

The changing face of the deep: Colonization of the Early Ordovician deep-sea floor, Puna, northwest Argentina

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ABSTRACT

An Upper Tremadocian deep-sea ichnofauna from the Chiquero Formation of Puna, northwest Argentina, represents a link between Ediacaran and Cambrian microbial-mat dominated ecosystems and younger Ordovician deep-marine trace-fossil assemblages. This ichnofauna is preserved at the base of thin-bedded turbidites formed in the lobe fringe of a back-arc deep-sea fan. While Ediacaran–Cambrian deep-marine trace fossils are typically linked to matground grazing and feeding, microbial textures in the Chiquero Formation are rare and not associated with trace fossils. Morphologic patterns (e.g. radial trace fossils and networks) of the Chiquero ichnofauna indicate the onset of novel trophic types, recording trapping of microorganisms and bacterial farming. However, in comparison with younger Ordovician deep-sea ichnofaunas, graphoglyptids are relatively rare, poorly diverse, and geometrically simpler. This study indicates that the Early Ordovician was a pivotal point in the ecology of deep-sea infaunal communities. This Upper Tremadocian ichnofauna records the arrival of the Agronomic Revolution to the deep sea. Comparisons with slightly older and younger deep-sea ichnofaunas demonstrate that the colonization of the deep sea was a protracted process spanning the Early Paleozoic, lagging behind colonization of nearshore and offshore substrates.

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1. Introduction

The early colonization of the deep-sea floor has attracted considerable attention in recent years (MacNaughton et al., 2000; Crimes, 2001; Orr, 2001, 2003; Buatois and Mángano, 2003; Uchman, 2004; Jensen and Palacios, 2005; Seilacher et al., 2005). The Early Ordovician was a pivotal point in the ecology of deep-sea infaunal communities. Ediacaran–Cambrian deep-sea ichnofaunas are represented by simple grazing trails and feeding trace fossils that reflect exploitation of microbial mats (MacNaughton et al., 2000; Orr, 2001; Buatois and Mángano, 2003; Seilacher et al., 2005). In essence, they still represent a pre-Agronomic-revolution world (Seilacher and Flüger, 1994; Seilacher 1999; Buatois and Mángano, 2003). By the Arenigian, the main lineages of deep-marine trace fossils, such as rosette, meandering, patterned and spiral ichnofossils, were established in the deep sea (Crimes et al., 1992; Orr, 2001; Mángano and Droser, 2004). Lower Ordovician deep-marine ichnofaunas are moderately diverse, and feeding trace fossils dominate over sophisticated grazing and traps/farming trace fossils. Ichnofaunas of more modern aspect and of higher diversity seem to be more typical of

the Upper Ordovician to Lower Silurian (Orr 1996, 2001; Mángano and Droser, 2004).

Exploration of Lower Cambrian to Lower Ordovician rocks is essential to unravel the early colonization history of the deep sea. However, some of these deep-marine units are metamorphosed, deformed, and dating becomes problematic (e.g. Uchman et al., 2005). Accordingly, little is known about the transition from an ecosystem dominated by microbial matgrounds to one in which the appearance of graphoglyptids started to change the face of the deep. In this paper we document a deep-marine Upper Tremadocian ichnofauna from Puna in northwest Argentina which records that transition.

2. Geologic setting, sedimentology, paleoenvironment, and age

The Puna region of northwestern Argentina and northern Chile (Fig. 1) is a large high plateau with an average elevation of 3700 m above sea level, uplifted during the Neogene crustal shortening related to the convergence of the Nazca and South American plates. The basement of this extensive, over 50,000 km² volcanic province, is formed mainly by Cambrian plutons and Ordovician volcano-sedimentary units folded in Ashgillian time during the Ocoyoc Orogeny (Turner and Méndez, 1975; Mon and Hongn, 1991).

The trace fossils discussed in this paper come from the eastern part of the Lower Paleozoic Puna basin named “Faja Eruptiva Oriental”

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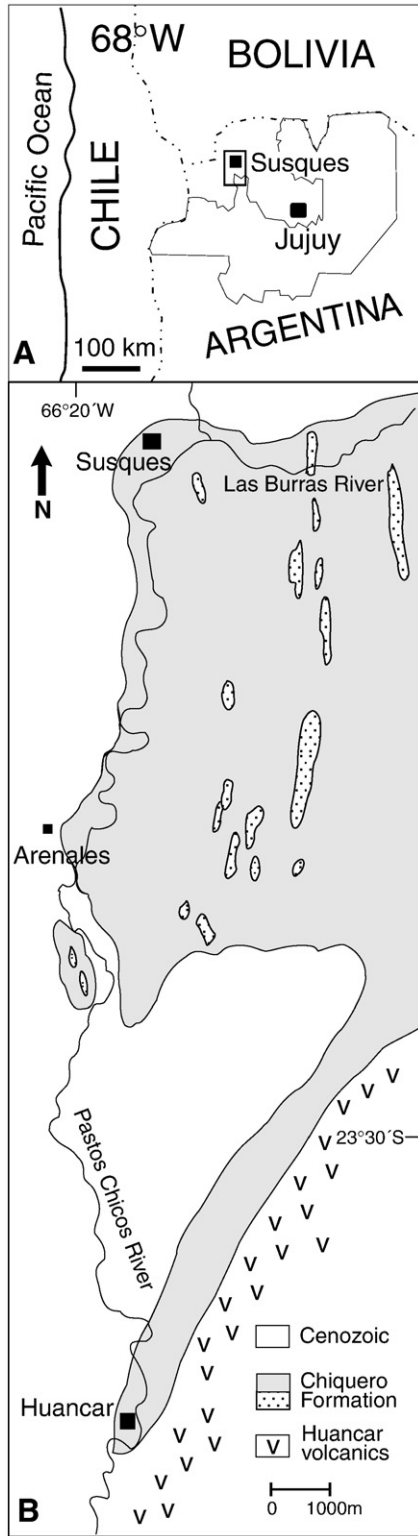


Fig. 1. A. Location map of the study area. B. Distribution of outcrops of the Chiquero Formation. Modified from Benedetto et al. (2002).

(Méndez et al., 1972). The stratigraphic succession in the Sierra de Cobres starts with shallow-marine quartz-sandstone, pebbly mudstone, conglomerate and shale of the Cobres Group (Schwab, 1973) of Cambrian?–Early Tremadocian age (Vaccari et al., 1999), which rests unconformably on Late Proterozoic–earliest Cambrian metamorphic rocks of the Puncoviscana Formation. The Cobres Group is overlain by the Chiquero Formation, a sedimentary and volcanic succession. In the

Sierra de Cobres this unit is capped by a 200 m-thick silicic volcanic unit (Cerro Huancar volcanic rocks) consisting of basalt and andesite lava flows and hialoclastites, sills, dykes and cryptodomes, interpreted as resulting from non-explosive submarine volcanism (Coira et al., 1999). The turbiditic nature of the Chiquero Formation has long been recognized (Breitkreuz, 1986; Bahlburg, 1990, 1991).

Petrographically, the turbidite sandstones of the Chiquero Formation are quartz intermediate (35–60% quartz), with monocrystalline quartz of magmatic origin. Glass shards are abundant in some horizons. Lithoclasts of volcanic rocks, mostly of basalt and andesite, vary between 25 and 50% (Bahlburg, 1998). This fact and the intercalated volcanic ash indicate that the turbidites were supplied from a volcanic arc, which is thought to have been located along the western margin of the Puna basin where rocks of volcanic-arc geochemical signature are widespread (Koukharsky et al., 1988; Rapela et al., 1992). It is believed that the Lower Ordovician volcano-sedimentary succession of the eastern Puna belt was deposited in a rapidly subsiding back-arc setting (Bahlburg, 1990). By the Middle Ordovician,

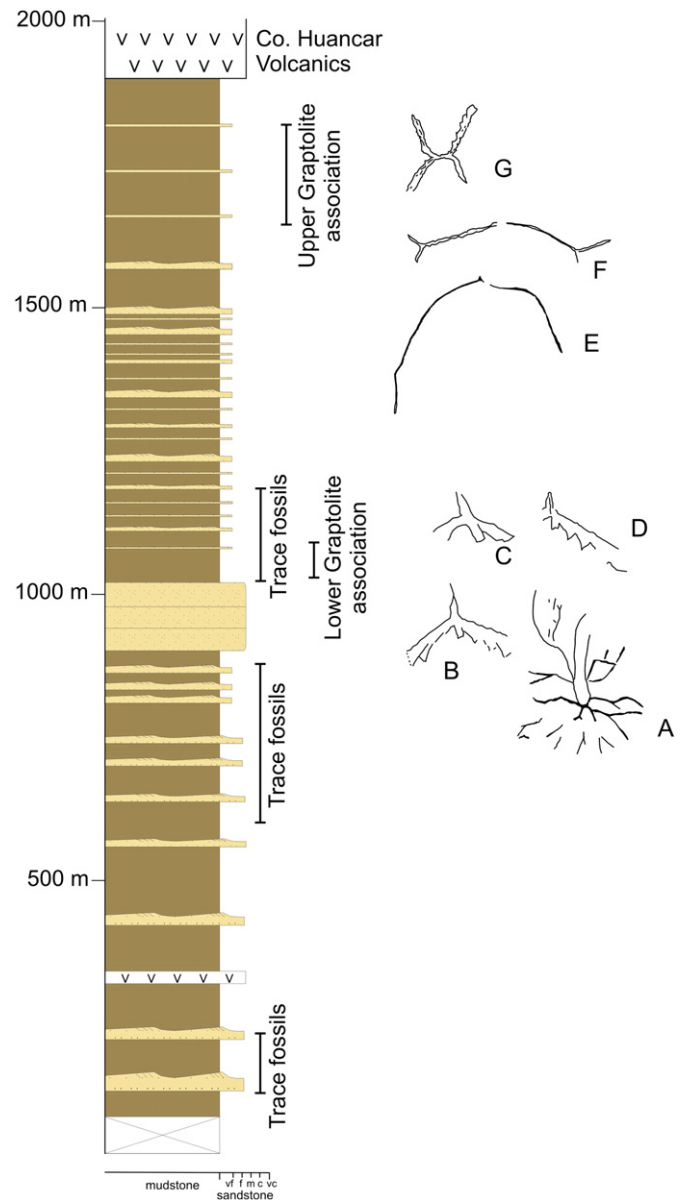


Fig. 2. Integrated stratigraphic section of the Chiquero Formation showing graptolite and trace-fossil occurrences. A. *Clonograptus* cf. *flexilis*. B–D. *Kiaerograptus* cf. *kiaeri*. E. *Paradelograptus* sp. F. *Hunnegraptus copiosus*. G. *Tetragraptus* sp. Modified from Benedetto et al. (2002).

the basin evolved to a foreland by overthrusting of the arc complex onto the back-arc basin. The Chiquero turbidite system occupied the back arc and was most likely fed from the volcanic arc located to the west. The volcanic arc was separated from the turbidite system by a narrow shelf. The delivery system may have consisted of multiple point sources.

In the Susques–Arenales–Huancar area, on the western slope of the Sierra de Cobres, the Chiquero Formation is ~2000 m thick (Fig. 2A–B). The lower half of the Chiquero Formation is exposed near Arenales. It is dominated by hemipelagic clays and very fine-grained turbidites characterized by parallel-laminated or graded siltstone and mudstone interbedded with scattered thin sandstone beds displaying incomplete T_{c-d} or T_{b-d} Bouma divisions (Fig. 3A–B). Current-ripple cross-lamination is common. Graptolites occur in some of these clay- and mud-rich layers. The bases of the graded very fine-grained sandstone beds contain trace fossils, and a wide variety of flute and tool marks and load casts. Textures indicative of microbial mats are extremely rare and only very locally patches of wrinkle marks have been recorded. Euhedral crystals of pyrite are widespread.

The upper interval of the Arenales section represents the middle part of the Chiquero Formation, and consists of a sandstone-dominated package that forms the top of the hills in the area. This interval consists of a ~90 m-thick package of amalgamated, erosionally based very coarse- to coarse-grained sandstone and pebbly sandstone beds lacking internal sedimentary structures or locally having coarse-tail grading and diffuse stratification. Trace fossils are absent in this facies. Thinly interbedded shale may occur in places. Individual beds range in thickness from about 0.60 m to many meters.

The upper part of the Chiquero Formation is exposed near Susques, in the Quebrada de Las Burras, and in the Huancar area (Fig. 3C). It consists mainly of hemipelagic clays and very fine-grained turbidites that pass into a monotonous alternation of 0.10–0.25 m-thick sandstone and shale, rarely up to 0.80 m thick. Most of these beds display complete T_{a-d} Bouma divisions and form well-defined up to 20 m-thick coarsening- and thickening-upward cycles. The thin-bedded turbidites contain trace fossils. Microbial-mat textures (e.g. wrinkle marks) are patchily distributed on some bedding planes. This large-scale coarsening-upward (approximately 500 m thick) culminates in sheet-like, amalgamated massive sandstone turbidites (Fig. 3D). A shale-dominated interval with scarce, thin, very fine-grained sandstone turbidites occurs at the top of the unit below the Cerro Huancar volcanic rocks.

The lower half of the Chiquero Formation is interpreted as deposited in basin-plain to depositional-lobe settings. The latter include distal-lobe or lobe-fringe deposits consisting of thin-bedded turbidites and proximal-lobe deposits characterized by sheet sands (*sensu* Weimer and Slatt, 2007). The massive amalgamated sandstone facies of the middle part records high-density turbidity currents and may represent the infill of large and confined multi-story channels. Basin-plain to distal-lobe environments were re-established in the upper interval, while the overlying thickening-upward successions of classical turbidites may record deposition of prograding lobes. Basin-plain deposits reappear near the top of the formation.

The age of the Chiquero Formation in the studied sections is well established based on an abundant graptolite fauna (Benedetto et al., 2002). The lower association occurs in the same interval as some of

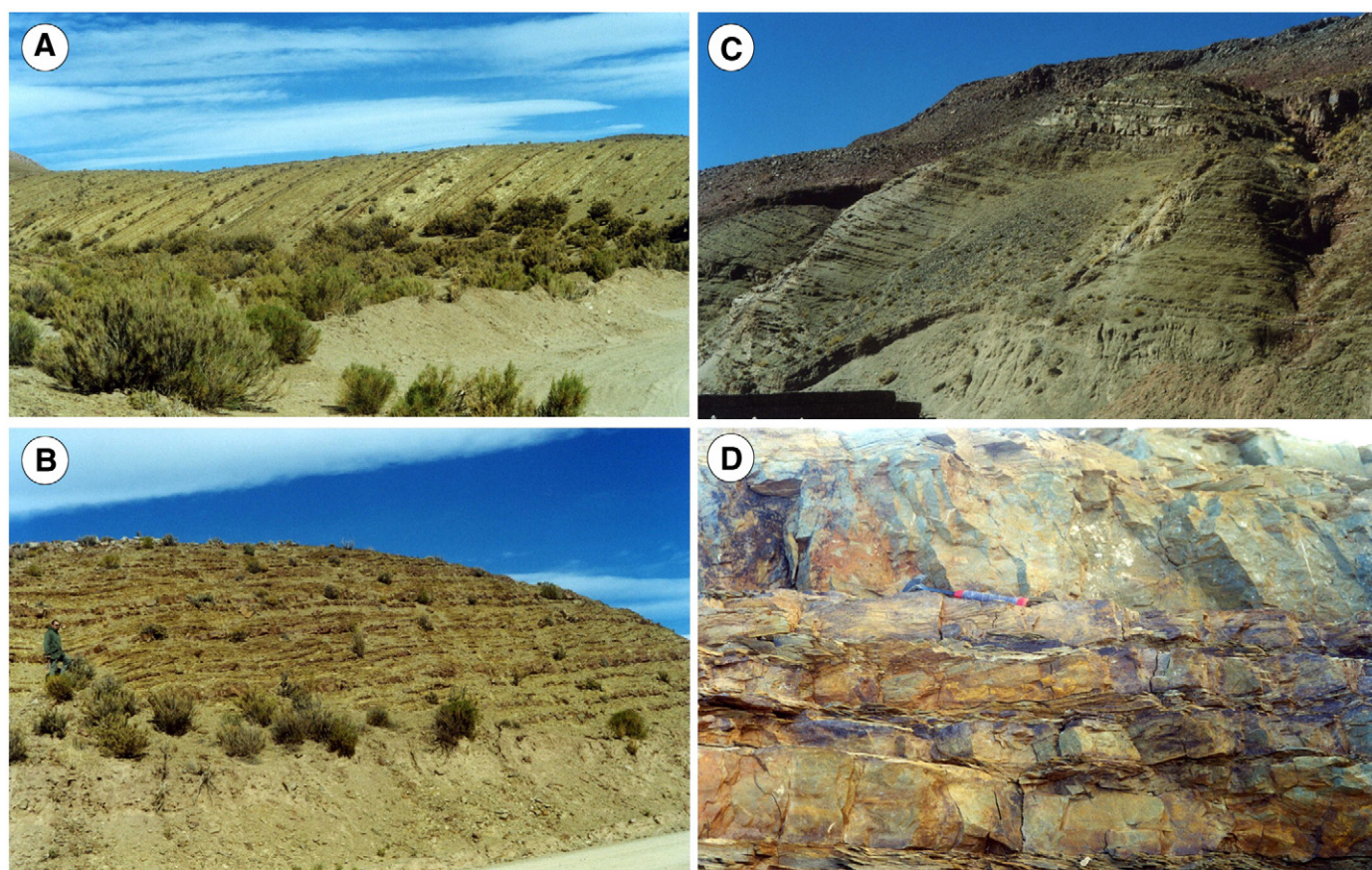


Fig. 3. Outcrop photos of the turbidite succession from the Chiquero Formation. A. Basin-plain deposits of the lower half of the unit exposed near Arenales. Note dominance of hemipelagic shale and scarce thin-bedded turbidites. B. Lobe-fringe deposits of the lower half of the unit exposed near Arenales. Note dominance of thin-bedded turbidites separated by shale layers. C. Coarsening-upward package showing transition from basin-plain to lobe-fringe and proximal-lobe deposits. Lower interval of the upper half of the Chiquero Formation in the Quebrada del Rio Las Burras. D. Amalgamated massive sandstone turbidites representing proximal-lobe deposits. Upper half of the Chiquero Formation near Huancar. Hammer is 28 cm.

the trace fossils, and contains *Kiaerograptus* cf. *kiaeri*, *Clonograptus* sp., and *Paradelograptus* sp. (Fig. 2). The upper association occurs near Cerro Huanca and consists of *Hunnegraptus copiosus*, *Tetragraptus* sp., and *Paradelograptus* sp. The presence of the *H. copiosus* indicates a Late Tremadocian age.

3. The Upper Tremadocian Chiquero ichnofauna

The ichnofauna occurs in the lower part of the Chiquero Formation in the Quebrada del Rio Las Burras (near the town of Susques), and in the vicinity of Arenales. Both sections consist of thickening- and coarsening-upward successions, representing the transition from basin-plain to lobe-fringe and lobe environments. The trace fossils occur in very fine-grained, silty sandstone (thin-bedded turbidites). Specimens are housed at the Paleontological Collections of the Centro de Investigaciones Paleobiológicas, Universidad Nacional de Córdoba with the prefix CEGH-UNC (collection is numbered CEGH-UNC 21729–21758). The ichnofauna consists of both pre- and post-depositional elements. The pre-depositional suite includes *Bergaueria* isp., *Helminthoidichnites tenuis*, *Lorenzina plana*, *Megagraptus irregularis*, *Multina magna*, *Paleodictyon* isp., and *?Treptichnus* isp. Elements of the pre-depositional suite are preserved in positive hyporelief (Fig. 4A–F). This pre-depositional suite records the activity of very-shallow to shallow tiers inhabiting the mud biotope, which were later cast by the sand-laden turbidity current.

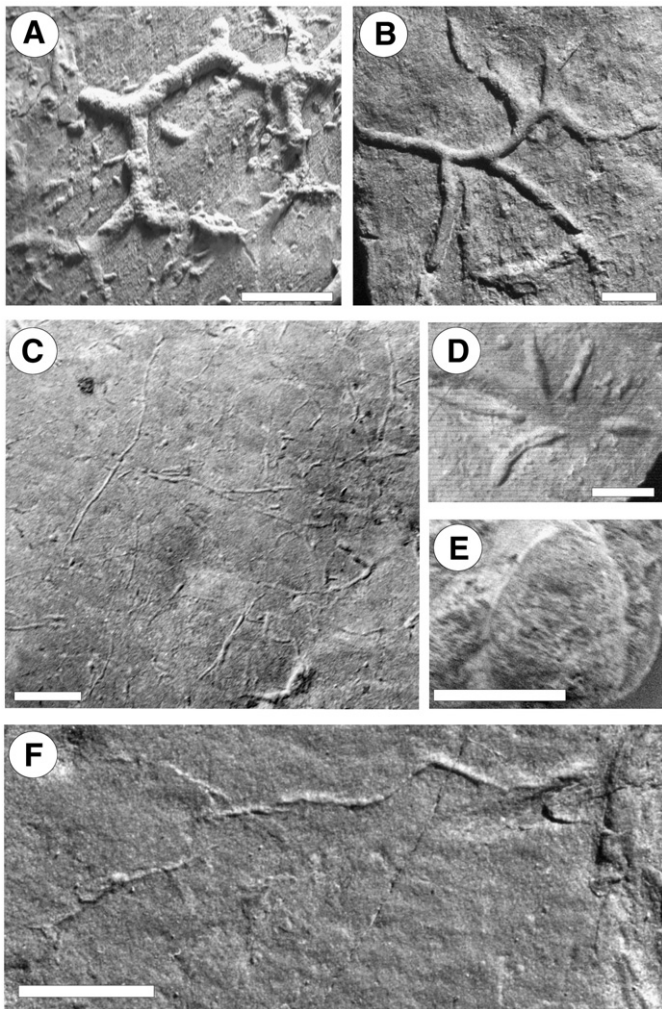


Fig. 4. Elements of the pre-depositional suite in the Chiquero Formation turbidites. A. *Paleodictyon* isp. B. *Megagraptus irregularis*. C. *Helminthoidichnites tenuis*. D. *Lorenzina plana*. E. *Bergaueria* isp. F. *?Treptichnus* isp. Scale bars are 1 cm.

Bergaueria isp. (Fig. 4E) is a shallow, hemispherical plug-shaped burrow with an elliptical cross-section. Wall is unlined. Base is rounded and filling structureless. Burrow is 11.3 mm long and 7.5 mm wide. This ichnotaxon is interpreted as a resting trace or cubichnion (Pemberton et al., 1988). *Bergaueria* has been recorded in Cambrian deep-marine deposits by Hofmann et al. (1994).

Helminthoidichnites tenuis (Fig. 4C) consists of straight to curved horizontal trails. Overlap among specimens is common. Trail width is 0.1–1.4 mm. *Helminthoidichnites* is a grazing trail or pascichnia (Buatois et al., 1998). This ichnogenus is common in Cambrian–Ordovician deep-marine deposits (e.g. Hofmann et al., 1994; Buatois and Mángano, 2003; Uchman et al., 2005).

Lorenzina plana (Fig. 4D) is a radial structure formed by one row of unbranched ellipsoidal elements around a smooth central area. Ridges are 4.2–15.5 mm long, 0.7–1.1 mm wide, and are irregularly distributed. External terminations are pointed or rounded. Central area is 4.2–5.3 mm wide and 8.9–11.0 mm long. Total radial structure is 19.3–35.0 mm long and 14.6–24.5 mm wide. *Lorenzina* is a graphoglyptid or agrichnion which has been occasionally recorded in Lower Ordovician (Arenigian) turbidites (Crimes et al., 1992). Uchman (1998) noted that *Phycodes coronatum* described by Crimes and Anderson (1985) from lowermost Cambrian shallow-marine deposits in eastern Canada may actually belong to *Lorenzina*.

Megagraptus irregularis (Fig. 4B) consists of slightly irregular networks with winding strings that typically branch at about 90°. String diameter is 1.0–1.3 mm. *Megagraptus* is a graphoglyptid or agrichnion (Seilacher, 1977; Uchman, 1998). This later author noted that many Lower Paleozoic occurrences of *Megagraptus* may in fact represent *Multina*, which display common overcrossing of the strings.

Paleodictyon isp. (Fig. 4A) is a distinctive ichnotaxon consisting of regular to slightly irregular hexagonal networks. Mesh size is 18.5–19.0 mm and string diameter is 1.0–1.7 mm. *Paleodictyon* is a graphoglyptid or agrichnion (Seilacher, 1977; Uchman, 1998). In Cambrian–Lower Ordovician strata, it has been recorded mostly in shallow-marine environments (e.g. Crimes and Anderson, 1985) and to a lesser extent in the deep sea (e.g. Jensen and Palacios, 2005).

?Treptichnus (Fig. 4F) isp. consists of simple, zigzag, straight, unlined, unornamented, horizontal burrow segments. It is interpreted as the bedding-plane expression of a three-dimensional burrow system. Burrow width is 0.5–0.8 mm and length observed is 47.0 mm. *Treptichnus* is a feeding trace (fodinichnion) (Maples and Archer, 1987; Buatois and Mángano, 1993a). It has been sporadically recorded in Ordovician turbidites (Uchman et al., 2005).

The post-depositional suite consists of *Protovirgularia* isp. (*Chevronichnus* preservation), *Lockeia* isp., *Multina magna*, *Palaeophycus tubularis*, and irregular knobs. With the exception of *Protovirgularia* isp., which is preserved as a negative epirelief, all the other ichnotaxa are full relief (Fig. 5A–C).

Lockeia isp. (Fig. 5A) is a seed-shaped trace with a pointed termination. Length is 15.5 mm and width is 7.0 mm. *Lockeia* is a resting trace or cubichnia (Seilacher and Seilacher, 1994; Mángano et al., 1998). In Lower Paleozoic rocks, *Lockeia* is mostly known from shallow-marine deposits (e.g. Kim, 1994).

Palaeophycus tubularis (Fig. 5B) consists of curved to straight horizontal to inclined, thinly lined burrows having the same fill as the host rock. Overlap among specimens is relatively rare. Width is 0.6–5.0 mm. Maximum observed length is 96.7 mm. *Palaeophycus* is a dwelling structure or domichnion produced by suspension feeders or active predators (Pemberton and Frey, 1982). This ichnogenus is common in Cambrian–Lower Paleozoic turbidites (e.g. Crimes et al., 1992).

Protovirgularia isp. (*Chevronichnus* preservation) (Fig. 5A) is a chevronate horizontal structure. Maximum length observed is 33.0 mm and width is 4.3–5.4 mm. The central furrow between rows of sediment pads is 0.6–1.8 mm wide. The sediment pads are 0.6–0.9 mm wide. *Protovirgularia* is a locomotion trace or repichnia

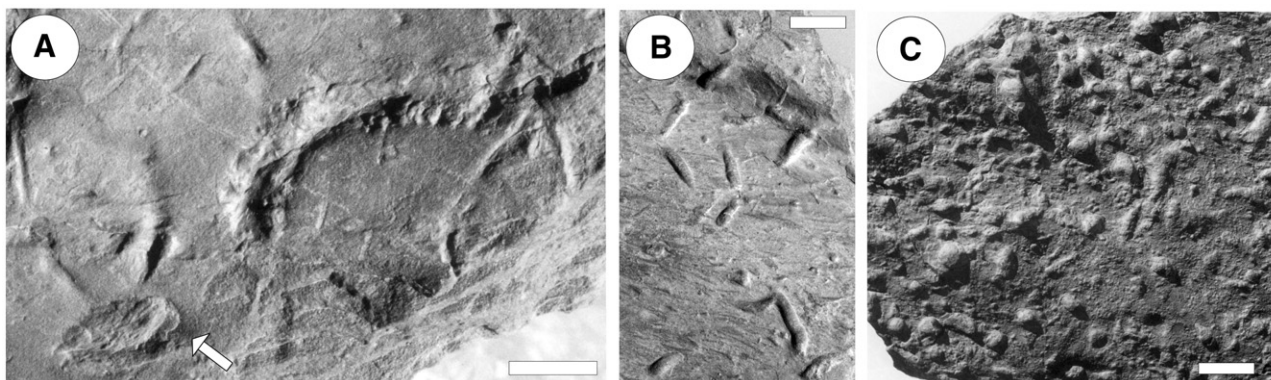


Fig. 5. Elements of the post-depositional suite in the Chiquero Formation turbidites. A. *Protovirgularia* isp. and *Lockeia* isp. (arrow). B. *Palaeophycus tubularis*. C. Irregular knobs. Scale bars are 1 cm.

(Seilacher and Seilacher, 1994; Mángano et al., 1998). *Protovirgularia* is relatively common in Ordovician turbidites (e.g. Uchman et al., 2005).

The irregular knobs (Fig. 5C) occur either isolated or forming dense concentrations. They are 1.5–5.5 mm wide. They may represent basal terminations of *Skolithos*, but vertical segments have not been detected. In some case, however, they may be inclined segments of *Palaeophycus tubularis*.

Multina magna (Fig. 6A–C) occurs in both the pre- and post-depositional suites as revealed by its variable cross-cutting relationships with flute marks. It consists of irregular overlapping networks having meandering to winding strings. Network size is 3.4–35.0 mm and string diameter is 0.7–2.4 mm. *Multina* is a feeding trace or fodinichnion (Buatois and Mángano, 2004). In Lower Paleozoic rocks this ichnogenus is mostly recorded in shallow-marine deposits (e.g. Orłowski and Żylińska, 1996; Buatois and Mángano, 2004).

Cross-cutting relationships among ichnotaxa are rarely observed and mostly represented by *Palaeophycus tubularis* overprinted to *Multina magna*. Vermiform organisms are regarded as the tracemakers of most of these ichnotaxa, with the exception of *Bergaueria* isp., which is attributed to sea anemones, and *Protovirgularia* isp. and *Lockeia* isp., which are produced by bivalves (Pemberton et al., 1988; Seilacher and Seilacher, 1994; Mángano et al., 1998). However, the poor preservational details of *Protovirgularia* in the Chiquero Formation, suggesting emplacement in soft sediment, do not allow ruling out arthropods as producers. Small crustaceans have been suggested as tracemakers of *Paleodictyon* (Garlick and Miller, 1993).

4. Discussion

4.1. Paleoenvironmental distribution of trace fossils

The Chiquero trace fossils are irregularly distributed throughout the unit, recording the interplay of environmental factors and

preservational conditions. Trace fossils seem to concentrate in certain facies, while other deposits are barren. Because trace fossils are preserved on bedding planes, no disturbance of the primary fabric is observed and bioturbation index (*sensu* Taylor and Goldring, 1993) is typically 0.

Basin-plain deposits contain very few trace fossils. Most of the hemipelagic shale seems to be non-bioturbated, which is unusual in younger basin-plain deposits. The only discrete trace fossils are isolated specimens of *Palaeophycus tubularis* which occur at the base of the thickest interbedded sandstone layers (approximately 4 cm thick) of this facies as post-depositional elements cross-cutting flute marks. This suite most likely represents opportunistic colonization of the sandy substrate emplaced due to low-density turbidity currents. Oxygen-depleted conditions may have been dominant during times of suspension fallout, with turbidity currents supplying oxygenated water. A link between oxygenation events and the arrival of turbidite flows has been noted in Arenigian slope deposits of the arc-related Famatina basin further south (Mángano and Buatois, 1997).

Lobe-fringe (distal lobe) deposits contain both pre- and post-depositional trace fossils, and display the highest ichnodiversity. Pre-depositional elements include *Paleodictyon* isp., *Megagraption irregulare*, *Lorenzina plana*, *Bergaueria* isp., *?Treptichnus* isp., and *Helminthoidichnites tenuis*. The pre-depositional suite occurs as positive hyporeliefs at the base of thin-bedded turbidite sandstones. The post-depositional suite consists of *Protovirgularia* isp. (*Chevronichnus* preservation), *Lockeia* isp., *Palaeophycus tubularis*, and irregular knobs. Elements of this suite are either preserved at the top or the base of turbidites as full-relief structures. In the latter case, they typically cross-cut flute marks. *Multina magna* is both pre- and post-depositional. Overall low-energy conditions and temporal stability promote the establishment of a resident fauna. Interruption of sediment fallout by dilute turbidity currents allows preservation of the biogenic structures formed in the mud biotope (Seilacher, 1977;

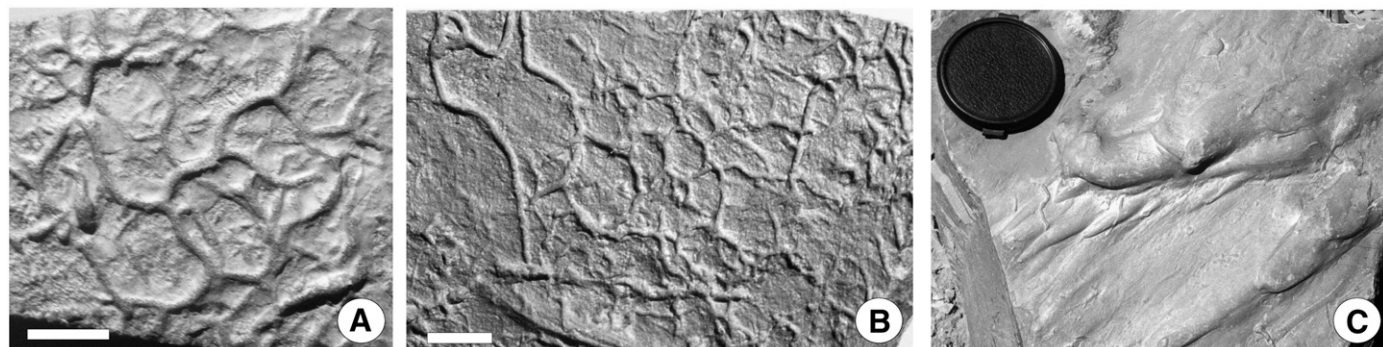


Fig. 6. *Multina magna*. A, B. General view of irregular networks. C. Poorly preserved networks associated with flute marks. Scale bars are 1 cm. Lens cover is 5.5 cm wide.

Miller, 1991; Uchman, 2007). The presence of thin-bedded sandstone turbidites separated by mudstone layers is ideal for preservation along lithologic interfaces. Subsequent to sand emplacement by turbidite deposition, the new substrate was colonized by an opportunistic suite.

Sheet-like, proximal-lobe deposits are sparsely bioturbated. Only post-depositional elements occur in the turbidite sandstones. These are represented by *Palaeophycus tubularis* and irregular knobs, preserved as full-relief structures. Repeated erosion and high rates of sedimentation are detrimental to development or preservation of trace fossils. However, the localized presence of *Palaeophycus tubularis* and irregular knobs indicates short-term colonization windows which allow the establishment of an opportunist infauna.

No trace fossils occur in the submarine-channel deposits. As in inner lobe zones, submarine channels are typified by intense erosion and high sedimentation rates, commonly preventing development or preservation of trace fossils. However, younger examples of channelized deposits elsewhere are at least locally burrowed (e.g. Buatois and Lopez Angriman, 1992; Uchman, 1995). Therefore, the absence of trace fossils in the Chiquero channelized deposits may reflect, at least in part, evolutionary constraints (see below).

Although abundance of trace fossils is more difficult to record than ichnodiversity, field observations indicate a relative scarcity of biogenic structures. Overall less than 5% of the beds contains trace fossils. The peak in abundance is coincident with the peak of ichnodiversity, and occurs in the lobe-fringe deposits. However, even in this facies trace fossils are still rare. Trace-fossil suites are commonly monospecific and in a few cases up to three different types are recorded. In this latter case, one of the forms is invariably the undetermined irregular knobs. An overall dominance of monospecific suites has been noted in other Ordovician deep-sea ichnofaunas (e.g. Uchman et al., 2005).

4.2. Significance in evolutionary paleoecology

Typical deep-sea ichnofaunas are dominated by ornate grazing trace fossils and graphoglyptids that record highly specialized feeding strategies (Seilacher, 1977; Miller, 1991; Uchman, 2007). Deep-marine ichnofaunas reveal adaptation to recurrent disruption by turbidity currents, and display complex feeding strategies, such as trapping of microorganisms and cultivation of bacteria. It has been hypothesized that these sophisticated feeding strategies were attained in order to solve the problem of the scarcity of food in deep-sea sediments (Seilacher, 1977).

The Chiquero ichnofauna records a transition point in the history of deep-sea ecosystems. In contrast to the Ediacaran to Early–Middle Cambrian, microbial mats were no longer a significant component of deep-sea ecology by the Late Tremadocian (Fig. 7). Earlier deep-sea ecosystems were dominated by benthic communities developed in direct connection with microbial mats. Ediacaran–Cambrian deep-marine trace fossils are typically associated with microbial-mat textures, revealing matground grazing and feeding (Buatois and Mángano, 2003). The earliest record of deep-marine trace fossils is Ediacaran, as indicated by poorly diverse, nonspecialized grazing trails (e.g. *Helminthopsis* and *Helminthoidichnites*) in connection with microbial mats (MacNaughton et al., 2000). These strategies linked to exploitation of microbial mats persisted in to the Cambrian with the addition of arthropod trackways (e.g. *Diplichnites*) and more sophisticated feeding strategies represented by different *Oldhamia* ichnospecies (Buatois and Mángano, 2003). In contrast, in the Chiquero Formation microbial textures are remarkably rare and patchy, and not associated with the documented trace fossils.

Interestingly, morphologic patterns of these Upper Tremadocian trace fossils display features that seem to indicate that a change in the ecology of deep-sea biotas was already underway. This is essentially suggested by the appearance of novel trophic types. Graphoglyptids, recording trapping of microorganisms and bacte-

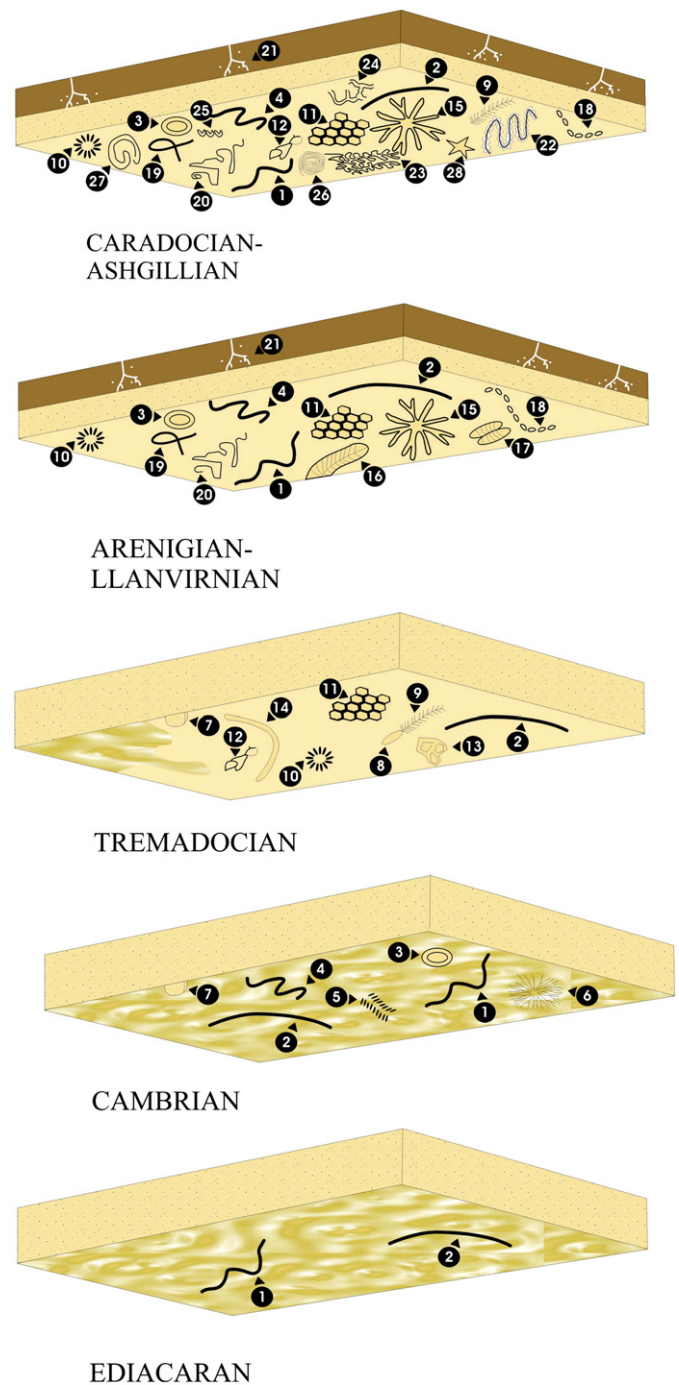


Fig. 7. Ichnofaunal changes in the deep sea through the Ediacaran and Lower Paleozoic. Secular trends include progressive restriction of microbial mats, and increase in graphoglyptid and overall diversity. 1 *Helminthopsis*, 2 *Helminthoidichnites*, 3 *Circulichnus*, 4 *Cochlichnus*, 5 *Diplichnites*, 6 *Oldhamia*, 7 *Bergaueria*, 8 *Lockeia*, 9 *Protovirgularia*, 10 *Lorenzina*, 11 *Paleodictyon*, 12 *Megagraption*, 13 *Multina*, 14 *Palaeophycus*, 15 *Glockerichnus*, 16 *Cruziana*, 17 *Rusophycus*, 18 *Saerichnites*, 19 *Gordia*, 20 *Dictyodora*, 21 *Chondrites*, 22 *Nereites*, 23 *Cosmorhaphis*, 24 *Protopaleodictyon*. 25 *Acanthorhaphis*, 26 *Spirorhaphis*, 27 *Spirophycus*, 28 *Asteriacites*.

rial farming, are present in this ichnofauna, as recorded by the ichnogenera *Paleodictyon*, *Megagraption*, and *Lorenzia*. Possible Cambrian examples of *Paleodictyon* and other graphoglyptids have been recorded mostly in shallow water (e.g. Crimes and Anderson, 1985; Paczeńska, 1985; Crimes and Fedonkin, 1994; Jensen and Mens, 1999), and only rarely in slope environments (Pickerill and Keppie, 1981; Jensen and Palacios, 2005).

In comparison with younger Ordovician deep-sea ichnofaunas, graphoglyptids in the Chiquero Formation are rare, poorly diverse in terms of morphologic patterns and geometrically simpler (Fig. 7). As noted by Uchman (2003), the contribution of graphoglyptids to overall diversity in Paleozoic ichnofaunas is low. Post-depositional elements are more abundant (although less diverse) than pre-depositional ones, which is highly unusual in the majority of younger turbidites. Arenigian turbidites contain much more varied morphologic patterns, including guided meanders, networks, and radial structures (Crimes et al., 1992). These patterns are marginally present in the Chiquero ichnofauna at the most.

In addition, the Chiquero ichnofauna shares with younger Lower to Middle Ordovician deep-sea assemblages the abundance of feeding and grazing trace fossils compared to graphoglyptids (Orr, 1996, 2001). By the Late Ordovician–Early Silurian, deep-marine communities dominated by graphoglyptids, illustrated by ichnofaunas displaying varied morphologic patterns, are established (Orr, 2001; Mángano and Droser, 2004; Uchman, 2004) (Fig. 7).

Multina is one of the dominant elements in the Chiquero ichnofauna and by far the most common network in this unit. This ichnogenus (and the similar ichnotaxon *Olenichnus*) are common in Cambrian shallow-marine deposits (e.g. Orłowski and Żylińska, 1996; Jensen, 1997; Buatois and Mángano, 2004). Its presence in Tremadocian deep-marine deposits may provide evidence of an onshore–offshore pattern. It has been noted that non-specialized, very-shallow-tier, small grazing trails, which are typical of Ediacaran–Cambrian deep-marine environments, reappeared as early colonizers of Late Paleozoic lakes (Buatois and Mángano, 1993b, 2003). These authors explained the recurrence of simple feeding patterns as a colonization strategy to exploit epifaunal to very-shallow infaunal empty ecospace. Interestingly, irregular networks (*Vagorichnus*) similar to those of *Multina* have been recorded at the base of Jurassic lacustrine turbidites in one of the early examples of infaunal colonization in deep lakes (Buatois et al., 1996). This recurrent pattern highlights that organisms develop similar strategies to colonize new habitats through the history of life. In addition, the abundance of *Multina* in Early Paleozoic deep-marine ichnofaunas predating the explosion of graphoglyptids suggests that these irregular networks may have been a precursor of the more complex graphoglyptid networks.

Integration of ichnologic and sedimentologic datasets indicates preferential colonization of distal-lobe settings in the Chiquero turbidite system. Basin-plain and proximal-lobe deposits are sparsely burrowed, and no trace fossils occur in the channel deposits. In the case of basin-plain deposits, oxygen-depleted conditions may have been responsible for the scarcity of trace fossils, although a delayed colonization of basin-plain environments cannot be completely ruled out. High-energy may be invoked to explain paucity of bioturbation in these proximal settings, but younger Phanerozoic deposits formed in high-energy areas of submarine fans are commonly colonized. Channelized areas and inner zones of depositional lobes, characterized by sandy substrates, organic particles in the water column and good oxygenation, allow establishment of a benthic fauna that produce trace fossils that commonly typify nearshore areas. These high-energy settings host ichnofaunas that contain elements typical of shallow water (e.g. *Skolithos* and *Diplocraterion*), representing deep-marine examples of the *Skolithos* ichnofacies (Crimes, 1977; Crimes et al., 1981). The presence of this ichnofacies in Cambrian to Lower Ordovician turbidites needs further study. Vertical burrows, referred to as *Arenicolites* and *Monocraterion*, have been mentioned in Cambrian deep-marine deposits of Ireland and Wales (e.g. Crimes and Crossley, 1968; Crimes et al., 1992), but no illustrations or descriptions are available. However, deep vertical burrows assigned to *Arenicolites* have been documented in turbidites from the Middle Cambrian to Lower Ordovician Meguma Group of eastern Canada by Pickerill and Keppie (1981; see also Pickerill and Williams, 1989). The age of this unit is constrained by trilobites (Pratt and Waldron, 1991) and graptolites (Cumming, 1985). Opportunistic suites in the Chiquero

Formation are overwhelmingly dominated by *Palaeophycus tubularis*. Elements of the *Skolithos* ichnofacies are absent. The irregular knobs may represent basal terminations of *Skolithos*, but vertical segments have not been detected. The colonization of these high-energy channelized and proximal-lobe areas of turbidite systems seems to have been relatively rare during the Cambrian–Ordovician. A dramatic change took place during the Late Jurassic, when some of these thick-bedded sandy turbidites became dominated by horizontal crustacean galleries attributed to *Ophiomorpha* (Tchoumatchenco and Uchman, 2001). As noted by several authors (e.g., Crimes et al., 1992; Orr, 2001; Buatois and Mángano, 2003), arthropod trackways, such as *Diplichnites* and *Dimorphichnus*, which are typical of shallow-marine environments, are relatively common in Cambrian–Ordovician deep-marine settings but subsequently are uncommon in turbidite deposits.

The Chiquero ichnofauna records the arrival of the Agronomic Revolution (Seilacher and Pflüger, 1994; Seilacher, 1999) to the deep sea. Available ichnologic evidence demonstrates that the colonization of the deep sea was a protracted process spanning the Early Paleozoic, which lagged behind colonization of nearshore and offshore substrates. The timing of expansion of bioturbation in the deep sea and the nature of early deep-marine ichnofaunas support the notion that bioturbation was a key factor in the closure of the deep-water slope-basin taphonomic window (Orr et al., 2003).

5. Conclusions

1. An Upper Tremadocian ichnofauna of moderate diversity is documented from deep-marine turbidites of the Chiquero Formation of Puna, northwest Argentina.
2. Basin-plain deposits contain very few trace fossils, being *Palaeophycus tubularis* the only discrete ichnotaxon recognized. Lobe-fringe (distal lobe) deposits display the highest ichnodiversity and contain both pre- and post-depositional trace fossils. Pre-depositional elements include *Paleodictyon* isp., *Megagraption irregulare*, *Lorenzina plana*, *Bergaueria* isp., *?Treptichnus* isp., and *Helminthoidichnites tenuis*. The post-depositional suite consists of *Protovirgularia* isp. (*Chevronichnus* preservation), *Lockeia* isp., *P. tubularis*, and irregular knobs. *Multina magna* is both pre- and post-depositional. Sheet-like, proximal-lobe deposits are sparsely bioturbated, and only post-depositional *P. tubularis* and irregular knobs are present. No trace fossils occur in the submarine-channel deposits.
3. The Chiquero deep-marine ichnofauna represents a transition between Ediacaran and Cambrian microbial-mat dominated ecosystems and younger Ordovician deep-marine trace-fossil assemblages. While Ediacaran–Cambrian deep-marine trace fossils are dominated by matground grazing and feeding, microbial textures in the Chiquero Formation are rare and not associated with trace fossils. Morphologic patterns (e.g. radial trace fossils and networks) of the Chiquero ichnofauna suggest the appearance of novel trophic types, recording trapping of microorganisms and bacterial farming.
4. However, in comparison with younger Ordovician deep-sea ichnofaunas, graphoglyptids in the Chiquero Formation are relatively rare, poorly diverse, and geometrically simpler.
5. The Early Ordovician was a pivotal point in the ecology of deep-sea infaunal communities. This Upper Tremadocian ichnofauna records the arrival of the Agronomic Revolution to the deep sea. Available ichnologic evidence demonstrates that the colonization of the deep sea was a protracted process spanning the Early Paleozoic, lagging behind colonization of nearshore and offshore environments.

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