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The ichnogenus *Dictyodora* from late Silurian deposits of central-western Argentina: Ichnotaxonomy, ethology and ichnostratigrapical perspectives from Gondwana

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ABSTRACT

The association of trace fossils from the Late Silurian Río Seco de los Castaños Formation in central-western Argentina (San Rafael Block) is mainly composed of *Dictyodora*, including *Dictyodora scotica*, *Dictyodora tenuis* and a new ichnospecies named *Dictyodora atuelica*. The latter shows a tendency to migrate to a deeper level – analogous to *Dictyodora liebeana*'s – which reflects more sophisticated behavioural patterns. The *Dictyodora* ichnospecies (one of the most diverse assemblages in Gondwana) coexists with *Nereites*. SEM observations and EDS analyses suggest that the wall structure of *Dictyodora* could be the result of an activity other than the traditional suggestion of respiration, e.g., feeding. The succession, including some of the levels containing *Dictyodora*, presents microbially induced sedimentary structures (MISS) that would indicate a photic zone. This discovery favours previous deltaic interpretations instead of the deep-sea fan deposits traditionally suggested for the Siluro-Devonian greywackes of the Cuyania terrane, and particularly for this unit. The abundant *Dictyodora*, *Nereites*, *Zoophycos* and undermat miners ichnofossils, as well as the scarce arthropod trackways, resemble older records in Europe and North America. The studied section is very well age-constrained, and the autochthonous Gondwana ichnofauna permits to cast doubt on previous interpretations, suggesting that after the Ordovician, microbial mats retreated to marginal marine environments and then spread later in the Carboniferous. More importantly, the occurrence of *Dictyodora* and *Nereites* in beds that bear abundant wrinkle structures or records of biofilms in some places is challenging with regard to deep-sea interpretations. *Dictyodora* is probably not a good stratigraphic indicator, and the provincialism suggested for this ichnogenus may be an artefact of the lack of more complete records in Gondwana.

1. Introduction

The ichnological record of *Dictyodora* in the European Lower Palaeozoic is well known (e.g., Delgado, 1910; Benton and Trewin, 1980; Benton, 1982a,1982b; McCann, 1990; Crimes and Fedonkin, 1994; Orr, 1995; Uchman, 2004; Uchman et al., 2005), but it is almost absent in the Lower Paleozoic of South America, with some exceptions (see Aceñolaza, 1978). *Dictyodora* occurs in deep-sea deposits. In the Ordovician in particular, it co-occurs with graphoglyptids (e.g., Seilacher et al., 2005). However, this ichnogenus has recently been documented in the Devonian successions of central-western Argentina (Vieira de Luca and Basilici, 2013) from a prodeltaic system developed on a platform (Basilici et al., 2012).

Dictyodora ranges from the Ordovician to the Carboniferous and includes several ichnospecies used as ichnostratigraphic markers (e.g., Seilacher, 1967b; Uchman, 2004). This ichnogenus is a member of the *Nereites* ichnofacies in the classical scheme of marine ichnofacies based on the bathymetric distribution of trace fossils (Seilacher, 1967a); in particular, it is a member of the *Paleodictyon* ichnosubfacies in Lower Paleozoic records of the *Nereites* ichnofacies (Wetzel and Uchman, 2012). *Dictyodora* is a complex three-dimensional structure. Its ichnospecies are mainly based on the morphology of their horizontal expressions, both epichnial and hypichnial, connected by a vertical wall of variable height in different ichnospecies (Benton, 1982a, 1982b). The morphology of this trace fossil is highly variable even within the same ichnospecies (see Benton and Trewin, 1980; Benton, 1982a, 1982b; Neto de Carvalho, 2001). The producer of this ichnogenus remains unknown, but a worm or a mollusc without a shell (Aplacophora) has been suggested (Benton and Trewin, 1980). It is attributed to a

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vagile deposit feeder connected to the water-sediment interface by a respiratory "snorkel-like" organ (Seilacher, 2007).

Dictyodora specimens from Devonian prodelta deposits of the Punta Negra Formation in Precordillera (Vieira de Luca and Basilici, 2013; Fig. 1a) derive from the same tectonic terrane (Cuyania) as the material studied here, as well as in deltaic deposits (see Bustos, 1996; Manassero et al., 2009; Basilici et al., 2012); the presumed environment differs from the original deep-sea fan interpretation of the succession proposed by González Bonorino and Middleton (1976) that is usually referred to as "deep water", "deep marine," or "deep sea". McCann (1990) retains the term "deep water" for all records below the storm wave base, which is reasonable. The use of "deep sea" in the sense of the seilacherian bathymetric scheme refers to abyssal deposits developed below the continental shelf break, including submarine fans, commonly named "deep-sea fans". In basins without a shelf break, however, large amounts of sediments are directly bypassed to "deep marine" settings, particularly in tectonically active basins (e.g., López-Cabrera et al., 2008) rather than in passive margins where the classical deep-sea fans in a sequence stratigraphy model are the result of a sea level fall (e.g., Van Wagoner et al., 1990).

The European occurrence of *Dictyodora* (e.g., Benton and Trewin, 1980; Benton, 1982a,1982b; McCann, 1990; Orr, 1995, 2001; Uchman et al., 2005) corresponds to turbidites of "deep-sea deposits", but direct bathymetric control is absent (see McCann, 1990). Ichnologically, Paleozoic deep-sea fans are differentiated from the archetypal Neogene records by the absence of *Ophiomorpha rudis* ichnosubfacies within the *Nereites* ichnofacies (e.g., Wetzel and Uchman, 2012; Buatois et al., 2013). Ichnologically, Palaeozoic deep-sea fans are differentiated from the archetypal Neogene records by the absence of *Ophiomorpha rudis* ichnosubfacies within the *Nereites* ichnofacies (e.g., Wetzel and Uchman, 2012; Buatois et al., 2013). According to McCann (1990), *Dictyodora* may be absent in Ordovician deep-water successions where graphoglyptids and *Nereites* are documented. Conversely, Uchman et al. (2005) documented *Dictyodora tenuis* (M'Coy, 1851) with *Nereites* from Norway. Other Ordovician records (Mikuláš, 1993) described *D. tenuis* with *Nereites missouriensis* (Weller, 1899), *Zoophycos* and *Rhizocorallium*, suggesting episodic sedimentation such as storms, which indicates a shallower environment, like a platform, rather than a bathyal and abyssal depositional setting. In the Ordovician of Germany (Haupquarzit) *Dictyodora* is documented without *Nereites* and graphoglyptids, while in the Carboniferous *Dictyodora liebeana* (Geinitz, 1867) co-occurs with *Nereites* but in some places without graphoglyptids, suggesting additional environmental controls (Benton, 1982b). In the Carboniferous successions from the Czech Republic

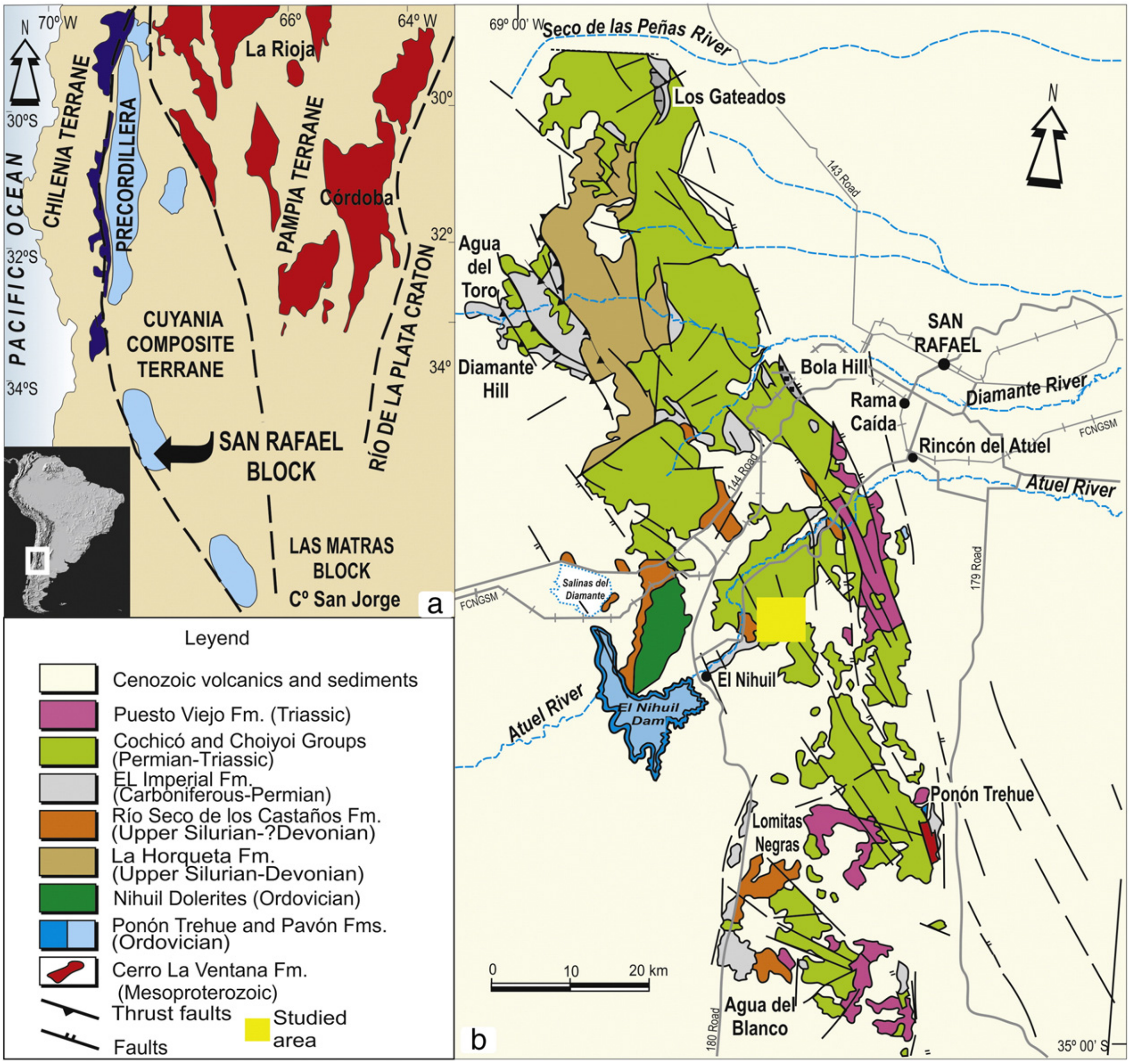

Fig. 1. Geological framework: a) Cuyania terrane and location of the San Rafael Block; b) geological map of the San Rafael Block with location of the studied localities.

(Pek and Zapletal, 1990) *D. liebeana* was reported with several graphoglyptids but scarce *Nereites*.

The stratigraphic record of *Dictyodora* is particularly scarce in the Late Silurian and Devonian around the world (Uchman, 2004). In the Ordovician (Arenigian–Llanvirnian) *Dictyodora* and graphoglyptids become common while microbial mats disappear from deep-water settings (Seilacher et al., 2005, Fig. 7). There is an increase in overall ichnodiversity in the Late Ordovician, while the absence of microbial mats remains (Seilacher et al., 2005). In the present work, *Dictyodora* occurs in bedding surfaces containing microbial mats and in others beds where microbial mats are absent but preservational variants of *Nereites* are present.

The material documented in this paper permits us to i) document the richest *Dictyodora* ichnofauna known from Gondwana; ii) define a new ichnospecies of *Dictyodora* and contribute to the behavioural interpretation of the ichnogenus; iii) discuss the validity of *Dictyodora*'s ichnostratigraphic scheme; and iv) analyse the relationship between "deep water facies", microbial mats and *Dictyodora* records. This paper is a starting point for the study of deep water middle Palaeozoic ichnofaunas of western Gondwana in Argentina. It is also evidence of previously biased conclusions based on the absence of data from Gondwana in the analysis of *Dictyodora* and probably other biased inferences, such as provincialism, where Gondwana data are crucial for a more complete analysis.

2. Geological framework

The Silurian–Devonian successions that crop out in central-western Argentina include a plethora of discontinuously folded and faulted units. They include the San Rafael Block and the Precordillera geological provinces (Fig. 1 a), which are part of the Cuyania terrane (Ramos et al., 1986), a portion of Laurentia that collided in the Late Ordovician with the western proto-Andean margin of Gondwana that has several affinities with the Appalachians (Thomas and Astini, 2003). The composed terrane was intensely tectonised during the collision of the Chilenian terrane from the west during the Late Devonian–Early Carboniferous (Ramos et al., 1986). The time spanning between the two collisional events permitted the development of a foreland basin filled, among other deposits, with thick turbidite-like deposits of Silurian and Lower to Middle Devonian successions traditionally interpreted as submarine fans (González Bonorino and Middleton, 1976) but later reinterpreted as extended deltaic systems (Bustos, 1996; Manassero et al., 2009; Basilici et al., 2012). The San Rafael Block is a morphostructural unit that includes a Palaeozoic record composed of a Grenvillian basement (Cerro La Ventana Formation), intensely deformed volcanic and metasedimentary units ranging in age from the Ordovician to the Late Silurian (Cingolani et al., 2003; Manassero et al., 2009), unconformably covered by a gently folded Pennsylvanian–Cissuralian succession containing Late Palaeozoic glacial deposits (López Gamundí et al., 1994; Pazos et al., 2007). These deposits are overlain by a volcano-sedimentary complex that records the eastern migration of a magmatic arc from the west (Kleiman and Japas, 2009), which itself is angularly covered by sedimentary red bed deposits of a rift basin developed during the Triassic (Kleiman and Japas, 2009). Miocene Andean foreland sedimentary deposits and post Miocene units, including basaltic flows, complete the stratigraphic column of the block (Manassero et al., 2009).

The most complete stratigraphic record of the San Rafael Block is exposed at the Atuel Canyon (Fig. 1b). Along the course of the Atuel River, magnificent exposures ranging from the Silurian to the Holocene are clearly distinguishable. Lower Palaeozoic units received several names in the block, but in the Atuel Canyon and surrounding areas where trace fossils were sampled, the sedimentary succession assigned to the Silurian–Lower Devonian was included in the Río Seco de los Castaños Formation (see Manassero et al., 2009), which differs from the La Horqueta Formation in its metamorphism grade. The Río Seco de los Castaños Formation is folded and faulted and shows a very low grade of metamorphism (Manassero et al., 2009). Near the canyon, the unit is intruded by a tonalite body dated as earliest Devonian by Cingolani et al. (2003); recent dating of detrital zircons indicated a maximum deposition age of post Early Silurian (Cingolani et al., 2014). The Río Seco de los Castaños Formation was compositionally, geochemically and lithofacially studied by Manassero et al. (2009), who also discussed the discrepancies in the assignment to the Late Silurian or Lower Devonian, taking into account palynomorphs, plant remains, and corals. The tonalite intrusion, Lower Devonian (Emsian) in age (401 Ma), brackets the age of the studied unit to the Ludlow–Pridoli Silurian to the earliest Devonian (see Cingolani et al., 2003), making possible a correlation with the Villavicencio Formation, which contains Wenlock Silurian zircons (Cingolani et al., 2013). Conversely, these ages disregard any correlation with the classical "greywacke" Lower–Middle Devonian unit of western Argentina called the Punta Negra Formation, which also overlies the marine Devonian unit named the Talacasto Formation (see Basilici et al., 2012). Plant remains (lycophytes) suggest a Devonian age while palynomorphs sampled at one of the localities also studied here were interpreted as Late Silurian by Rubinstein (1997). Ordovician metasedimentary rocks and Grenvillian basement rock units are the source area (see Manassero et al., 2009, for discussion). According to SHRIMP results in zircons (Cingolani et al., 2003), the metamorphism of the unit is related to the Chanic Orogeny (Late Devonian–Early Mississippian).

The Grenvillian basement (Cerro La Ventana Formation), the Ordovician Pavón and Ponón Trehue Formations were exposed to the east, as was the source of the immature sediments that composed the sedimentary record of the studied unit (Manassero et al., 2009). Lithologically, several types of lithotypes were described by Manassero et al. (2009) in a regional study of the unit. Particularly, in the Atuel Canyon thickening-upward sandstone-dominated packages, several metres thick (Fig. 2a) and showing no internal sedimentary structures, sharp basal contacts with uncommon flute marks at the base are exposed. The beds' thickening-upward arrangement is up to 25 m thick and ends abruptly in heterolithic deposits, and microbial mat structures (Fig. 2b) are recognised on top surfaces, locally exhibiting asymmetrical ripples. These heterolithic deposits, up to 35 m thick (Fig. 2c), are composed of very fine-grained sandstones and siltstones intercalated with claystone beds, and exhibit more sedimentological variability in sedimentary structures. The basal contacts are usually planar and sharp or are deformed by load casting. Internally, some beds (mainly sandstones) present convolute lamination (Fig. 2d) or asymmetrical climbing ripples (Fig. 2d, top). Microbially induced sedimentary structures (MISS) are locally abundant (Pazos et al., 2015–in this issue). These two main lithotypes were described by Manassero et al. (2009), but they recorded beds with hummocky cross stratification in another locality, situated at the basin border, as well as the channelised conglomerates and shallow marine deposits where trace fossils of the *Cruziana* ichnofacies were documented (Poiré et al., 2002).

3. Materials and methods

The material studied in this paper was collected or photographed in the field in the Atuel Canyon (Locality 1 in Fig. 1b) and surrounding creeks and hills. This locality is equivalent to the Locality 2 studied by Manassero et al. (2009). The intense faulting precludes any accurate correlation between short distance outcrops inside the canyon where subvertical exposures are dominant. Slabs were sampled and outcrop walls were photographed, particularly where subvertical exposures of the succession were found. The collected material is housed at the Collection of the Área de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires with the prefix CPBA and identification numbers 21650–21653, 21659, 21682–21683. A vertical section of the uppermost millimetres of the paratype sample CPBA 21651 was analysed

Fig. 2. Sedimentary features, each black square is 10 mm wide: a) coarsening and thickening-upward sandstone-dominated deposits in outcrops close to the Atuel River inside the Atuel Canyon; b) top surface of a sandstone bed with MISS; c) heterolithic deposit interval (person for scale); d) convolute laminations (below) and current ripples (top) in the heterolithic interval.

under a scanning electron microscope (SEM; Zeiss Supra 40 with ultrahigh-resolution field-emission scanning) and photographed at 300× magnifications using standard sample preparation (thin goldcoat). Energy-Dispersive X-Ray Spectroscopy analyses, commonly known as EDS analyses, were also conducted on particular areas of the sample. The stratigraphic divisions used in this paper follow the ICS International Chronostratigraphic Chart (Cohen et al., 2013, updated).

4. Ichnology

4.1. Systematic ichnology

Ichnogenus *Dictyodora* Weiss, 1884.

Diagnosis: Complex three-dimensional burrow, roughly conical, vertical to bedding; apex of cone upward; very thin spreite with exterior surface delicately striated. On bedding plane, the structures appear as a meandering (or roughly spiralling) "band", which corresponds to the intersection of the three-dimensional spreite with the bedding surface (after Häntzschel, 1975).

Type ichnospecies: *Dictyodora scotica* (M'Coy, 1851).

Dictyodora atuelica isp. nov.

Figs. 3a–d.

Derivation of name: From the Atuel River.

Type locality: Atuel Canyon. GPS coordinates: 34°57.529′ S and 68°36.623′ W plus the surrounding areas.

Material: more than 10 specimens were observed in the field; one is illustrated in Fig. 5 with white arrows. Three complete specimens were collected: the holotype (CPBA 21653, Fig. 3a, c), the paratype (CPBA 21651), the basal section (CPBA 21683, Fig. 3b), and a fourth partially preserved specimen (CPBA 21650).

Diagnosis: *Dictyodora* with differentiable lower (basal section) and a vertical section that ends in an upper level (stratinomic level). The lower section is composed of a basal horizontal meandering part, wider than the vertical wall that is differentiable in three morphological types of meanders. The lower meanders are very similar in shape but thinner than the basal section, with always divergent limbs and rounded turns. The meanders of the upper level are subtriangular, with almost orthogonal angles between limbs and pointed turns. The vertical connection between the two meander types consists of asymmetrical, tilted and curved meanders of variable shape pointed in one direction. In full relief, the shape is helical to irregular, but never coiling; vertical striations in the wall may be observable in lateral views.

Description: Helical structures to irregular in full relief with a full diameter of 60 mm and a variable vertical expression (13–18 mm in height between the lower and upper meandering types). The diagnostic shape with two types of vertically displaced meanders is clearly observable in the holotype specimen (Fig. 3a) that lacks the true basal section (CPBA 21683, Fig. 3b). The upper level shows regular triangular meanders with an almost orthogonal angle between limbs (see arrow in Fig. 3c), and with more or less constant length (8–9 mm) and wavelengths 10–15 mm. The meanders show inverted turning points with respect to the lower meanders (e.g., in the holotype), and the course of the trace also shows a 90° change in direction (in the holotype, Fig. 3a) but may be also variable. The

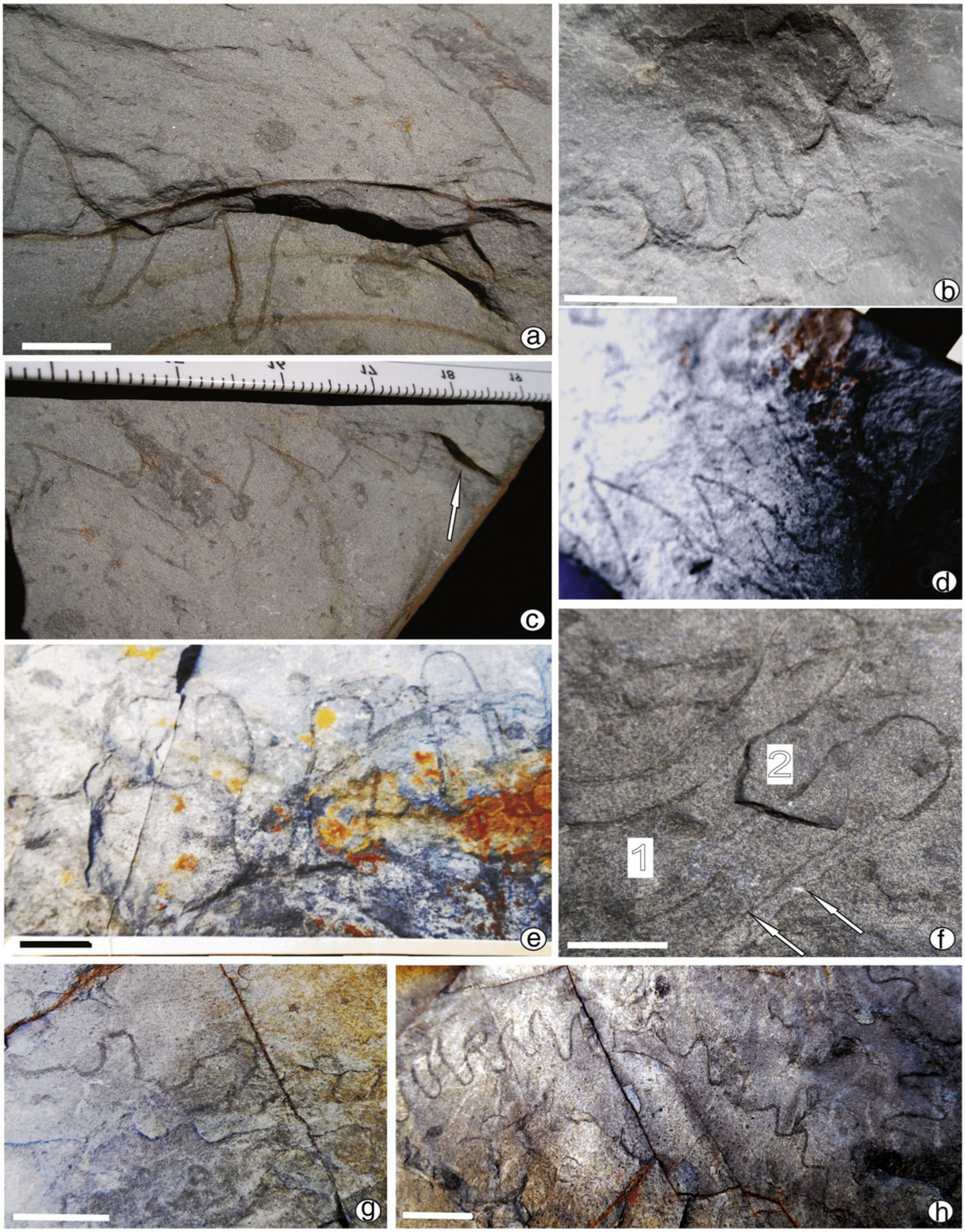

Fig. 3. *Dictyodora* from the Atuel Canyon, scale bar in all photographs is 1 cm: a) *D. atuelica* (holotype: CPBA 21653) showing the lower tier meanders, parts of the “wall” and the upper tier meanders. Note the gradual passage to an upper level with helical shape; b) *D. atuelica*, showing the basal section preserved as hyporelief (CPBA 21683); c) *D. atuelica* detail of the holotype specimen showing the upper tier meanders with triangular shape; the vertical wall is indicated by an arrow; d) *D. atuelica*, displaying meanders that are tilted and pointed in one direction (CPBA 21650). e) *D. scotica*, bedding plane view of the section of the wall showing large amplitude meanders with subparallel to slightly divergent limbs, field image; f) *D. scotica* with a very thin wall in an upward level (2), displaced vertically in some places and a short exposure of the basal section in a lower level (1) with dark borders (arrows); g) *D. tenuis*, bedding plane section across vertical wall showing moderately developed second-order meander, field image; h) *D. tenuis*, with regular meanders; different order sinuosity.

lower level (almost the basal section) shows meanders with rounded turns (Figs. 3a, 5). The amplitude of each meander is variable, but larger than in the upper level (10–13 mm in length). The wavelength is also variable (8–13 mm, and 5–8 mm, respectively). The transition between both meanders shows tilted meanders in one direction (CPBA 21650, Fig. 3d), with pointed turns and acute angles. This is more similar to the morphology of the meanders of the upper level than the lower one, and the vertical separation is shorter than the 15 mm of the meandering “wall”. The width of the vertical expression of the trace fossil is very thin, approximately 1 mm, and it is almost vertically constant. Vertical striations are subtly visible in the paratype. The basal section is wider than the vertical wall and the upper level meanders, but shows a meandering pattern similar to the lower section (Fig. 3b). It was also observed in lateral view as an oval 2 mm wide infilled with fine-grained and dark-coloured sediment. The traditionally tapered upward expression of the vertical wall was not observed as in the basal section and the "wall" is preserved in different specimens.

Distribution: Atuel Canyon, Locality I, at the top of thickening-upward packages and in silty light or dark grey beds within heterolithic deposits.

Comparison: *Dictyodora* Weiss is a complex trace fossil that requires three-dimensional exposures to be reconstructed and not confounded with other bedding plane trace fossils with meandering, irregular or looping pattern. *Paradictyodora* Olivero et al., 2004, is an ichnogenus recorded in Neogene deposits, and it is distinguishable from the simple forms of *Dictyodora* and is even further differentiated from *D. liebeana* and *D. atuelica* by the lack of basal spiralling as well as by the presence of basal branching.

Dictyodora includes under the present knowledge some ichnospecies originally assigned to *Crossopodia* and *Myrianites* by M'Coy (1851). A clear, complete and unambiguous diagnosis of the ichnogenus is lacking, but a wall as part of a three-dimensional structure is the most important ichnotaxobase. Some changes were introduced by Häntzschel (1975), although not without errors (Benton and Trewin, 1980). Benton and Trewin (1980) and Benton (1982a) discussed the ichnospecies that remained valid at that moment. For instance, because of the absence of a vertical "true wall", *Dictyodora simplex* Seilacher, 1955 documented from the Lower Cambrian of Asia must be excluded from *Dictyodora* according to Benton and Trewin (1980). Aceñolaza and Yanev (2001), in contrast, assigned to this ichnospecies some material from the Cambrian, but without illustrations. Another intriguing ichnospecies is *Dictyodora major* (mentioned and not figured by Rindsberg and Martin, 2003), from shallow marine turbidite-like deposits from the Silurian Red Mountain Formation in the United States. Previously, Frey and Chowns (1972, plate 3a–c) studied the unit and figured *Dictyodora* with winding to irregular pattern. The status of *D. major* is regarded as *nomen nudum* in this paper.

The remaining ichnospecies analysed by Benton and Trewin (1980) and Benton (1982a, 1982b) are all valid. The simplest ichnospecies is *Dictyodora zimmermanni* Hundt, 1913 common in the Ordovician of Germany (Benton and Trewin, 1980), which presents an irregular to broadly meandering, sometimes looping, course, and is the less specialised form of *Dictyodora* according to Seilacher (1967b) and Benton (1982a). It is also one of the ichnospecies with highest wall (25 mm). Following Benton and Trewin (1980) and Benton (1982a,b), with the exception of *D. liebeana* (Geinitz, 1867) (a corkscrew form in full relief), the rest of the ichnospecies are differentiated on the basis of the horizontal expression of the wall. *D. zimmermanni* in some cases loops and winds, and meanders with several orders are diagnostic of *D. tenuis* (M'Coy, 1851; Benton, 1982a), while regular meanders are diagnostic of *D. scotica* (M'Coy, 1851) or a complex meandering pattern without looping define *Dictyodora silurica* Yang and Hu, 1992 documented only in the Silurian of China. The existence of a structure differentiable in one basal level with also distinguishable meandering expression (vertical wall) and an upper meandering level; a helical to irregular meandering structure, does not allow to be assigned to any previously known ichnospecies. In fact, the material described in this paper permits us to conclude that the characteristics of the meanders and the helical shape in full relief are morphologically closer to that of *D. liebeana*. This provides evidence of unequivocal migration of the tracemaker to a different stratinomic level and presents morphological variations of the meanders as the result of this migration. The corkscrew shape typical of *D. liebeana* was never observed; nor was the spiralling basal section and coiling, therefore precluding the assignment to this ichnospecies.

Interestingly, Neto de Carvalho (2001) re-examined the material studied by Delgado (1910), and considered *Myrianites lorioli* Delgado, 1910 and *Myrianites andrei* Delgado, 1910 as junior synonyms of *D. tenuis* (M'Coy, 1851), also documenting an early evidence that some specimens migrated to a different stratinomic level as earlier than the Ordovician, and emphasizing that the correct description of morphology and meander orders in some cases demands largely exposed areas. This migration to another stratinomic level is a behaviour only previously documented in *D. liebeana* later in the Carboniferous. However, the morphology described by Neto de Carvalho (2001, Fig. 2b) and interpreted as the ability to migrate to a different stratinomic level is in partial disagreement with the diagnosis of *D. tenuis*. Other specimens described by Neto de Carvalho (2001) are puzzling because they combine the looping typical of *D. zimmermanni*, with a different order of meander (Neto de Carvalho, 2001, Figs. 1c, 2a) characteristic of *D. tenuis*. He also suggests that the meandering pattern is not observable in the basal section (Neto de Carvalho, 2001, Fig. 2b). When Neto de Carvalho (2001) assigns these specimens to *D. tenuis*, the meandering order rather than the migration of the tracemaker to a different level is implicitly considered as the most important ichnotaxobase, but vertical migration or looping is lacking in the original diagnosis of this ichnospecies. Taking into account the complexity in the variability of bedding plane meanders observed even within the same ichnospecies; it is, however, reasonable to emphasise that the full relief morphology rather than the bedding plane expressions are necessary for a more accurate diagnosis. Neto de Carvalho (2001, Fig. 2b) shows that the basal sections of the trace fossils are not meandering and that only the upper level is comparable with *D. tenuis*. Even the more sophisticated *D. liebeana* exhibits a meandering pattern only in the upper level, according to Seilacher (1967b, Fig. 5). Interestingly, Neto de Carvalho (2001) also mentioned wrinkle marks attributed to biofilms, something also noted by Pazos et al. (2015–in this issue) in this studied succession. *D. tenuis* was also documented in the Ordovician flysch deposits of Norway by Uchman et al. (2005) and the Ordovician and Silurian of Scotland (Benton and Trewin, 1980). As previously mentioned, it was also documented from the Middle Devonian of Gondwana by Vieira de Luca and Basilici (2013, Fig. 11c). In the specimens assigned in this paper to *D. scotica*, the meanders show higher amplitude and are more regular than the lower level meander views of specimens of *D. atuelica* (Figs. 3a, 4a). The morphological differences observed between the lower and upper level of *D. atuelica* – including the meander pattern – are recognisable in one specimen of *D. scotica* documented in Benton and Trewin (1980, Fig. 3e), even when *D. scotica* does not present a vertical migration.

D. liebeana has the most complex morphology. The upper level is meandering while the lower one is spiralling, and the transition between them is corkscrew-shaped (Seilacher, 1967b). This morphology results from the migration of the producer to different levels (e.g., Benton, 1982b, Fig. 8a,b). *D. liebeana* was only documented in the Mississippian of Germany (Benton, 1982a,1982b), in Moravia by Pek and Zapletal (1990) and Uchman (2004), and also in Menorca (Balearic Islands) by Orr et al. (1996). Interestingly, the *Dictyodora* isp. documented by Vieira de Luca and Basilici (2013, Fig. 11b) shows similarities with specimens illustrated as *D. liebeana* in the literature (a circular external shape and the spiralling tendency), and it may be the oldest record of this ichnospecies.

Uchman (2007, fig. 15.12) shows an upper view of *D. liebeana* where in certain parts, the sub-triangular tilting and meanders pointed in one direction are distinguishable. These meanders partially resemble the morphology of the vertical migration and the lower level shape of the meanders observable in *D. atuelica*. Mikuláš et al. (2004) documented several specimens from the Carboniferous of Moravia, but one of them (plate IV, 3) clearly shows that the meandering part is wider than the spiralling downward movement of the producer. This case exhibits

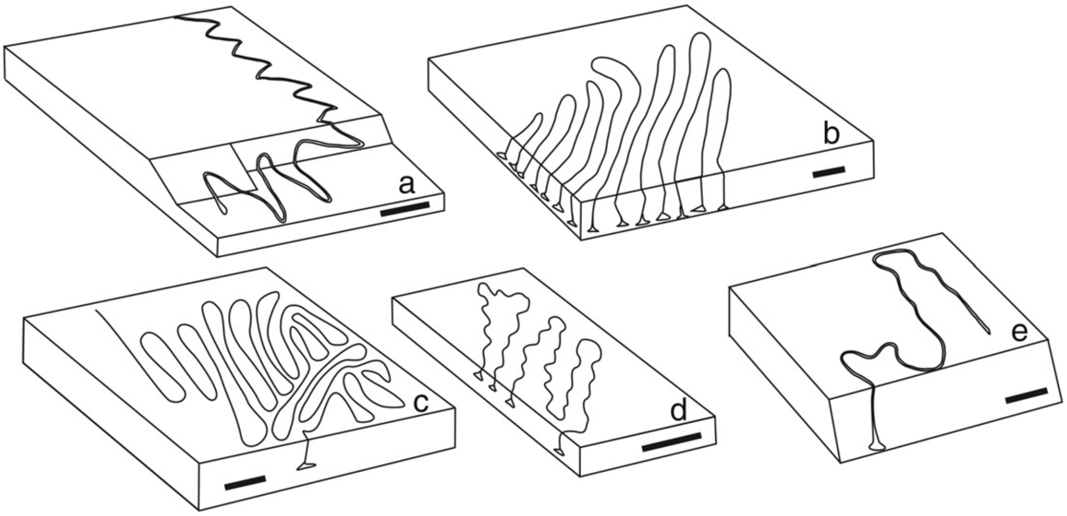

Fig. 4. Pre-Carboniferous ichnospecies of *Dictyodora*, scale bar is 1 cm: a) *D. atuelica* based on the holotype (CPBA 21653); b) *D. silurica* Yang from China modified from Yang and Hu (1992); c) *D. scotica* showing regular meanders, modified from Benton (1982a, Fig, 12 a); d) *D. tenuis* showing different order of meanders, modified from Benton (1982a, Fig. 12b); e) *D. zimmermanni* showing typical irregular pattern. Note the higher wall compared to other ichnospecies, modified from Benton (1982b, Fig. 10a).

meanders that are morphologically similar to some of the material shown here (Fig. 3d). *Paradictyodora.*

Dictyodora scotica (M'Coy, 1851).

Figs. 3e–f.

Material: CPBA 21659 (incomplete specimen), CPBA 21682 (a basal section) and a field specimen.

Description: Regular meanders that constitute the horizontal expressions of a vertical wall are preserved as epichnial forms. They present darker and more fine-grained infill than the host rock and diffuse menisci. Regular, subparallel and slightly divergent limbs up to 40 mm in amplitude are observed. The wavelength of meanders is approximately 15–18 mm. The width of the wall is variable, depending on the exposed level (e.g., approximately 2 mm wide in Fig. 3a). In the specimen CPBA 21682 the basal section is observed, and the wall is also present in a different level (labelled 1) where it is 0.25 mm wide (Fig. 3f). The collected specimen confirms that the morphology does not change vertically. *D. scotica* presents the largest meander size of all *Dictyodora* ichnospecies documented in this paper.

Comparison: Regular meanders are common in *D. scotica* (Fig. 4c) according to Benton (1982a). Absence of the second order sinuosity differs from *D. tenuis* (Fig. 4d). The regularity of the meanders is not frequent in *D. zimmermanni* (Fig. 4e), which is generally irregular and exhibits frequent looping (Benton and Trewin, 1980; Benton, 1982a,1982b). *D. silurica* (Fig. 4b) is a meandering *Dictyodora* but its meanders are complex, with higher amplitude and width and in some places curved. Additionally, the overall structure is more complex than that of the specimen illustrated here. Finally, *D. liebeana* and *D. atuelica* (Fig. 4a) have spiralling or helical structures with meanders of lower width and amplitude. However, isolated and partially exposed records of the *D. silurica* and some parts of *D. liebeana* may be indistinguishable from *D. scotica* and always distinguishable from *D. atuelica.*

Dictyodora tenuis (M'Coy, 1851).

Fig. 3g,h.

Material: Two specimens observed and photographed in the field.

Description: Epichnial forms of *Dictyodora* recorded in silty beds with an incompletely developed second-order meander (Fig. 3g). The total length of the structure is 46 mm in one case (Fig. 3g) and 120 mm in the other (Fig. 3h). Two clear orders of sinuosity were observed in one specimen (Fig. 3h), while in the other specimen, the first order sinuosity is not clear and the assignment to this ichnospecies is tentative. The wall is approximately 2 mm wide and meanders are irregular but with quite rounded turns, and they exhibit divergent rather than subparallel limbs.

Comparison: The partially developed second-order meander allows a tentative assignment to *D. tenuis*. Benton (1982a) used a multivariate approach (principal components analysis) to differentiate *D. scotica* from *D. tenuis*, but in the latter, the second order sinuosity is the diagnostic ichnotaxobase (Benton, 1982a) and was also used by Uchman et al. (2005). *D. silurica* is a more complex structure with long and morphologically complex meanders that lack the second order sinuosity. Until recently, this ichnospecies was restricted to the Late Ordovician and early Silurian; however, a *Dictyodora* specimen from the Devonian of Precordillera (Argentina), illustrated by Vieira de Luca and Basilici (2013, Fig. 11c), and reported as *Dictyodora* isp., exhibits the second order sinuosity and can be ascribed to this ichnospecies. Neto de Carvalho (2001, Fig. 1a) illustrated an Ordovician specimen very similar to one of those included in this paper (Fig. 3h), but he also suggested that looping and migration to other stratinomic levels is frequent in some specimens, as was discussed previously in the analysis of *D. atuelica.*

Nereites Mc Leay, 1839

Nereites isp.

Fig. 5 (black arrows).

Material: Several specimens observed in the field.

Description: *Nereites* with a central tunnel showing a clear backfill pattern. The tunnel is notably wider than the lateral reworked lobes; these consist of darker and more fine-grained material than the central tunnel and the host rock. The external width is 2–4 mm (Fig. 5) and the length is several centimetres, does not show meandering or coiling, but looping is frequent.

Comparison: *Nereites* includes several valid ichnospecies (see Mángano et al., 2000) that have been the focus of intense ichnotaxonomical debate. For instance (see Rindsberg, 1994; Uchman, 1995). *Nereites* now includes ichnospecies previously pertaining to other ichnogenera (e.g. *Helminthoida irregularis* Schafhäutl, 1851; *Neonereites biserialis* Seilacher, 1960 and *Scalarituba missouriensis* Weller, 1899). See Pazos et al. (2015–in this issue) for the detailed analysis of the *Nereites* record in this succession.

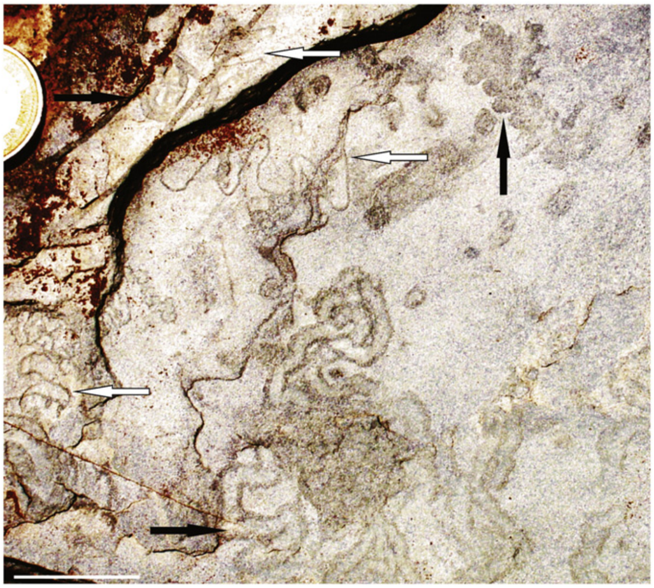

Fig. 5. *Dictyodora–Nereites* taphonomy: *Dictyodora* (white arrows) and *Nereites* isp. (black arrows) co-occurring in the same slab. Note that one *D. atuelica* specimen, close to the coin in the figure, exhibits two tier meanders, both of which cross-cut *Nereites* isp.; *Nereites* shows frequent looping, central backfill and a narrow sides. Scale bar is 2 cm.

5. Discussion

5.1. Ethology and producers of Dictyodora

The three-dimensional morphology of this ichnogenus is not always recorded (Benton, 1982b). The producer assignment is closely linked with the functional interpretation of the wall. For instance, Benton and Trewin (1980) interpreted the wall as the result of a respiratory organ resembling a "snorkel", quite rigid and displaced backward and inward with respect to the basal section, which represents the activity of a deposit feeder. The reconstruction of *D. liebeana* (Benton, 1982b) indicates that a connection with the surface must be permanent and suggests a relatively large animal to explain the 160 mm height structure in full relief. Benton (1982b, p.127) found it difficult to believe that an organ could be up to 160 mm in length and less than 2 mm wide. Seilacher (1967b) attributed this structure to siphons of a worm-like animal. The size of the total structure and the very thin wall make it difficult to accept the "snorkel-like" organ hypothesis. In *D. liebeana*, the conical structure may be inverted; it thus becomes even more difficult to explain the respiratory device interpretation. As a result of the progressive movement, the wall presents vertical striations (Benton, 1982a; Seilacher, 2007). These are not always observable and are a secondary character that is likely not always preserved due to the grain size of the host sediment (Benton1982b).

A variety of producers have been suggested by Benton (1982a), including molluscs and worms. Neto de Carvalho (2001) suggested primitive, shell-less molluscs for the Ordovician records from Portugal, and proposed endobenthic aplacophorans as tentative producers. As noted by Todt (2013) the taxonomy of the Aplacophora is a "secret science" due to difficulties in their taxomomic study. Within Aplacophora, the Solenogastres (neomeniomorphans) are carnivorous and largely symbiotic on various cnidarians, while the Caudofoveata (chaetodermomorphans) are infaunal burrowers and detritus feeders. Recent aplacophorans are slender, between 5 mm and 30 cm long, and they have external calcareous sclerites or spicules (Todt, 2013). The latter represent most of their fossil record. Caudofoveates' life habits (vertical burrowers) and the posterior position of the gills close to the water-sediment interface (Jones and Baxter, 1987) do not support the "wall-organ" or "snorkel" interpretation suggested by Benton and Trewin (1980), Benton (1982b) and Seilacher (2007). Moreover, the aplacophorans lack a well-developed foot: locomotion is primarily by slow ciliary gliding movements through or upon the substratum (Brusca and Brusca, 2003). Nevertheless, the vertical and angled striations documented in the literature in *Dictyodora* may be produced by the spicules. In particular, Caudofoveata known from the Cambrian are today more abundant in very shallow platforms but also reach very deep environments and live in soft, muddy substrates (Salvini-Plawen and Öztürk, 2006).

The specimen documented but not described by Benton and Trewin (1980, Fig. 3e) favours the interpretation of an animal occupying the structure living in a vertical position. The spreiten reported in the wall by Benton and Trewin (1980) and Benton (1982a) may be related to the animal's progressive movement.

The ichnospecies that remain in the same stratinomic level (*D. scotica*, *D. silurica*, *D. tenuis*, *D. zimmermanni*) and only vary in the morphology and pattern of the meanders (Fig. 4) may only be differentiated by paths of food searching, which is clearly more sophisticated and advanced in *D. scotica* and *D. silurica*. The meandering pattern would indicate foraging, while looping or spiralling would optimise exploitation around food patches, as previously suggested (e.g., Seilacher, 1967b; Benton, 1982b; Baucon and Neto de Carvalho, 2008). Conversely, as previously mentioned, in *D. liebeana* and now in *D. atuelica*, and probably in some of the records assigned to *D. tenuis* by Neto de Carvalho (2001), the animal acquired the ability to migrate to another level is evidenced as early as the Ordovician. The shape of *D. atuelica*, a basal level and lower meanders that mimics the pattern of the lower level meanders, and the absence of spiralling but incipient coiling suggests constant deposit feeding rather than exploitation around food patches as in *D. liebeana*.

Fig. 5 shows that *Nereites* and *Dictyodora* concur and *Nereites* might represent the basal section of *Dictyodora*, something already suggested in previous works (e.g., Benton, 1982b). There are clearly observable features that disregard such an interpretation, foremost i) the trace fossils attributed to *Nereites* are intensely looped, never meandering or spiralling as expected in *Dictyodora* basal sections; ii) more importantly, *Nereites* is a pioneering coloniser that is cross-cut by *Dictyodora*, probably when the substrate was more cohesive (Fig. 5). It is interesting to note that the co-occurrence of both ichnogenera only takes place in heterolithic intervals and has been documented in only one case. Several square metres of surface exposing the top of silty sandstones contains only scarce specimens of *D. atuelica* but lacks *Nereites*, which are abundant and varied in silty claystone beds in these intervals (Pazos et al., 2015–in this issue). A common producer of *Nereites* and *Dictyodora* was suggested in pioneering works (see Benton, 1982a). All of the possible producers of *Dictyodora*, except for shelly molluscs, were suggested for *Nereites* (see Rindsberg, 1994), including enteropneusts, annelids, polychaetes, and holothurids, among others. As microbial mats evidenced by MISS were observed at several levels in the interface of both lithotypes, it is plausible that *Dictyodora* was produced prior to the development of the microbial mat or in beds lacking them. This permits us to disregard a possible undermat miner feeding behaviour. Microbial mats enhanced the preservation of the trace fossils.

Macroscopically, the wall is composed of finer-grained and darker infill than the host rock, as documented by previous authors (Orr and Howe, 1999). In SEM observations, this material exhibits different features. The infilling of the wall and the host rock were examined under scanning electron microscopy (SEM-EDAX) to verify whether there were any differences in fabric and composition. Fig. 6 shows a smooth surface at the border of the wall probably related to the reorientation of platy minerals (*sensu* Benton and Trewin, 1980). EDAX analyses, however, show that the carbon content in the wall is up to 18% in weight, relatively high compared to the host rock, whose carbon content is up to 1%.

Under the assumption that the wall was produced by a "snorkel-like" respiratory organ, Benton and Trewin (1980) concluded that the animal could have fed by sediment ingestion at the basal level, which would

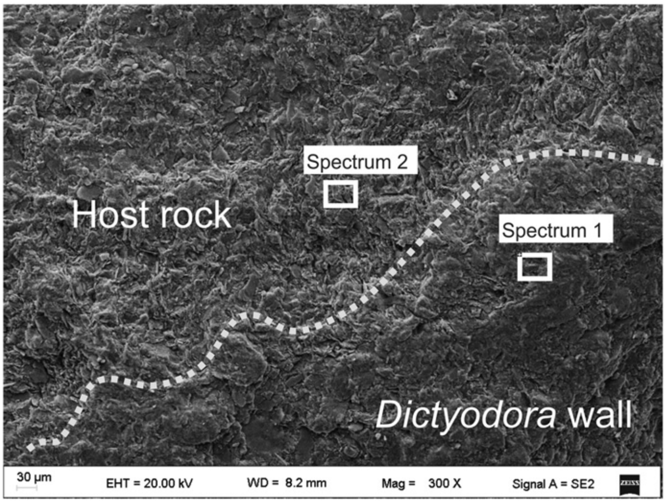

Fig. 6. SEM analysis: image showing a section through a bedding plane expression of the wall of the *Dictyodora atuelica* (paratype, CPBA 21651). The dotted line is the approximate boundary showing a notable texture differentiation between the smoother wall and the host rock. Both squares represent the areas in which the spectra were obtained and EDAX calculated. 300×.

imply the digested waste must remain behind in the same level; however, if the wall is not a result of the activity of a respiratory organ but the space occupied by tracemaker itself, it is also not evidence of food collection as stated by Benton and Trewin (1980). The absence of bacteria in the wall infilling thus far discredits a more sophisticated behaviour such as cultivation.

5.2. Palaeoenvironment and ichnostratigraphy

The *Nereites* ichnofacies during the lower and middle Palaeozoic is composed of ichnogenera such as *Dictyodora*, *Nereites*, *Oldhamia* and several types of graphoglyptids (see Seilacher, 2007), and represents the colonisation of the deep sea in the early Palaeozoic (Seilacher et al., 2005). *Dictyodora* is normally used as indicator of deep-sea environments (e.g., Benton and Trewin, 1980; Benton, 1982a,1982b; Uchman, 2004). However, the reexamination of the material described by Delgado (1910) from the Ordovician of Portugal by Neto de Carvalho (2001) includes wrinkle marks, clear evidence of biofilms, showing the morphologies extensively described by Noffke (2010) for MISS identification. These MISS were noted also by Pazos et al. (2015–in this issue), who cast doubt on the deep-sea origin of the Ordovician succession.

According to Buatois and Mangano (2011, phase 4) microbial mats retreated to marginal marine setting during the middle Palaeozoic and reappeared in the Upper Palaeozoic in a wide bathymetric range. The documented MISS suggests that they persisted in a wide bathymetric range during the middle Palaeozoic.

Mikuláš (1993) reported *Dictyodora* from an Ordovician succession containing other ichnogenera not frequent in the *Nereites* ichnofacies like *Zoophycos* and *Rhizocorallium* and also suggested a shallow marine depositional setting containing storm deposits. The new palaeoenvironmental evidence in the studied section including storm related turbidite-like deposits, the abundance of microbial mats with wrinkle marks and biofilms studied under SEM (Pazos et al., 2015–in this issue) and the presence of *Zoophycos* also indicate that *Dictyodora* is not a direct indicator of deep-sea environments and most of *Dictyodora* ichnospecies are probably frequent in muddy substrates rich in nutrients below the storm wave base but not necessarily slope or bathyal.

Deep-tier trace fossils such as *Dictyodora* and *Zoophycos* have been documented in the Ordovician and Silurian of Bolivia by Toro et al. (1990); those specimens of *Dictyodora* are probably assignable to *D. scotica*.

This Late Silurian record is intriguing because in some aspects it resembles relicts from the early Palaeozoic ecosystems where microbial mats were abundant and graphoglyptids were absent (e.g., Buatois et al., 2009, 2013). Conversely, *D. liebeana* occurs with graphoglyptids among other ichnofossils, including *Nereites*, in deep-water deposits from the Carboniferous of Moravia by Mikuláš et al. (2004), suggesting that at least this ichnospecies is restricted to deep-sea environments, someplace co-occurring with *Nereites*. Buatois et al. (2009) reinterpreted deposits from the Lower Palaeozoic of northwestern Argentina as shallower records, in contrast to the previously assigned deep-sea *Nereites* ichnofacies (Seilacher et al., 2005). In the case described in the present paper and in Pazos et al. (2015–in this issue), the abundance of microbial mats is in disagreement with a deep-sea environment. This represents an invitation not to use *Dictyodora* as an indicator of deep-sea deposits in turbidite-like records. In this sense, microbial mats and the related sedimentary structures are an independent source of evidence to suggest a platform setting related to a prograding deltaic system, as was suggested by Manassero et al. (2009).

The evolutionary trend in *Dictyodora* (e.g., Uchman, 2004) is based on the overall complexity of this three-dimensional structure. A varied meandering patterns starting with *D. zimmermanni* and ending in *D. scotica*, *D. silurica*, and *D. tenuis* might be reasonable, but a rigorous dating of the age of the successions involved must be performed. Clearly, *D. tenuis* is recorded in the Ordovician by Mikuláš (1993), Uchman et al. (2005) and Neto de Carvalho (2001), as well as by Vieira de Luca and Basilici (2013) from the late Lower Devonian in Gondwana; this casts doubt on the validity of the stratigraphic use of *Dictyodora* ichnospecies. Until now, the only ichnospecies with a stratigraphic use is *D. liebeana*, which remains restricted to the Carboniferous (Mississippian) but also to deep-sea environments. The record of *Dictyodora* documented in this paper includes several ichnospecies and is also one of the few well age-constrained (late Silurian–earliest Devonian) examples of this ichnogenus (see Uchman, 2004). Interestingly, the ichnogenus is eurybathic in pre-Carboniferous records with a possible restriction to deep-sea environments during the Carboniferous. The intriguing specimens documented in the Lower Devonian of Argentina may complete the scarce Devonian record of the ichnogenus and permit us to cast further doubts on the use of ichnostratigraphy as a powerful tool.

6. Conclusions

The record of *Dictyodora* Weiss is analysed in detail from the late Silurian unit (Río Seco de los Castaños Formation) from western Gondwana. This record constitutes one of the most diverse documented outside Europe and North America but also one of the few well age-constrained examples for the Late Silurian-earliest Devonian worldwide. The ichnospecies recognised include *D. scotica* and *D. tenuis* — and a new ichnospecies, *D. atuelica*. This new ichnospecies evidence the ability of the producer to migrate to a different stratinomic level to exploit organic matter for feeding as was suggested for *D. liebeana*, and also suggested for some Ordovician records (Neto de Carvalho, 2001). The resultant morphology of such behaviour is more complex in the late Silurian in *D. atuelica* and became sophisticated during the Carboniferous with *D. liebeana*.

The succession studied in this paper contains abundant microbial mats (wrinkle marks) as either extended surfaces or patches and suggests that an ichnofauna dominated by *Dictyodora* and *Nereites* does not necessarily indicate deep-sea environments as they co-occur with *Zoophycos* precluding any deep-sea interpretation (see Pazos et al. 2015–in this issue).

Several organisms have been proposed as tracemakers of *Dictyodora* mainly in the attempt to explain the vertical wall of this three-dimensional structure. Shell-less molluscs such as aplacophorans, particularly the deposit-feeding Caudofoveata, have been suggested as candidate producers (Neto de Carvalho, 2001); however, the “snorkel-like” respiratory organ currently used to explain the vertical wall is dorsally located, and it is not consistent with such primitive molluscs, which lack a dorsal respiratory system and live in a vertical position in muddy substrates. The vermiform shell-less molluscs may be plausible producers as they were able to live in structures connected to the surface, and modern counterparts live on platforms in up to deep-sea depths. The producer of *Dictyodora* is not the same as that of *Nereites*, at least in the studied case, due to taphonomical relationships that indicate that *Nereites* preceded *Dictyodora* as well as differing morphologically.

The succession studied in this paper contains abundant microbial mats (wrinkle marks) as either extended surfaces or patches and suggests that they were not restricted to marginal marine settings during the middle Palaeozoic; an also suggest that an ichnofauna dominated by *Dictyodora* and *Nereites* does not necessarily indicate deep-sea environments due to they co-occur with *Zoophycos*, precluding any deep-sea interpretation (see Pazos et al. 2015–in this issue), as historically was suggested for the co-occurrence of *Dictyodora* and *Nereites* ichnofaunas.

The record in the Cuyania terrane and the Late Silurian age suggests that it is probably the oldest studied autochthonous west Gondwanan ichnofauna composed of *Dictyodora* (this paper) and *Nereites* (Pazos et al. 2015–in this issue) that co-occurs in the same unit and stratigraphic interval.

The lack of studies in Gondwana successions is the simplest explanation for the bias in the absence of varied ichnospecies of *Dictyodora* in Gondwana. These new data cast doubt on the value of the most of *Dictyodora* ichnospecies as ichnostratigraphic markers. However, *D. liebeana* is the only remaining well documented ichnospecies restricted to the Carboniferous.

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