

The unusual record of *Nereites*, wrinkle marks and undermat mining trace fossils from the late Silurian–earliest Devonian of central-western margin of Gondwana (Argentina)



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ABSTRACT

Silurian–Devonian deposits of central western Argentina contain one of the most diverse Palaeozoic records of *Nereites* in Gondwana. *Nereites* cf. *camprensis*, *Nereites irregularis*?, *Nereites jacksoni*, *Nereites macleayi*, *Nereites missouriensis* and *Nereites pugnus* are documented in a turbidite-like succession of the San Rafael Block (Río Seco de los Castaños Formation). The succession, historically assumed as deep-sea deposits or interpreted as a deltaic system, also contains abundant microbially induced sedimentary structures (MISS) such as wrinkle marks. Glossy surfaces indicate abundant biofilms, where the fossil record comprises *N. macleayi*, *N. missouriensis*, scarce arthropod trackways (*Diplichnites*?) and undermat-miner structures. *Nereites*, the pioneer colonizer, is in some cases cross-cut by *Dictyodora*, while undermat miners are the late bioturbators. The succession is dominated by gravity flow deposits, including storm related, turbidite-like deposits and abundant wrinkle marks. These suggest deposition on the shelf rather than the deep sea. This study shows that microbial mats were not restricted to marginal marine environments during the mid Palaeozoic, and documents one of the most diverse Palaeozoic records of *Nereites* in western Gondwana. It also contributes to the record of *Nereites*, *Dictyodora*, and *Zoophycos* found, for first time, in association with microbial mat structures in the late Silurian–earliest Devonian, the *Nereites* ichnofacies together with abundant wrinkle marks.

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1. Introduction

The ichnogenus *Nereites* MacLeay (Murchison, 1839) is a conspicuous component of the homonymous ichnofacies in the bathymetric scheme defined by Seilacher (1967) to characterize deep-sea environments. However, from an ichnotaxonomic approach, several morphological features suggested as ichnotaxobases make ichnospecies assignment difficult; comparison is dependent on which scheme is followed (e.g., Rindsberg, 1994; Orr and Pickerill, 1995; Uchman, 1995). Research by Mángano et al. (2000) shed light on the status of several ichnospecies, but the debate about *Neonereites* Seilacher (1960) as a valid ichnogenus is not completely resolved.

Nereites ranges from Cambrian to Holocene (Callow and McIlroy, 2011) and, in the Palaeozoic, is particularly common in the Silurian (Crimes and Crossley, 1991). It occurs in Recent sediments in the South China Sea (Wetzel, 2002), and is mainly recorded in deep-sea rather than shallow-marine deposits (see Wetzel, 1983; Orr et al., 2003; Uchman, 2004).

Nereites is very common in Palaeozoic successions of North America and Europe where pioneering studies took place and most of the ichnospecies were defined (e.g., Murchison, 1839; Emmons, 1844; Delgado, 1910). Additional Palaeozoic successions bearing *Nereites* have been documented in several papers from the Northern Hemisphere (e.g., McCann, 1990, 1993; Crimes, 1992; Crimes and Fedonkin, 1994; Crimes and McCall, 1995; Orr, 1995).

In South America, Palaeozoic records of *Nereites* are scarce. For instance, the record of *Nereites saltensis* Aceñolaza and Durand, 1973 from the Puncoviscana Formation (Ediacaran–Early Cambrian) from NW Argentina (Aceñolaza and Aceñolaza, 2007; Aceñolaza et al., 2009) is controversial. This ichnospecies was retained in *Nereites* by Aceñolaza et al. (2009) but Seilacher et al. (2005), Seilacher (2007) and Buatois and Mángano (2012) relocated it to *Psammichnites* Torrell, 1870.

Indisputable records of *Nereites* with *Neonereites* preservation (see Uchman, 1995 for the *Nereites* and *Neonereites* dilemma), were also documented by Aceñolaza and Aceñolaza (2007) in the Cambrian interval of the Puncoviscana Formation. Specimens described as *Parahelminthoida* isp. by Aceñolaza and Peralta (1985) from the mid Palaeozoic of the Argentinian Precordillera were later included in *Nereites* by Uchman (1995). More recently, Melchor et al. (2013)

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documented specimens of *Nereites* with tight meanders from the Ordovician? of central-western Argentina. The Ordovician ichnofauna documented in Bolivia by Toro et al. (1990) includes *Dictyodora*, *Cosmoraphe* and material assigned to *Neonereites* (= *Nereites missouriensis*). In Brazil, abundant specimens of *Nereites* isp. were documented in the Devonian Pimenteira Formation by Campanha (1974).

The *Nereites* ichnofacies was subdivided by Seilacher (1974) into *Paleodictyon* and *Nereites* ichnosubfacies, in order to differentiate substrates. The archetypal features of the *Nereites* ichnofacies can be found mainly in Mesozoic and Cenozoic deep-sea fan examples, where it was subdivided into the *Ophiomorpha rudis* ichnosubfacies (characterising sand-rich channel and channel proximal lobe) and the *Paleodictyon* ichnosubfacies typifying thin-bedded turbidites in sand-rich lobe fringes (Uchman, 2001) and external shale flysch deposits for the *Nereites* ichnosubfacies (Uchman, 2004). The ichnogenus *Nereites* is a conspicuous constituent of the *O. rudis* ichnosubfacies, but not exclusively. In contrast to Seilacher (1974), Orr (1995) considered oxygenation level, rather than substrate, to be the controlling factor in deep-sea settings. A combination of both oxygenation and substrate controls was suggested by Callow et al. (2014). Wetzel (2002) analysed this relationship in detail and found oxygen deficient substrates in records of incipient *Nereites* from Recent sediments.

The evolution of the *Nereites* ichnofacies during the lower Palaeozoic was addressed by Buatois et al. (2009), who pointed out some characteristics of the deep-sea ecosystem. For instance, the relationship between graphoglyptids (sensu Seilacher, 1977), microbial mats and structures produced by undermat mining was analysed. It was concluded that the disappearance of microbial mats from the deep sea during the Ordovician allowed the diversification of graphoglyptids. More recently, Buatois and Mángano (2011) suggested that microbial mats persisted, but were restricted to marginal marine environments during the mid Palaeozoic (Silurian–Devonian), before becoming more widespread in the late Palaeozoic (Buatois et al., 2013). Interestingly, *Nereites* ichnofacies is bathymetrically well constrained and characterises deep-sea fan systems in the Mesozoic and Cenozoic times (e.g. Uchman, 2003; Buatois and Mángano, 2011; Heard and Pickering, 2008; Wetzel et al., 2007, among others).

Callow and McIlroy (2011) suggested that *Nereites* is more common in turbidite-bearing formations of the Palaeozoic than the Mesozoic and Cenozoic. The palaeobathymetric control of *Nereites* during the Palaeozoic is therefore questionable. In some cases the *Nereites* ichnofacies is used as an indicator of the deep-sea following the seminal work of Seilacher (1967). However, Uchman (2007) discussed examples within sedimentary rocks deposited very close to storm wave base, raising the possibility of at least some exceptions in the Palaeozoic fossil record.

The relationship between *Nereites* and microbial mats has not been previously explored in Palaeozoic records. Conversely, the relation between graphoglyptids and matgrounds has been examined (e.g., Buatois et al., 2009). This paper documents the ichnogenus *Nereites* with microbial mat structures (wrinkle marks and glossy surfaces) from the late Silurian–earliest Devonian Río Seco de los Castaños Formation (González Díaz, 1981) in the San Rafael Block, in western Argentina.

2. Geological setting

2.1. Tectonic framework

The mid-Palaeozoic successions of central-western Argentina include a plethora of folded, faulted and discontinuously outcropping units. These are part of the San Rafael Block and other blocks included in the Cuyania terrane (Fig. 1a) that collided with the western proto-Andean margin of Gondwana in the Late Ordovician (Thomas and Astini, 2003). Cuyania was intensely deformed from the west during the collision of the Chilenia terrane (Ramos et al., 1986) in the Late

Devonian–Mississippian. The units underlying the resulting unconformity usually present a variable grade of metamorphism while the post-collisional units (Mississippian and younger units) are unmetamorphosed. During the time spanning the Cuyania and Chilenia collisions (Late Ordovician–Mississippian), a foreland basin developed and was filled, in some stratigraphic intervals, with thick turbidite-like deposits.

The San Rafael Block is a morphostructural unit that includes a varied Palaeozoic record that is well exposed in Atuel Canyon. The succession there begins with intensely deformed volcanic and meta-sedimentary units ranging in age from Ordovician to late Silurian—earliest Devonian (Cingolani et al., 2003, 2014; Manassero et al., 2009). These are unconformably overlain by a gently folded Pennsylvanian–Cisuralian succession, volcanic units (Choiyoi volcanism), Triassic sedimentary rift basin deposits (Kleiman and Japas, 2009) and finally Miocene and Quaternary units, including lava flows.

2.2. The Río Seco de los Castaños Formation

Atuel Canyon exposes the stratotype of the Río Seco de los Castaños Formation (RSLC) of late Silurian—earliest Devonian age. This unit is a succession of flysch deposits more than 600 m in thickness, and is distinguishable from other similar units in the region by its very low grade of metamorphism (González Díaz, 1981).

The age of the unit has been approximated using detrital zircons, dating of an intrusion, and by fossil remains. Detrital zircon studies constrain the age of the rocks and trace fossils to the Ludlow–Lochkovian (Cingolani et al., 2013, 2014). Near Atuel Canyon the RSLC Formation is intruded by a tonalite body dated through Sensitive High Resolution Ion Microprobe (SHRIMP) as of Lower Devonian (Emsian) age by Cingolani et al. (2003). Fossil remains (palynomorphs, plant and coral remains) indicate a late Silurian–Lower Devonian age for the unit (see Manassero et al., 2009).

In a regional study, Manassero et al. (2009) recorded gravity flow deposits to the west and storm deposits to the east; these are organised into coarsening-upward and heterolithic intervals. Based on the stacking pattern, the facies trend, charcoal abundance, and plant remains, they interpreted them as the record of a deltaic system.

Pazos et al. (2015) described turbidite-like deposits with convolute lamination and asymmetrical climbing ripples, and also documented wrinkle marks that provide evidence of patchy microbial mats on bedding planes (Pazos et al., 2015, fig. 2b, and this paper). They interpreted the turbidite-like units as storm deposits that were emplaced below normal storm wave base, concluding that they, in combination with wrinkle marks, indicate deposition on the outer shelf.

Ichnologically, the unit has received little study, but Manassero et al. (2009) mentioned the *Cruziana* ichnofacies (following Poiré et al., 2002) from the basin margin and the *Nereites*–*Mermia* ichnofacies (sic Manassero et al., 2009, page 234) for the trace fossils documented in locality 2 of this paper. Recently, Pazos et al. (2015) studied the ichnogenus *Dictyodora* Weiss, 1884 in Atuel Canyon and also mentioned the ichnogenus *Nereites*.

3. Methodology

Special attention was given to precise location of sampled sections in order to allow the comparison with previous work (e.g. Manassero et al., 2009). Locality 1 coincides with the outcrops recently revisited by Pazos et al. (2015) where *Dictyodora* was studied in detail. It is situated between Nihuil dams 1 and 2 along the Atuel River in Atuel Canyon (GPS coordinates: 34°57.529' S and 68°36.623' W). Locality 2 is represented by a series of exposures on Road 144 (Fig. 1b), approximately at kilometre 703. The intense faulting precludes any accurate correlation at the same locality or between them for an integrated logged section, even over short distances. Localities 1 to 4 of Manassero et al. (2009) were numbered from distal to proximal deposits. In this paper, localities 3 and 4 (proximal settings) were not studied; locality 1 of Manassero

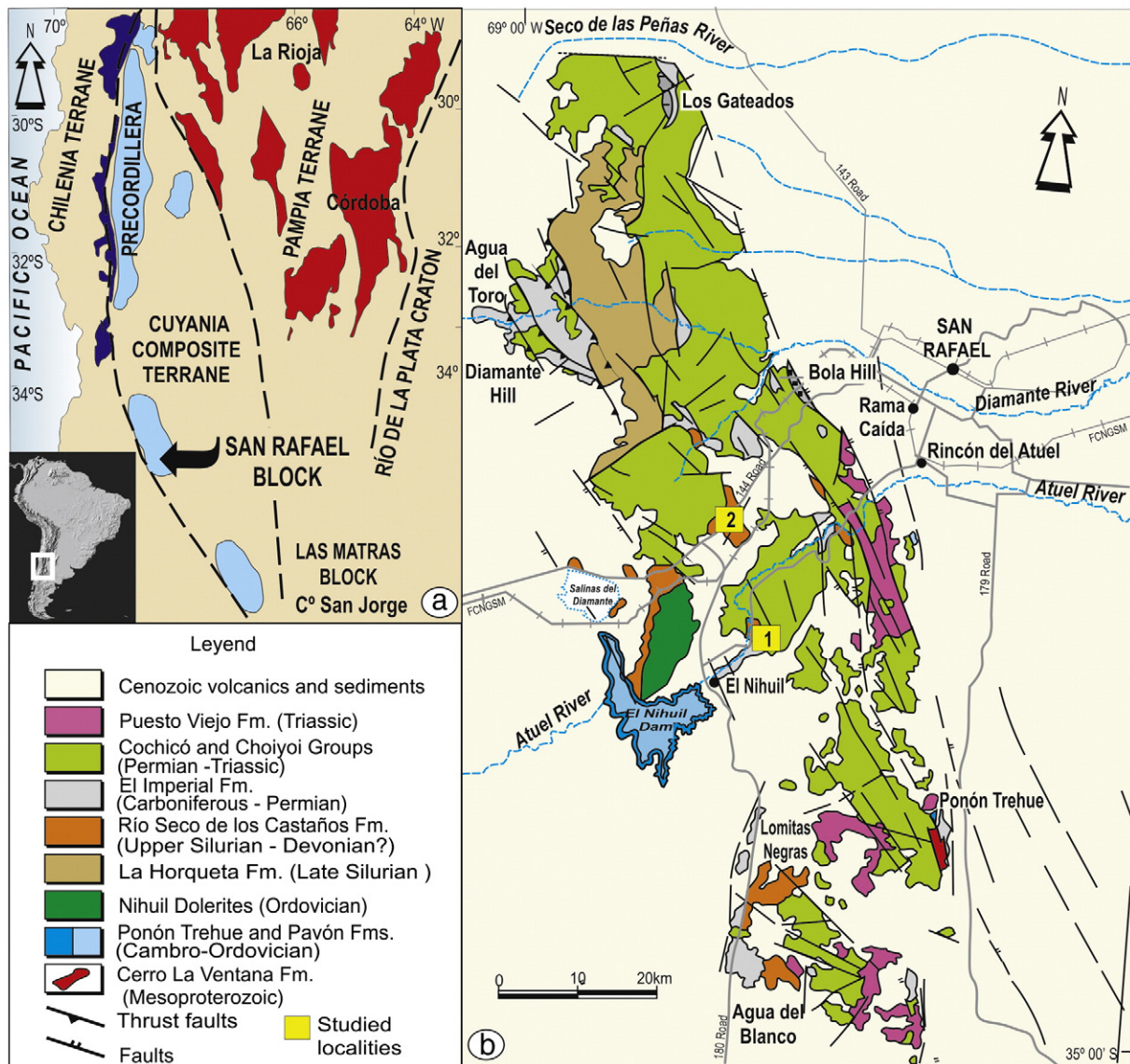


Fig. 1. Geological framework: a) Geological location of the San Rafael Block in the Cuyania terrane; b) Geological map and location of the studied localities. Modified from Manassero et al. (2009).

et al. (2009) is our locality 2 and their locality 2 is our locality 1, following a proximal to distal trend. The term MISS is used following Noffke et al. (2001), where wrinkle marks are just one example, and is also used to describe corrugated surfaces (after Porada and Bouougr, 2007). Recognising that the “mid Palaeozoic” is an informal chronostratigraphic subdivision; we use it here for the Silurian–Devonian periods.

The sampled ichnological specimens are housed in the Collection of the Área de Paleontología (Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales) of the University of Buenos Aires (UBA, Buenos Aires, Argentina) with the institutional abbreviation CPBA.

For the ichnogenetic diagnosis of *Nereites* we follow Rindsberg (1994) and Uchman (1995) rather than Orr and Pickerill (1995). At the ichnospecific level, we used criteria such as the morphology of the lobes or pustules (envelope) and the ratio of tunnel width to external width (which is clearer than the morphology of pustules alone; Benton (1982a), Rindsberg (1994), Orr and Pickerill (1995) and Uchman (1995). The differences in both schemes are clear (compare Uchman, 1995, fig. 8a, b) to Orr and Pickerill, 1995, fig. 8). The trace

fossils studied by Pazos et al. (2015) referred to the ichnogenus *Dictyodora* and associated ichnospecies are only briefly described here to avoid duplicated descriptions. Trace fossils associated with microbial mats are described separately as a record of undermat mining and are only identified to ichnogenus level, since more material is necessary for a more precise assignment.

Vertical sections of the uppermost millimetres of wrinkle marks were analysed under a scanning electron microscope (SEM; Zeiss Supra 40 with ultrahigh-resolution field-emission scanning), using standard sample preparation (thin gold-coat). Energy-dispersive X-ray spectroscopy (EDS) analyses were also conducted on areas of presumed organic origin.

Callow and McIlroy (2011) studied the ichnological record of turbidites and used the term “turbidite bearing formation” to refer to any rocks deposited by turbidity currents in deep-marine (slope or basin floor) environments. However, turbidite-like is here used for comparison with the archetypal turbidite sequence (Bouma, 1962) without any specific bathymetric implication, and both are considered as part of gravity flows, in particular low-density turbidite deposits, following Talling et al. (2012).

4. Ichnology

4.1. Systematic ichnology

4.1.1. *Nereitids* (sensu Seilacher, 2007)

Nereites MacLeay in Murchison, 1839

Type ichnospecies: *Nereites cambrensis* Murchison, 1839.

Diagnosis: Usually selectively preserved, winding to regularly meandering, more or less horizontal trails, consisting of a median back-filled tunnel enveloped by even to lobate zone of reworked sediment. Commonly, only the external part of the enveloping zone is preserved as a densely packed chain of uni- or multi-serial small depressions or pustules (Uchman, 1995).

Nereites cf. *cambrensis* Murchison, 1839

Fig. 2a

Material: One specimen (CPBA 21663).

Occurrence: Locality 2 in dark coloured fine-grained heterolithic intervals of the fine-grained couplets.

Description: Horizontal specimen preserved as epirelief with the diagnostic central tunnel and an envelope zone comprising lobes or pustules at both sides up to approximately 3–6 per centimetre. The pustules exhibit an elongate and almost arcuate form with pointed ends; they are disposed at an acute angle rather than perpendicular to the central tunnel, which is poorly exposed with no observable backfill. Maximum width is 12 mm and the course of the trace is regularly meandering. The meanders exhibit rounded curves which are enlarged in some cases (cf. Orr and Pickerill, 1995).

Remarks: In *N. cambrensis*, the pointed ends of the lobes or pustules are arranged at angles from 45° to 65° with respect to the central furrow or tunnel (Benton, 1982a; Orr and Pickerill, 1995; Uchman, 1995). This is observed in specimen CPBA 21663. This, rather than the course of the trace, is diagnostic of *N. cambrensis*. According to Seilacher (2007), tight meanders dominate in deep water, Early Palaeozoic records. In our case, the course is meandering but not as tight as illustrated by Benton (1982a, fig. 6b). *Nereites pugnus* exhibits large lobes with diagnostic arcuate pustules (Benton, 1982a, fig. 6.4f), or clavate pustules according to Orr and Pickerill (1995). Therefore, *N. pugnus* is not comparable with this specimen. Rounded lobes (ovate in the sense of Crimes and McCall, 1995; Orr and Pickerill, 1995) preclude any comparison with *Nereites macleayii* and with *Nereites jacksoni* (two ichnospecies that may overlap due to toponymic reasons; Orr and Pickerill, 1995, fig. 8). *Nereites irregularis* is characterised by a wide median tunnel with respect to the reworked sides; backfill is not always present (Uchman, 1995). In the studied specimen, the median tunnel is thin with respect to the size of the lobes. *N. missouriensis* presents widely different preservational variants: i) *Neonereites* preservation, with a succession of pustules and no central tunnel; and, ii) preservation with a wide median tunnel with backfill, an envelope zone of similar proportion than the lobes, and occasional low side lobes (Rindsberg, 1994; Uchman, 1995). The small median tunnel of this specimen negates assignment to *N. missouriensis*. *Nereites imbricata* has a median tunnel enveloped by obliquely arranged, arcuate laminae, externally resulting in a uniserial row of imbricated and tightly packed, subspherical to annulate, large sediment pads (Mángano et al., 2000) which are completely different from this material.

N. irregularis? (Schafhäutl, 1851)

Fig. 2b

Material: One specimen (CPBA 21667).

Occurrence: Heterolithic deposits of locality 2.

Description: *Nereites* with *Helminthoida*-type preservation with a central, light-coloured backfilled tube; the reworked sediment is darker and more fine-grained, or absent. The meanders are tight. It appears in the same slab with other small forms of *Nereites*, possibly assignable to *N. macleayii*, without any clear relationship between them.

Remarks: The tunnel is wide with respect to the reworked sediment at both sides, which is diagnostic of the *Helminthoida* preservation of

Nereites (Uchman, 1995), and is characteristic of *N. irregularis*. The material described as *Nereites* isp. by Pazos et al. (2015) presents some of the diagnostic features of this ichnospecies, such as a wider central tunnel with backfill and thin reworked sediment at both sides. However, another feature diagnostic of *N. irregularis*, the guided and frequently tight meanders, as in *N. cambrensis*, is not present here.

N. jacksoni Emmons, 1844

Fig. 2c

Material: Two specimens (CPBA 21658.1, 21658.2)

Occurrence: Locality 1, recorded in fine-grained siltstone-claystone couplets from the heterolithic intervals.

Description: A narrow central tunnel is very distinctive; it is 2 mm wide, dark coloured and without backfill. Its brownish colour is different than that of the host rock and the sediment reworked in the lobes. The course of the trace is very straight and lobes are ovate; these are preserved as concave and convex reliefs (the specimen is preserved in both forms in two adjacent slabs). The pustules are ovate with rounded ends, convex or concave and very large compared with the tunnel that, in parts, is laterally displaced rather than central. The specimens contain no more than 1.5 pustules per centimetre. The ovate lobes show strong variability along the same side of the trace, but also with the lobes of the other side; in certain areas, convex pustules are vertically prominent rather than flat. The length of the trace is 6 cm and the external width is variable with a maximum of 1.2 cm.

Remarks: These are remarkable specimens that show contrasting features that might suggest different ichnospecies. Material assigned by Benton (1982a) to *N. jacksoni* was partially placed in *N. missouriensis* by Uchman (1995), with doubts. That seems a correct decision because the specimen figured by Benton (1982a, fig. 6c) has a wide central tunnel and lobes similar to those characteristic of *N. missouriensis*. However, Benton (1982a, fig. 6f) illustrated the different ichnospecies of *Nereites* through drawings, including *N. jacksoni* with the central tunnel very thin with respect to the lobes, and similar to the specimen here described. Taking into account the proportions between the central tunnel and lobes as stated by Uchman (1995) the specimen resembles the material illustrated by Benton (1982a) and later included in *N. missouriensis* by Uchman (1995). However, these specimens with a thin central tunnel resembles a “large *N. macleayii*,” something already noted by Orr and Pickerill (1995), thus suggesting some overlap between ichnospecies. In our case, specimens assigned to *N. macleayii* do not present a displaced median tunnel with almost straight course but, more importantly, the proportion between the central tunnel and lobes is distinguishable in both ichnospecies. In *N. macleayii* some of the studied specimens exhibit a central tunnel of similar width to that of *N. jacksoni*, but with smaller pustules that sometimes are of equal width than the tunnel which makes them more similar to *N. missouriensis*.

The high lobe/tunnel width ratio in *N. jacksoni* may suggest that the differences may not be due to an ontogenetic variation of the same producer of *N. macleayii*. Notably, the laterally displaced tunnel suggests the ability of the producer to move the organ that produces the envelopes, but not due to vertical displacement, because the tunnel remains with a constant width. *Nereites* figured by Orr et al. (1996) from the Carboniferous of Menorca, exhibit more elaborate ornamentation in the lobes, a wider, backfilled central tunnel, and are comparable with *N. jacksoni* described by Delgado (1910) and discussed by Orr and Pickerill (1995) as “morphology (iii)”.

N. jacksoni has been recorded in Upper Ordovician successions of Portugal (Delgado, 1910), in the Upper Ordovician–lower Silurian of North America (Pickerill et al., 1987), in the Silurian of North America and Europe (Emmons, 1844; Benton, 1982a,b; Orr and Pickerill, 1995), in the Upper Carboniferous of Portugal (Delgado, 1910), and in the Miocene of Iran, Crimes and McCall (1995). The latter is the youngest record of this ichnospecies.

N. macleayii (Murchison, 1839)

Fig. 2d, e

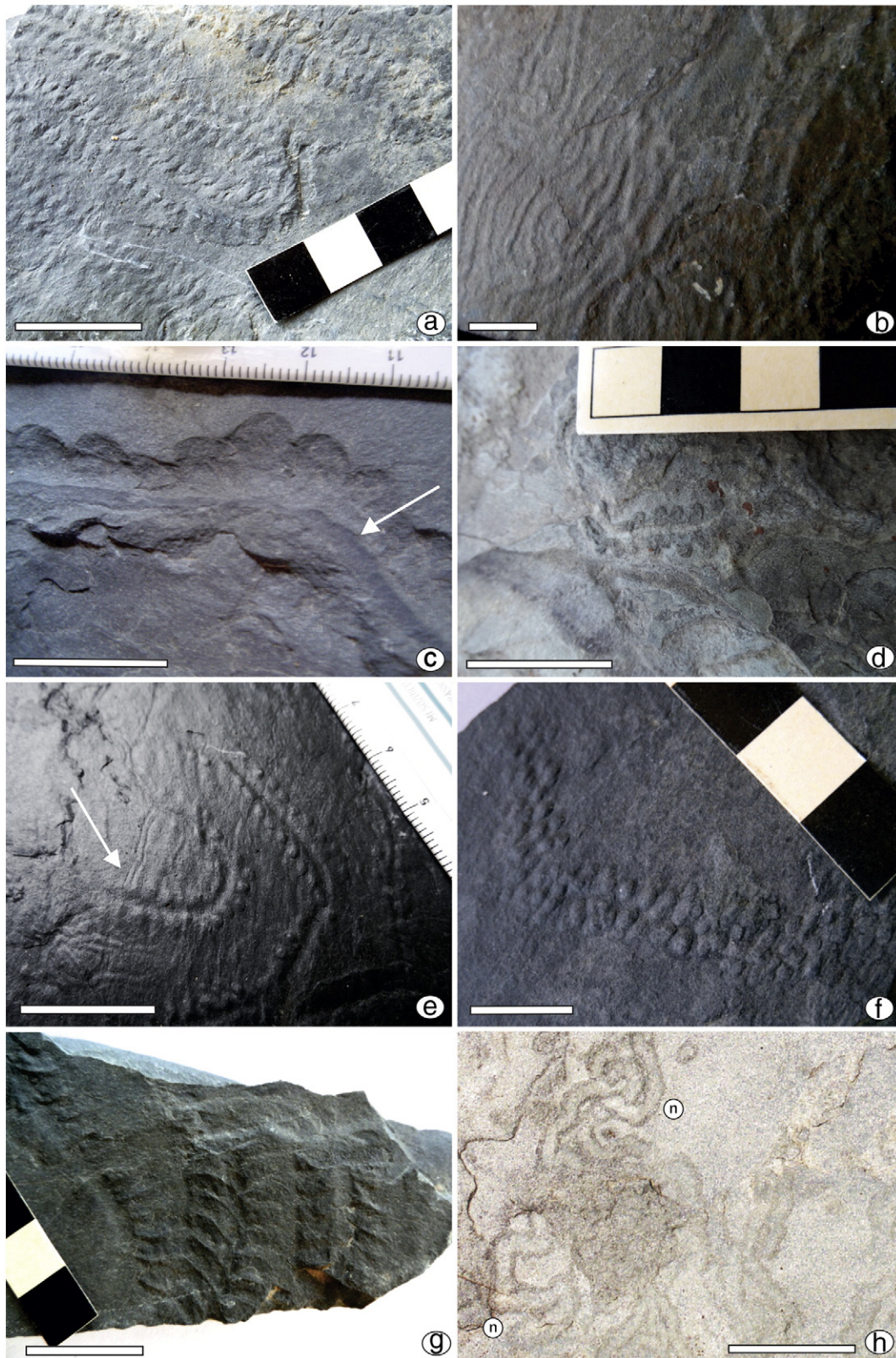


Fig. 2. Nereitids: a) *N. cf. cambrensis* (CPBA 21663); b) *N. irregularis?* (CPBA 21667); c) *N. jacksoni* with a defined central tunnel (CPBA 21658); d) *N. macleayii* (CPBA 21662); e) *N. macleayii* (CPBA 21673) in a microbial mat (glossy type) and undermat mines (arrow); f) *N. missouriensis* with *Neonereites* preservation (CPBA 21666); g) *N. pugnus* with leaf-shaped lobes (CPBA 21660); h) Field photograph showing *Nereites* isp. with (n) distinct backfilling menisci and very narrow lateral lobes.

Material: Five collected specimens (CPBA 21654, 21655, 21662, 21665, 21671) and several field photographs.

Occurrence: Fine-grained deposits from localities 1 and 2.

Description: This is the most common type of *Nereites* recorded in the studied sections. The lobes or pustules show rounded endings and are sometimes completely ovate and connected with the central tunnel

(Fig. 2d), or disconnected (Fig. 2e) and resembling the *Neonereites* preservation of *N. missouriensis*. The distance between pustules is variable and sometimes it differs between sides; they are perpendicular with respect to the median tunnel (Fig. 2d, e). The median tunnel is present in some specimens but in others it is recorded as a depression (see Fig. 5d). Backfill is not distinct in any specimen. The course of the traces is winding to irregularly meandering and sometimes with a coiling tendency. Winding is the most common course.

Remarks: Lobes with rounded ends, and small pustules with variable distance between them (more than 3–4 per centimetre) are diagnostic of *N. macleayii* according to Benton (1982a), Orr and Pickerill (1995) and Uchman (1995). Some specimens resemble a transition between *N. macleayii* and *N. missouriensis* (*Neonereites*-like preservation) particularly in bedding planes with glossy surfaces or patchily preserved wrinkle marks (Fig. 2e). They show rounded to slightly ovate pustules disconnected from the central tunnel, probably representing another preservational variant intermediate between the classical *N. macleayii* and *N. missouriensis*. This type of preservation may be influenced by microbial mats. *N. jacksoni* is a similar form but has different proportions (see above).

N. missouriensis (Weller, 1899)

Fig. 2f

Material: Four specimens (CPBA 21661, 21664, 21666 and 21673).

Occurrence: Heterolithic deposits of locality 1.

Description: Aligned, rounded to slightly elongate or ovate pustules in overlapping groups of two or more. The central tunnel is absent, and the convex hyporelief preservation is frequent but one specimen is preserved as convex epirelief. In one specimen (CPBA 21673) the central tunnel is partially preserved and wrinkle marks are present on the same surface (see Section 5). The course of the traces is straight or slightly winding but never meandering. One specimen (CPBA 21661) presents the pustules and a surrounding lobate area that clearly comprises a bigger envelope than the serial pustules (Section 5, Fig. 5a, b). Remarks: These specimens are very similar to: 1) the material illustrated by Pickerill (1981, fig. 4) from the Silurian; 2) "*Neonereites biserialis*" sensu Seilacher (1960); 3) the specimens illustrated by Crimes and Anderson (1985) from shallow-marine Ediacaran–Cambrian deposits of Canada; and 4) *N. missouriensis* figured by Uchman et al. (2005) from the Ordovician of Norway. Transitions between these forms have been documented in the Ordovician of Portugal (Delgado, 1910) and in the Ordovician–Silurian successions of UK analysed by Benton (1982a) and described as *Neonereites biserialis*. Some specimens of *N. macleayii* exhibit transitions to this type of preservation (see above) but in these cases pustules are more separate and sometimes isolated. Interestingly the material documented in this paper indicates that this ichnospecies is frequent in levels containing microbial mats structures, such as wrinkle marks. More importantly, the epirelief and hyporelief preservation, that in the first case provide evidence of a large reworked area, strongly support the interpretation of a tridimensional origin for this ichnospecies, with several preservational variants as was suggested by Uchman (1995) instead of a separate ichnogenus as originally proposed by Seilacher (1960).

N. pugnus Emmons, 1844

Fig. 2g

Material: Three specimens (CPBA 21660.1–3) (recorded on the same slab) and one more documented in the field.

Occurrence: Heterolithic deposits of locality 1.

Description: *Nereites* with an external width of 0.9–1.5 cm and preserved length of 6 cm. The overall morphology resembles branches and is preserved as endichnial traces with narrow median tunnels. The lobes are elongated, arranged and inserted at an acute angle with respect to the middle tunnel; these are individually arcuate, with a sharp line that gives them a leaf-like appearance. The burrow is short and two of the specimens recorded in the same slab are very similar; a partial juxtaposition of lobes is present. A third specimen shows a median tunnel but no clear lobes; it resembles in part the pustules observed

in *N. cambrensis*. On the same surface, very short and thin burrows resembling undermat mining trace fossils are sparsely recorded.

Remarks: These specimens are extremely similar in all features to those figured by Benton (1982a, fig. 6d, e). *N. pugnus* is apparently one of the rarest ichnospecies of *Nereites*; it has been seldom reported in the literature (e.g., Emmons, 1844; Delgado, 1910; Orr and Pickerill, 1995). Uchman (1995) did not illustrate this ichnospecies but his drawing of *N. cambrensis* resembles *N. pugnus*, which might indirectly indicate that proportions and minor differences in lobe morphology are insufficient to retain separate ichnospecies. Conversely, Orr and Pickerill (1995) considered this ichnospecies to be the most distinctive within the ichnogenus, without any possibility of confusion with any other ichnospecies. One of the reasons for such a statement is the shape of the lobes and the straight to gently curved course. However, the angle of insertion of the lobes figured by Benton (1982a) and the characteristics of the material studied here are comparable with *N. cambrensis*, but the lobe/tunnel ratio is very different in the two ichnospecies. Some specimens shown by Orr and Pickerill (1995, fig. 8) also exhibit a flat V shape in cross section. For those authors, this is the only ichnospecies that does not show transitions with others. The shape of the lobes precludes assignment to any ichnospecies other than *N. pugnus*.

Nereites isp.

Fig. 2h

Material: Several specimens observed in the field, one collected (CPBA 21670).

Occurrence: Heterolithic deposits of locality 1.

Description: Short trail with a wide central backfill and diffuse, fine-grained reworked sediment at both sides. The course of the trace is curly and irregular. The material was recently described and analysed by Pazos et al. (2015).

Comparison: *Nereites* with the classic *Helminthoidea* preservation shape (Uchman, 1995); the absence of tight meanders typical of *N. irregularis* prevents the assignment to this ichnotaxon. The specimens differ from *Taenidium* isp. documented from locality 1 (see below) in the presence of a wall, lined or reworked material, and the different colour and grain size of the arcuate backfilling.

4.1.2. Other ichnogenera

Dictyodora Weiss, 1884

Dictyodora isp.

Pazos et al., 2015, fig. 3a–d

Material: Several specimens (CPBA 21650, 21651, 21653, 21657, 21659, 21668, 21682, 21683) and field specimens.

Occurrence: Heterolithic deposits at locality 1.

Description: This material represents the new ichnospecies *Dictyodora atuelica* Pazos et al., 2015. It is characterised by a spiralling to irregular pattern and differentiation between a lower (close to basal) and upper meandering levels, showing different morphology. Also, examples assigned to *Dictyodora scotica* M'Coy, 1851 (Pazos et al., 2015, fig. 3e, f) and *Dictyodora tenuis* Hundt, 1912 (Pazos et al., 2015, fig. 3g, h) were found in the heterolithic intervals and also described in detail by Pazos et al. (2015, figs. 3–5).

Diplichnites Dawson, 1873

Diplichnites? isp.

Fig. 3a

Material: Two trackways from the same slab (CPBA 21679.1–2).

Occurrence: Fine-grained sandstone from locality 2.

Description: Trackways preserved as convex hyporeliefs and associated with delicate tool marks. They are short, biserial, and contain thin and arcuate imprints, externally tapered and disposed perpendicular to the median axis. Rows of imprints of different specimens display a partial overlap, making difficult a complete characterization of individual trackways. However, their width is probably less than 1.3 cm.

Comparison: These trackways are tentatively assigned to *Diplichnites?* Dawson, 1873 given the shape and disposition of the imprints, but more material is necessary to confirm this assignment, and allow



Fig. 3. Associated trace fossils: a) *Diplichnites?* isp. (CPBA 21679), scale bar 1 cm; b) *Taenidium* isp., scale bar in cm (field specimen); c) *Zoophycos* isp. (CPBA 21464), scale bar in mm.

accurate differentiation from other arthropod trackways like *Tasmanadia* Chapman, 1929, as figured by Seilacher et al. (2005, fig. 22e).

Taenidium Heer, 1877

Taenidium isp.

Fig. 3b

Material: One field specimen.

Occurrence: Fine-grained sandstones showing thickening-upward packages from locality 1.

Description: Winding, unlined burrow preserved as flat hyporeliefs and composed of a succession of menisci (backfilling). Menisci are arcuate; no differences in grain size are observed between successive menisci. The width is 5 mm and the length is 40 mm.

Remarks: Meniscate burrows without a wall are the diagnostic feature of *Taenidium* Heer, 1877 (D'Alessandro and Bromley, 1987). The absence of reworked sediment and wall lining precludes comparison with *N. missouriensis*.

Zoophycos Massalongo, 1855

Zoophycos isp.

Fig. 3c

Material: Two specimens (CPBA 20664 and 20665).

Occurrence: Heterolithic couplets from locality 1.

Description: Tongue-like structure (CPBA 20664) with almost no relief, showing arcuate lamellae and a poorly preserved external tube. The long-axis length is 13 cm and the maximum width in this incomplete specimen is 8 cm (CPBA 20664), while the vertical expression of the lobe is very thin, less than 0.5 cm. The specimen CPBA 21665 is a fragment from close to the axial apex.

Remarks: The documented specimens preserved in fine-grained siltstone deposits present the diagnostic characteristics of *Zoophycos*, including double lamellae (e.g., Olivero, 2007; Kotake, 2009). The ichnospecies assignment is not possible due to the scarce material, but similarities with the ichnospecies *Zoophycos villae* Massalongo, 1855 are favoured given the curvature of the lamellae, particularly in the specimen CPBA 21665 (not figured) while the specimen CPBA 21664 is more similar to *Zoophycos brianteus* Massalongo, 1855. Although an ichnotaxonomic revision of *Zoophycos* is pending, this ichnogenus is generally considered an indicator of palaeobathymetry in most Palaeozoic records. *Zoophycos* "migrated" from shelf areas to the deep sea after the Palaeozoic (Olivero and Gaillard, 2007; but see Bottjer et al., 1988). Its producer is considered a worm-like, deep-tier burrower and either interpreted as a deposit feeder or strip miner.

Different organisms have been proposed as possible tracemakers. *Zoophycos* is an enigmatic and complex ichnogenus (Olivero, 2007). In South America, some mid-Palaeozoic *Zoophycos* are found in the Silurian of Argentina (Aceñolaza, 1978; Astini and Marengo, 2006) and the Devonian of Bolivia and Brazil (e.g., Campanha, 1985; Assis, 2001; Gaillard and Rebeauchef, 2006), all from shelf deposits.

4.2. *Nereites*: ichnotaxonomy, producers and records

The ichnotaxonomic study of *Nereites* is a complex task because of the different existing ichnotaxobases at the ichnogenus level and the fact that an acceptable diagnosis of the ichnogenus was proposed much later than the erection of most of its ichnospecies. Several papers addressed the study of the ichnogenus and emended the diagnosis (e.g., Häntzschel, 1975; Rindsberg, 1994; Orr and Pickerill, 1995; Uchman, 1995) or revised partially the status of several ichnospecies, but in an informal way (e.g. Benton, 1982a,b; Rindsberg, 1994; Orr and Pickerill, 1995; Mángano et al., 2000). Most of the erected ichnospecies date from pioneer papers in the Northern Hemisphere (e.g., Murchison, 1839; Emmons, 1844; Delgado, 1910). Rindsberg (1994) emended the *Nereites* diagnosis of the ichnogenus previously used (e.g. Häntzschel, 1975) and included a central faecal ribbon as an ichnotaxobase; he also remarked on the variability of preservation and the importance of complete three-dimensional records for an accurate assignment at the ichnospecific level. It was an important ichnotaxonomic observation by Rindsberg (1994) that transferred *Scalarituba* Weller, 1899 and *Neonereites* Seilacher, 1960 into *Nereites*. Orr and Pickerill (1995) stated that the ichnogenus did not have a proper diagnosis and proposed one, but did not define a type ichnospecies. They suggested an ichnospecific differentiation based on a combination of shape and amount of pustules per centimetre without regarding the central tunnel or furrow as a crucial ichnotaxobase. Uchman (1995) again emended the diagnosis of the ichnogenus (used here) and introduced changes that affected the stability of other ichnogenera, expanding the work of Rindsberg (1994), and synonymizing *Nereites* with *Helminthoidea irregularis* Schafhäütl, 1851. *Neonereites* was considered a toponymic expression of *Nereites*, an interpretation that was widely accepted with some exceptions (e.g., Orr, 2001; Orr et al., 2003; Seilacher, 2007). There has been some confusing combination of names subsequently, including *Nereites biserialis* (sic) used by Shi et al. (2009).

The ichnotaxonomy of *Nereites* is still quite confusing due to preservational variants and transitional forms (Orr and Pickerill, 1995; Uchman, 1995). Benton (1982a) and Orr and Pickerill (1995) focused their ichnospecific diagnoses on the morphology of lateral lobes and lobes per centimetre and did not use the ratio between the central tunnel or furrow and envelope (lobes) as a primary ichnotaxobase (contra Uchman, 1995). Mángano et al. (2000) introduced *N. imbricata* and revised the status of all previously proposed ichnospecies and commented on the material documented by Delgado (1910), reducing substantially the number of possible ichnospecies. The following ichnospecies are here considered valid after these partial revisions: *N. cambrensis* Murchison, 1839 (the type ichnospecies), *N. macleayii* (Murchison, 1839), *N. jacksoni* Emmons, 1844, *N. pugnus* Emmons, 1844, *N. irregularis* (Schaffhäutl, 1851), *N. missouriensis* (Weller, 1899) and *N. imbricata* Mángano et al., 2000.

Nereites might be produced by worm-like animals such as enteropneusts, polychaetes, and sipunculans, but also by mollusks and arthropods (Rindsberg, 1994). *Nereites* represents the combined locomotion and feeding behaviour (pascichnion) of a producer that selectively sorts out coarse grains and passes the fine grains through the gut; these later form part of the central tunnel or backfilled faecal ribbon (Seilacher, 1986; Rindsberg, 1994; Mángano et al., 2000). Interestingly, enteropneusts are more frequently found in shallow-marine rather than deep-sea deposits (Maletz, 2014). More importantly, their traces are spiral faecal forms, at least in modern analogues (Smith et al., 2005), casting doubts on this group as possible producers of *Nereites*. Other suggested producers are unknown worm-like animals that might also produce *Dictyodora* (Benton and Trewin, 1980).

Shallow-marine controversial records of *Nereites*-like traces documented in modern tidal flats by Martin and Rindsberg (2007) are considered to be the result of the activity of juvenile limulids. Morphologically, these traces resemble *Nereites* and are comparable to *N. missouriensis* (as emended by Rindsberg, 1994; Uchman, 1995) from the Carboniferous of USA. Martin and Rindsberg (2007) suggested that *Nereites*-like modern traces in shallow-marine records might suggest xiphosurans as plausible trace-makers. These could include some examples from shallow-marine records in the Carboniferous. This indicates that, in the Palaeozoic, this ichnospecies was clearly eurybathic. The remaining ichnospecies (with the exception of *N. imbricata*) were recorded in turbidite-like deposits. *Nereites* has also been reported from slope to abyssal plains in the Holocene (Wetzel, 1983, 2002).

5. Microbial mats and undermat miners

Matgrounds involve substrate modification mediated by microbial activity. Evidence of this activity includes macroscopic and microscopic features, where processes like binding, baffling and trapping of grains are involved (Noffke, 2009). This may produce microbially induced sedimentary structures (MISS) or it can just form thin and glossy surfaces containing extrapolymeric substances (EPS), termed “bioglue” by Seilacher (2008).

Microbial mats have an important role in the enhancement of trace fossil preservation (e.g. Fernández and Pazos, 2013) and undermat activity, through the formation of biofilms or bioglue (Seilacher, 2008) and the reduction of the erosion rate compared to surfaces free of microbial mats (e.g. Carmona et al., 2012). Microbial mats dominated by cyanobacteria depend on photosynthesis and are bathymetrically controlled (Noffke et al., 2001). Other types of microbial mats formed by sulfate reducing bacteria are not related to wrinkle marks and are very common in environments with reduced oxygen levels or are stratified beneath cyanobacterial mats, as observed in lagoons in Brazil by Vasconcelos et al. (2006). The rapid reduction in oxygen content under the mat was analysed by Gingras et al. (2011) in hypersaline Caribbean tidal flats. Other shallow records are very common in the Precambrian (e.g., Gerdes et al., 2000; Noffke et al., 2001, 2003; Lan and Chen, 2012; Buatois et al., 2014).

Microbial structures may be easily detected with scanning electron microscopy, but in some cases remain unnoticeable in macroscopic observation. Microbially induced sedimentary structures (MISS) include elephant skin textures, wrinkle marks, “Kinneyia” structures, mud crack-like, gas domes, palimpsest ripples and mud chips, among others (see Noffke et al., 2001). They are not all produced in the same environments. MISS are very common in shallow marine to marginal marine settings (Porada et al., 2008). They are particularly common in modern, marginal marine, hypersaline environments (Vasconcelos et al., 2006; Gingras et al., 2011). In particular, wrinkle marks are palaeobathymetric indicators (e.g., Buatois et al., 2014), recorded in shallow marine settings, above of the shelf edge.

Gerdes et al. (2000) summarised the MISS common in peritidal environments, but did not include wrinkle structures. Noffke (2009) pointed out that storm and fair-weather waves above ancient shelves led to frequent reworking of endobenthic microbial mats, and that wrinkle structures are associated with epibenthic microbial mats mainly in quiet zones.

Mata and Bottjer (2009) analysed the Phanerozoic record of wrinkle structures and concluded that two depositional settings favoured their development: offshore transition zones and intertidal environments. Thomas et al. (2013) pointed out that wrinkle marks are dominant in microbial mat-bearing littoral environments as a result of Kelvin–Helmholtz-type instability, which induces ripple corrugations in a viscoelastic film under flowing water. In their experiments, the ripple corrugations are spontaneously induced in the film, which grow in amplitude over time, and were correlated with oscillatory flows.

Evidence of macrofauna feeding on wrinkle marks is scarce, though it was reported from Cambrian shallow-marine deposits by Bayley et al. (2006). Most of the evidence recorded in the literature of trace fossils produced by undermat miners is from endobenthic mats where wrinkle marks are not generated.

The trace fossils described in this paper occur on glossy surfaces (Fig. 2e) and corrugations. In the present case, a supratidal setting can be completely disregarded; the succession analysed is deeper than shoreface and lacks most of the MISS found in very shallow depositional settings (e.g., Noffke, 2009; Lan and Chen, 2012).

The evidence of microbial activity observed in the successions studied in this work is composed of two types: i) patchy (Fig. 4a, b; Pazos et al., 2015, fig. 2b) and extended wrinkle marks (Figs. 4c, 5c); and ii) very reflective, contrasting glossy surfaces (biofilms).

The trace fossils associated with patchy wrinkle marks in this study are scarce and mostly represented by *N. macleayii* (Fig. 5a). Interestingly, one very well preserved specimen of *N. missouriensis* (Fig. 5a, b) occurs on a bedding plane with well-developed wrinkle marks. However, in most cases this type of MISS remains unbioturbated (Figs. 4 c, d, 5c; Pazos et al., 2015, fig. 2b).

Scanning electron microscopy shows isolated sheaths and coccoidal forms (Fig. 5e, f), confirming the presence of microbial activity on wrinkle marked surfaces (Fig. 5c). Semi-quantitative EDS analyses reveal carbon as the main component indicative for organic substances together with Si, Al, K, Fe, Mg, and Ca, suggesting silicate mineral phases. Some features observed under SEM resemble clusters of rounded irregular grains (Fig. 5f) that could be interpreted as pyritised microbes (sensu Schieber, 2002). EDS analyses do not confirm the presence of sulfide minerals. The glossy surfaces contain structures produced by undermat grazers: simple structures assignable to *Helminthoidichnites* (Fig. 5d, e), gently curved to irregular forms that resemble *Gordia* (Fig. 5f). Loops, however, are not clear, and also very peculiar parallel epichnial ridges similar to *Caridolites* are present (Fig. 2e, arrow). These trace fossils are less than 2 mm wide and no more than 10 mm long. Some crosscut *N. macleayii* specimens which are preserved intergrading to *N. missouriensis* (Figs. 2e and 4a). The trace fossils assigned to *Caridolites* by Benton (1982a) were attributed to the juvenile producers of other trace fossils such as *Nereites* and *Dictyodora*.

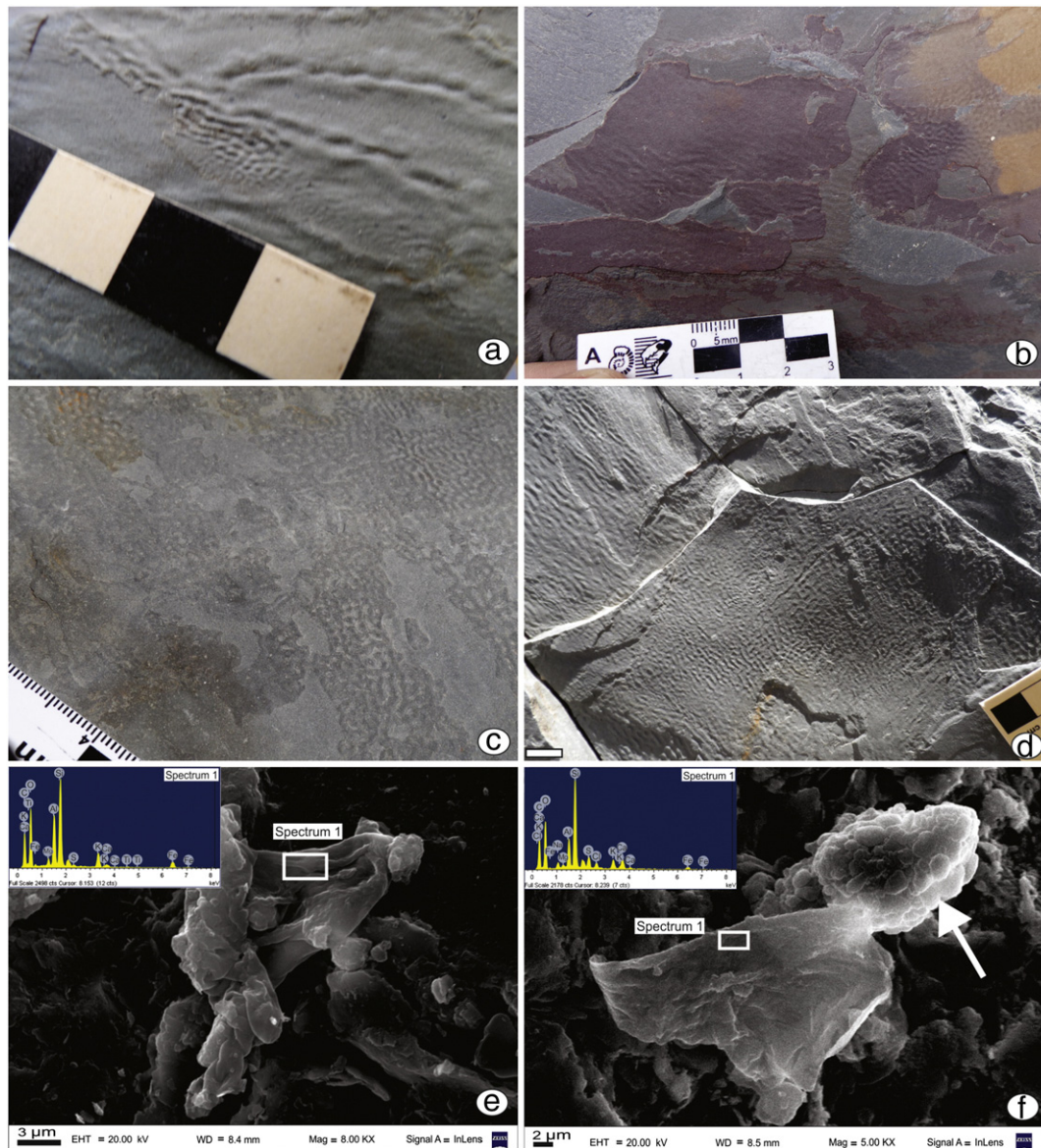


Fig. 4. Macroscopic and microscopic features of microbial mats: a) *Nereites missouriensis* and transition to *N. macleayii* (CPBA 21673) with wrinkle marks; b) patchy wrinkle-marked surface showing different morphologies of the structures; c) wrinkle-marked bedding plane where the sample was taken for SEM analysis (Fig. 5e, f); d) bedding plane with laterally extended microbial mats (wrinkle marks). Scale: black square is 1 cm; e) Rod-like organic bodies and EDX analysis; f) round to oval isolated coccoids (arrow) and EDX of the EPS.

6. Discussion

The *Nereites* ichnofacies from the Ordovician have been described from deep-sea fan systems in which microbial mats are scarce and the graphoglyptids are widespread (Buatois et al., 2009). However, there are some occurrences of the *Nereites* ichnofacies described from just below storm-dominated deposits (Uchman, 2007). However, in the Upper Ordovician–Early Silurian of Portugal, graphoglyptids, *Nereites*, *Dictyodora* and microbial mats with trace fossils of undermat miners are illustrated by Delgado (1910, pl. 8, fig. 6, pl. 12, fig. 3). In his figures, wrinkle structures and corrugated surfaces are documented. In some cases, like those shown in his plates 12a (figs. 1, 2), 20 (fig. 3) and 21 (fig. 2), there are trace fossils comparable with *Helminthoidichnites* and *Gordia*. Interestingly, Delgado (1910, pl. 10, fig. 4) documented a network resembling *Paleodictyon* (*Squamodictyon*) but showing the morphology of *Nereites*.

Undermat mines have been documented in Ordovician deposits of Norway in association with *Dictyodora* and *Nereites*. In particular, the record of *N. missouriensis* (*Neonereites* preservation) was observed in the

material figured by Uchman et al. (2005, fig. 17 a, c). Buatois et al. (2009, fig. 4c) documented *Helminthoidichnites* in the upper Tremadocian succession of northwestern Argentina, which is similar to the material here assigned to this ichnogenus. Benton (1982a) analysed the record of lower Palaeozoic trace fossils including the Silurian succession of Maine, where Emmons (1844) documented *Nereites* and *Gordia*. Interestingly, Benton (1982a, fig. 12) assigned all the records of *Dictyodora*, “*Neonereites*”, *N. pugnus* and *Caridolites* from a “*Nereites* subfacies” (sic; ichnosubfacies) which in his work was not related to turbidites. Benton (1982a) also included *Nereites* and *Gordia* in a pre-turbiditic “*Paleodictyon* ichnosubfacies.”

Irregardless of the ichnotaxonomic assignment of these trace fossils, undermat mining is present in the same stratum previously bioturbated by *Nereites*. In a few cases *Nereites* was observed either with wrinkle marks (Figs. 4a; 5a, b) or with glossy surfaces (Figs. 2e; 5d) and careful study of the surfaces shows that *Nereites* is crosscut by traces of undermat miners in slabs from locality 2. In the present work, the facies trend indicates that undermat mines are mainly present in the distal section (locality 2) with *N. macleayii* and transitions to *N. missouriensis*

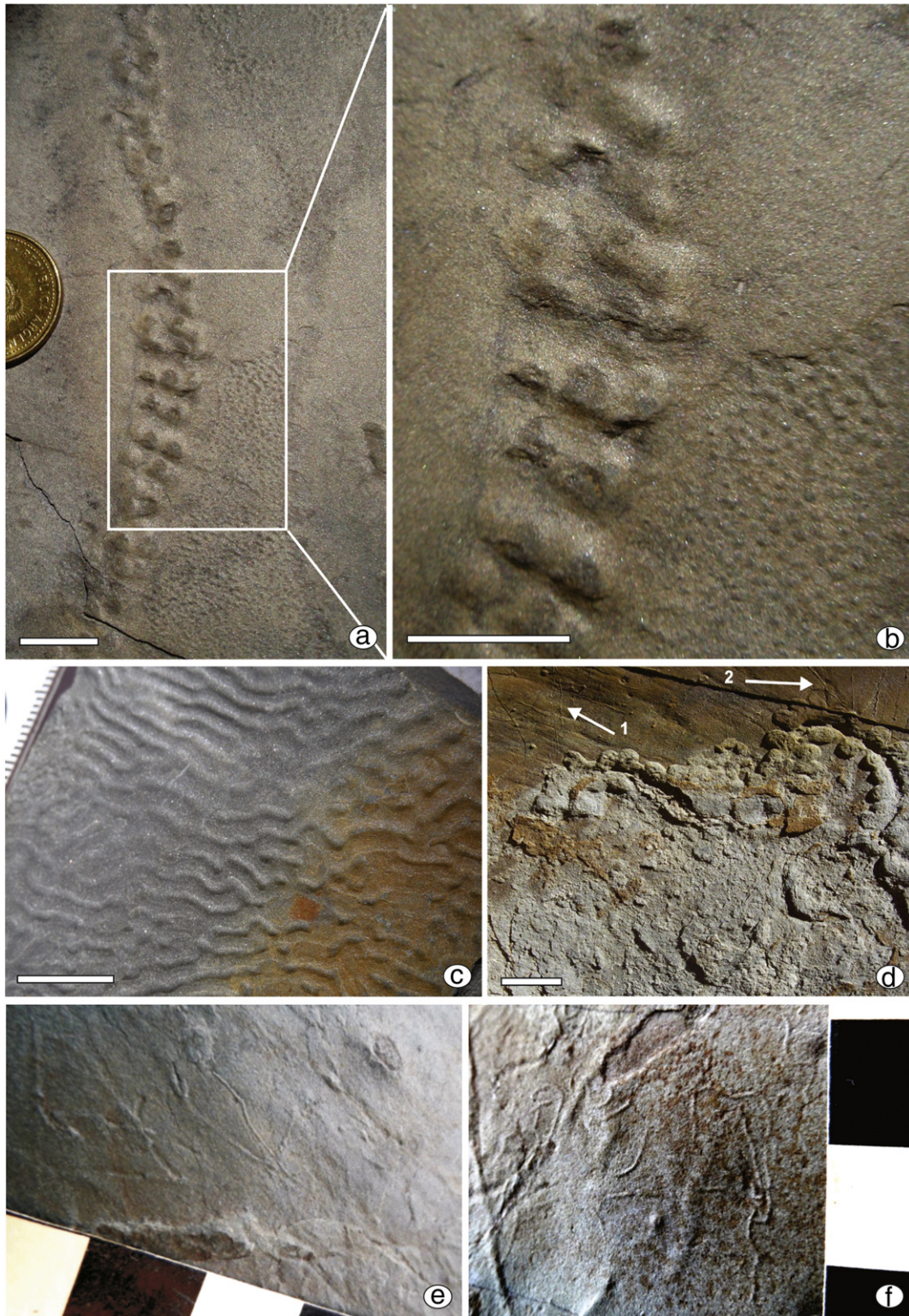


Fig. 5. *Nereites* and undermat-mining trace fossils: a) *Nereites missouriensis* preserved as convex epirelief. Note the surrounding bulge area denoting an envelope bigger than the pustules (CPBA 21661). Scale bar: 1 cm; b) details of panels showing the microbial mat and *Nereites* taphonomic relationship. Scale bar 1 cm; c) common wrinkle marks observed in the succession. Scale bar: 1 cm; d) *Nereites macleayii* with eroded median tunnel with size variations. Arrows 1 and 2 point out undermat mines. Note that the microbial mat is a glossy surface. Scale bar: 1 cm; e) *Helminthoidichnites* isp. (CPBA 21675); f) *Gordia* isp. (CPBA 21677). Fig. 5e and f are from the same slab; scale of each black box is 1 cm.

(= *Neonereites*) and *Diplichnites*? isp. In locality 1, *Nereites*, recorded in heterolithic deposits, is the pioneer trace fossil and is disrupted by *Dictyodora* (Pazos et al., 2015, fig. 5); wrinkle marks do not disrupt the specimen of *N. missouriensis* (Fig. 5 a, b). Conversely, with the exception of *N. missouriensis*, all the ichnospecies of *Nereites* are documented in

distal parts of the basin in the assumed facies trend proposed by Manassero et al. (2009). All the ichnospecies of *Dictyodora* are documented in locality 1, and the microbial mat structures (which are very conspicuous) post-date the bioturbation. In this depositional setting, undermat mines are nearly totally absent. Manassero et al. (2009)

mentioned for their basinward area, coincident with the locality 2, an ichnofauna assignable to the *Nereites*–*Mermia* ichnofacies, where *Nereites* and “other trace fossils” were recognised, but microbial mats were not mentioned. A possible explanation of such apparent disparity in the coexistence of the contrasting ichnofacies is the abundance of levels with *Nereites*, undermat mines and scarce arthropod trackways that somehow resemble the ichnofauna documented in the Puncoviscana Formation during the Cambrian (Buatois and Mángano, 2003). The ichnocoenosis studied in this paper shows more varied and complex feeding behaviours including deposit feeders (*Dictyodora*, *Nereites*, *Taenidium*); a cache style, or strip-mining (*Zoophycos*), undermat mining (*Gordia*, *Helminthoidichnites*), locomotion (*Diplichnites?*) and possibly grazing (*Caridolites*). The association of undermat mines and scarce arthropod trackways is also found in glacial to post-glacial transitions in the late Palaeozoic (Buatois and Mángano, 1995). The arthropod trackways were not originally included in the definition of the *Mermia* ichnofacies (Buatois and Mángano, 1995), but later suggested by Uchman et al. (2009). Similarly, arthropod trackways and traces by undermat miners were documented by Pazos (2002, fig. 3c), where the “irregular networks” are clearly modifying arthropod trackways. Other well-preserved records were documented by Pazos et al. (2007, fig. 3) in post-glacial sections containing *Cochlichnus*, *Gordia* and *Helminthoidichnites*.

The association of *Nereites* with *Dictyodora* and scarce, flat and large *Zoophycos* is uncommon and suggests the exploitation of shallow and deep tiers, while the absence of marine macrofaunal body fossils could be the result of muddy substrates, oxygen restrictions and high sedimentation rates. This suggests stressful palaeoenvironmental conditions.

7. Conclusions

The trace fossils documented from the late Silurian–earliest Devonian Río Seco de los Castaños Formation are dominated by: *Nereites* cf. *cambrensis*, *N. irregularis*, *N. jacksoni*, *N. macleayii*, *N. missouriensis*, *N. pugnus* and *Nereites* isp. Several ichnospecies of *Dictyodora* (*D. atuelica*, *D. scotica* and *D. tenuis*) studied in detail by Pazos et al. (2015) and *Taenidium* isp. and *Zoophycos* isp. have been documented. This likely constitutes the most diverse record of *Nereites* and *Dictyodora* in the mid Palaeozoic of western Gondwana.

N. macleayii is the most abundant ichnospecies and it is associated with microbial mats and we document frequent transitions between *N. macleayii* and *N. missouriensis* (*Neonereites* preservation).

Microbial mats are documented in two forms; i) wrinkle marks in patchy or extended surfaces, on top of fine-grained siltstones; and ii) glossy surfaces. They contain trace fossils related to the activity of undermat miners resembling *Gordia*, *Helminthoidichnites* and *Caridolites* and arthropod trackways tentatively assigned to *Diplichnites*. *N. missouriensis* is related to the microbial mats, with glossy surfaces or with wrinkle marks.

The presence of *Zoophycos* in the same stratigraphic interval with several ichnospecies of *Nereites* and *Dictyodora* and with abundant wrinkle marks is unusual. This trace fossil assemblage is in agreement with the interpretation suggested by Manassero et al. (2009), an environment dominated by gravity flows above the shelf edge rather than a submarine fan. However, a detailed facies analysis is necessary to further constrain the depositional setting.

This paper sheds light on late Silurian–earliest Devonian records of a trace fossil assemblage dominated by *Nereites* and *Dictyodora* and is a starting point for further discussions about the bathymetry of the *Nereites* ichnofacies and the role played by matgrounds during this time interval, which is poorly understood compared to those from the remainder of the Palaeozoic.

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