic section of the Bajo de Veliz Formation, showing the members and sedimentary settings (after Césari & Hünicken, 1991). The arrow indicates the level from which *Meanderovalichnus huenickeni* was collected.

Fenton, 1937 and from *P. conica* Pieńkowski & Uchman, 2009 since these two ichnospecies have distinctive traces due to the ‘relocation’ of the bivalve’s shell after each movement (Uchman *et al.*, 2011, fig. 6) and that are lacking in this case.

The general plan, active fill, cross-section and especially the constrictions along the course of *M. huenickeni* show similarities to certain *Planolites* Nicholson, 1873 ichnospecies such as *Planolites annularis* Walcott, 1890 and ?*Planolites reinecki* Książkiewicz, 1977. *P. annularis* is horizontal, straight, sinuous, and exhibits prominent annulations. The annuli may be of regular or irregular size and spacing; otherwise, this burrow tends to be more or less constant in diameter (Pemberton & Frey, 1982). Uchman (1998) reviewed the status of *Planolites reinecki*

Książkiewicz. Although *Planolites reinecki* was reservedly included in *Palaeophycus alternatus* Pemberton & Frey (1982), the holotype of *P. reinecki* does not display a lining or any other features of *Palaeophycus* (*sensu* Uchman, 1998). *Planolites constriannulatus* isp. n. Stanley & Pickerill, 1994 is distinguished for trace fossils that display the same features as *P. reinecki*, thus, *P. constriannulatus* is the junior subjective synonym of *P. reinecki* Książkiewicz (Uchman, 1998).

In the same sense can be mentioned –although passively filled– the constrictions and overall pathway of some annulated ichnospecies of *Palaeophycus* Hall, 1847: *P. alternatus* Pemberton & Frey, 1982 and *P. crenulatus* Buckman, 1995. Buckman (1995) reviewed the status of these ichnospecies. *P. alternatus* is slightly curved in plan view and displays alternate annulate and striate section, and *P. crenulatus* is curved or sinuous in plan view, with continuous annulate ornament, which is more distinct than all other annulate ichnospecies of *Palaeophycus* (Buckman, 1995, fig. 7). Also *P. annulatus* Badve, 1987 and *P. serratus* McCann, 1993 (including *P. anulatus sensu* Buckman, 1995) respectively possess annulations that suggest an active mode of backfill, and consequently are considered *nomina dubia* by Buckman (1995). In wide sense the annulations in these ichnogenera presumably reflect peristaltic movements by the tracemaker, probably worm, to moving and/or feeding (*sensu* Pemberton & Frey, 1982; Buckman, 1995 and references). Another ichnospecies that need to be considered is *Torrowangea rosei* Webby, 1970. *T. rosei* also exhibits a meandering course in plan view, with regularly distributed constrictions (Webby, 1970). It displays in some cases tight meanders, cutting previous structures and forming “nodes” (Webby, 1970, fig. 18B, C). In similar way that *M. huenickeni*, *T. rosei* is interpreted as burrow of worm-like deposit feeders (see discussion in Webby, 1970). The similarities between *M. huenickeni* and the mentioned ichnospecies of *Planolites*, *Palaeophycus* and *Torrowangea* could be related to a tracemaker with morphological and ethological affinities, using body parts that are not necessarily the same anatomically, even if they have a similar function and the end efficiency of the locomotion process is the same (see DISCUSSION). The most remarkable difference are the strong constrictions and swellings of *M. huenickeni*, which displays interconnected ‘ovals’ in plan view. Finally we need to consider the ichnogenus *Halimedides* Lorenz von Liburnau, 1902. *Halimedides* consists of straight to slightly curved, horizontal to oblique, tubular burrows, someplace with annulations and scratch marks on the burrow margin and a series of symmetrically distributed heart-shaped, angular, trapezoid, oval, semispherical, or bilobate chambers along its length (after Uchman, 1999; Gaillard & Olivero, 2009). The chambers are used for food capture and storage, maybe used for microbial farming by the trace-maker – probably a small crustacean – in deep

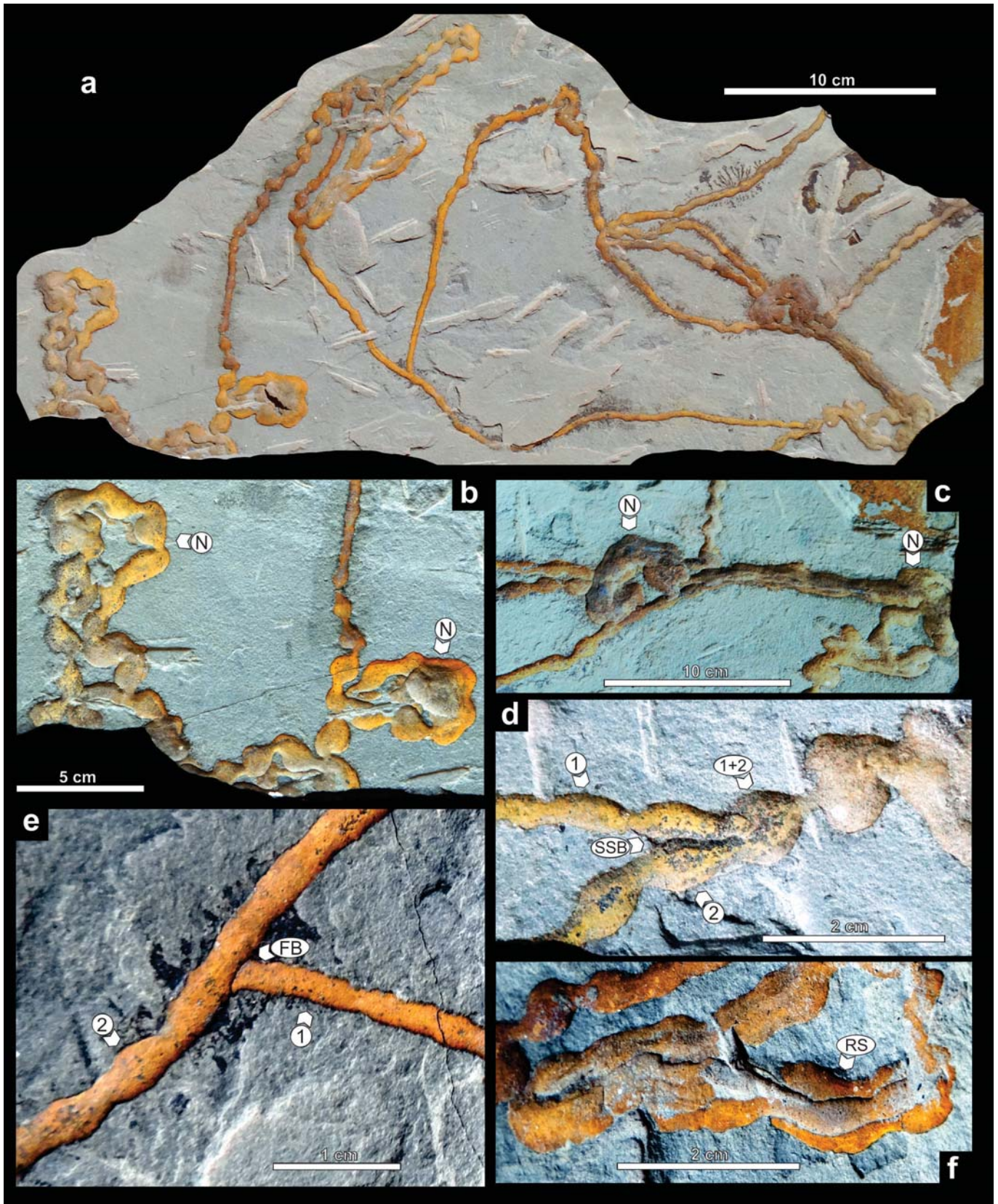


Figure 4. *Meanderovaleichnus huenickeni* from the Bajo de Véliz Formation, San Luis, Argentina. **a)** General view of holotype, PIL 15.769. **b)** Detail of nodes (N) in trace course. **c)** Nodes (N) cutting across pre-existing trajectories. **d)** Secondary successive branching (SSB). Course 1 is pre-existing. The organism moves nearby (course 2) and re-enters structure 1. From there, the resulting structure is deformed and wider (1+2). **e)** False branching (FB). Course 1 is cut by course 2. **f)** Reworked structure (RS). There is a pre-existing structure that contains a smaller, later structure within it.

sea environments (Gaillard & Olivero, 2009). Even though these constrictions and chambers in plan view resembling some parts of *M. huenickeni*, there are more differences than similarities. The morphology of each chamber in *Halimedides* suggest a different mode of construction and use – agrichnion – (*sensu* Gaillard & Olivero, 2009). In *Halimedides* is common a high “chamber spacing”, and are frequent lapses of course without chambers. Moreover *M. huenickeni* always displays constrictions and swellings along their course. Also, some *Halimedides* exhibit scratch marks, which are not observed in *M. huenickeni*.

4. DISCUSSION

4.1. Trace construction

Certain features presented above suggest the mode of construction: the general morphological plan of the trace, its meandering path, its orientation parallel to the bedding surface, the regular constrictions along the length of the course, fill and a semi-circular morphology in cross-section. These features are compatible with the scenario of a worm-like organism moving across the substrate by peristaltism. This mechanism was analysed in detail by Trueman (1975) and Seilacher (2007 and references) and involves in *s.l.* the following process: The head section of the worm digs into the substrate, inflates (forming a penetrating anchor), and then, through peristalsis, travels the length of the organism in a more-or-less continuous action, thereby pushing the animal forwards. In the case of *M. huenickeni*, there are two alternatives whose construction processes are interpreted in Figure 5. In the first alternative (Fig. 5a), which is the most common, the trace has maximum widths after each constriction, corresponding to the maximum possible dilation of the tracemaker’s diameter. This configuration occurs when the worm is in a softer substrate with a consistency forcing it to anchor itself more effectively in order to progress. The second case is shown in Figure 5b. In this alternative, the trace displays a more regular width along the course. This suggests that due to a local increase in substrate consistency, the worm needs less effort to progress. This translates into less body dilation for anchoring during substrate penetration and therefore a more regular width to the trace. In overcrossing points (Figs 4b-f) the burrow crossing its earlier segment displays distinct margins. This shows that the earlier segment was already filled when was crossed by the later segment. This suggests an active filling just behind the tracemaker. The haematitic surface can be interpreted as differential alteration due to diagenesis and weathering, probably because of an

original substrate change by the tracemaker (i.e. mucus secretion). In Figure 5, *L* is the stride, which is the distance advanced by the worm during a peristalsis period (*sensu* Quillin, 1999). This dimension comprises the progress lapse in which the worm’s parts advance over the substrate and the resting time during which the parts are holding onto the substrate.

4.2. Tracemaker identity

Based on its morphological and construction features, *M. huenickeni* is interpreted as a worm trace fossil produced during peristaltic burrowing. The term “worm” covers a wide variety of cylinder-shaped organisms from different phyla. Seilacher (2007) noted that annelids, molluscs (i.e., *Natica*, *Polinices*), and even anemones (i.e., actinians), among others, can employ similar mechanisms to travel across the substrate by peristaltism (“worm-type burrowing” *sensu* Seilacher, 2007). As to the identity of the possible tracemaker, the absence of traces of setae, cirri, or parapodia (that might have been preserved given the texture of the host rock) suggests (although not definitively) that we can discard earthworms (Lumbricidae) and a great number of polychaetes with these anatomical parts. For instance, rhythmic constrictions and ‘scratches’ are common in *Scoyenia* (which has an active infill). The locomotion inferred for it is similar to that of *M. huenickeni* although, as Seilacher (2007) mentions, there is still debate as to whether ‘pure’ peristalsis is compatible with active infill. As mentioned above, the absence of shell relocation traces suggesting gastropods and similar organisms can be discarded. It is highly likely that the *M. huenickeni* tracemaker was a coelomate worm-like organism with bilateral symmetry and a body axis oriented in the sense of movement, with cephalization and sensory organs. The coelomate feature is important since the hydrostatic pressure produced by the internal cavity is what allows peristaltic movement and therefore locomotion of the animal (Pechenik, 2010). It is likely it was a segmented organism, which makes peristaltism more efficient since the hydrostatic pressure of the coelom is evenly distributed to the individual segments or to groups of segments, which also allows energy savings compared to non-segmented worms (Turbeville & Ruppert, 1983). These aspects suggest a link to Annelida although, given all the data, a definitive assignation is postponed until new material is found and/or new records are reported.

4.2.1. Ethological classification

As regards the interpretation of this trace fossil, and based on the information given above, we speculate on the following alternatives:

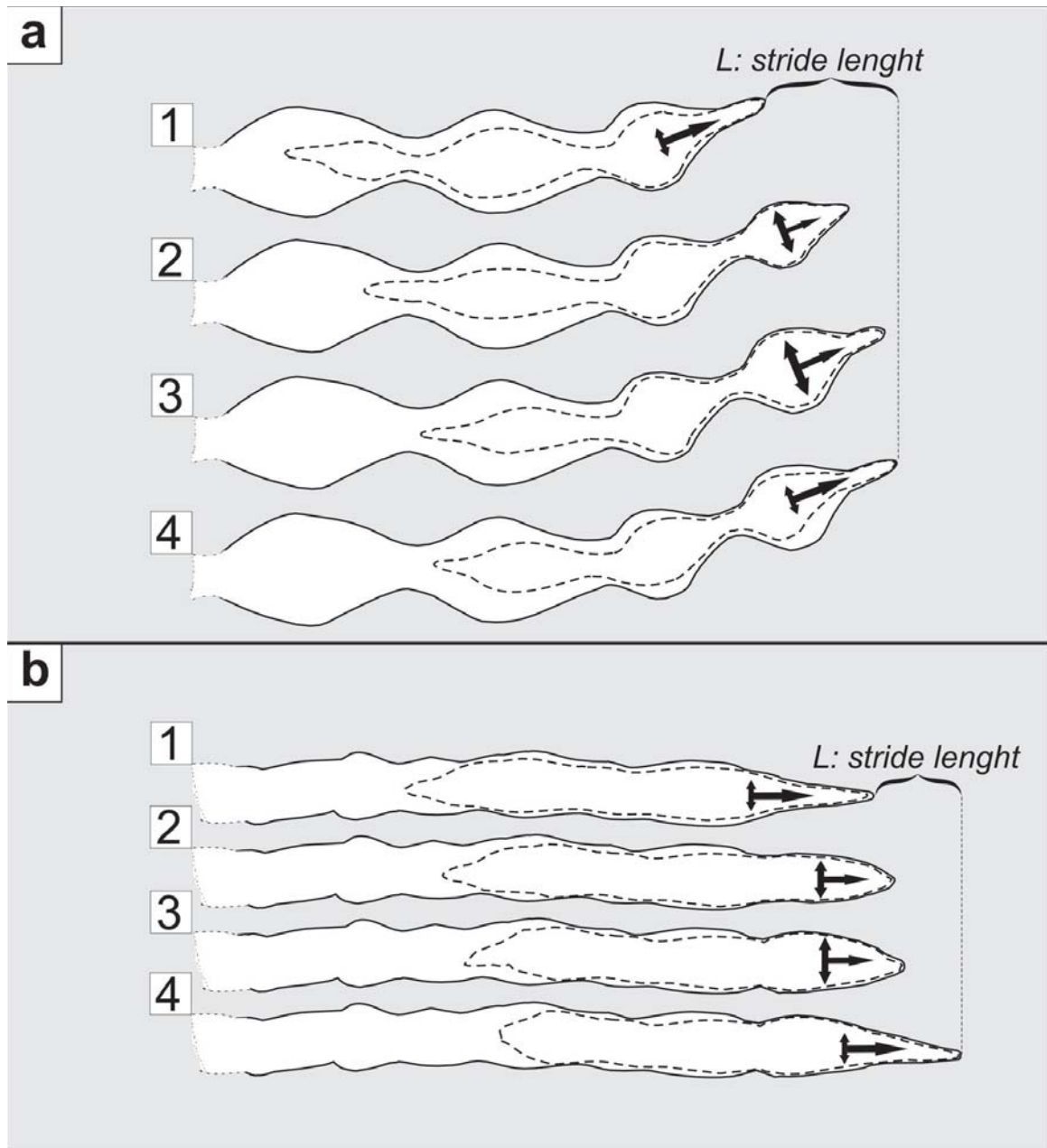


Figure 5. Construction patterns of *Meanderovaleichnus huenickeni*. **a)** Softer substrate. 1) The anterior part of the worm extends to the maximum possible and penetrates the substrate. 2) Advancing, the anterior part of the worm widens and anchors itself firmly to the substrate. 3) The maximum body width is reached. 4) The anterior part of the worm extends once again to penetrate the substrate. This completes one stride (L). **b)** Increasing substrate consistency. In this case, stages 1 to 4 are analogous to A. Since the substrate is firmer, it requires less effort, and so the body dilation in each length does not need to reach the maximum possible body width.

1) Locomotion. The construction characteristics suggest a crawling trace (repichnion). 2) Shelter. It is possible these structures were produced by the trace maker in search of a burrow in addition to by simple movement. This strategy has been documented in some types of earthworms (anecic species) (Bastardie *et al.*, 2002), which build sub-horizontal burrows for protection from which they travel to the surface to feed.

5. FINAL COMMENTS

Meanderovaleichnus huenickeni is an ichnotaxon whose features suggest it is the product of peristaltic burrowing by a worm, probably a non-marine annelid. Ethologically it is a locomotion trace (repichnion) being a new element for the discussion of peristaltism as a locomotion mechanism in worm-like organisms. This is particularly

interesting in the stratigraphic context of this first record from a unit characteristic of the South American Upper Paleozoic. Finally, we expect new records of *M. huenickeni* and of neoichnological analogues, which will certainly enable more discussion on the ichnotaxonomic and palaeobiological details of this trace fossil.

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