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Nereites in Lower Cretaceous marginal-marine facies from Patagonia: Ichnotaxonomic and ethological implications

Diana Elizabeth Fernández [a, b, *], Marcos Comerio [c], Pablo José Pazos [a, b]

[a] Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Geológicas, Intendente Güiraldes 2160, C1428EGA, Buenos Aires, Argentina
[b] CONICET – Universidad de Buenos Aires, Instituto de Estudios Andinos Don Pablo Groeber (IDEAN), Intendente Güiraldes 2160, C1428EGA, Buenos Aires, Argentina
[c] Centro de Tecnología de Recursos Minerales y Cerámica (CETMIC), Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), C.C. 49 – Camino Centenario y 506, Manuel B. Gonnet, B1897ZCA, Buenos Aires, Argentina

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ABSTRACT

Detailed descriptions of *Nereites* are uncommon. In this work, *Nereites* are thoroughly described from tidally influenced and wave dominated deposits in the Cretaceous of the Neuquén Basin (northern Patagonia). These *Nereites* show a great morphological variety in bedding-plane view. The application of different possible tracemakers for this renowned ichnogenus is discussed. Besides the well known morphology consisting of median tunnel surrounded by a halo composed of reworked material, a tripartite burrow structure has been observed that comprises in addition a disturbed, but not reworked zone at the external side of the reworking halo. The studied material provides evidence that the producers of these *Nereites* were shallow infaunal deposit-feeding organisms, a feeding strategy mentioned in many studies of the ichnogenus as matching a worm-like tracemaker, while the subsurface characteristics, particularly the disturbed outer zone, support a burrowing arthropod as tracemaker. Consequently, for interpretation of the potential trace producer, basic feeding strategy and burrow construction method should be differentiated and neither should be automatically linked with one particular tracemaker. The different morphologies of these *Nereites* allow referral of part of this material to *N. missouriensis*, but some cases of transitional forms remain problematic. The ratio between the width of the median tunnel and the enveloping zone (used as an ichnotaxobase) is not always due to variation in the burrowing depth of the producer. The same individual was able to produce wider or narrower enveloping areas in the same level along its course. In such cases, the use of this ichnotaxobase even at the ichnospecific level seems questionable.

1. Introduction

The ichnotaxonomic status of *Nereites* MacLeay, 1839 including its ichnospecies and relationships with other ichnogenera has been thoroughly discussed (e.g., Seilacher and Meischner, 1965; Chamberlain, 1971; Fillion and Pickerill, 1984; Rindsberg, 1994; Orr and Pickerill, 1995; Uchman, 1995; Mángano et al., 2000; Pazos et al., 2015). According to the diagnosis of Uchman (1995) slightly emended by Mángano et al. (2000) this ichnogenus includes diverse winding to meandering traces consisting of a median backfilled tunnel enveloped by an even to lobate zone.

Nereites is known from Cambrian to Holocene deposits and has been reported from different paleoenvironmental settings (e.g., Conkin and Conkin, 1968; Wetzel, 2002; Callow and McIlroy, 2011). In Patagonia *Nereites* are known from the Jurassic of the Neuquén Basin and the Lower Cretaceous basin plain deposits in the eastern Fuegian Andes (Olivero et al., 2009; Canale et al., 2013). In the Antarctic Peninsula *Nereites* was found in Lower Cretaceous deposits (Buatois et al., 2009; Olivero and López Cabrera, 2016). Cenozoic (mainly Eocene and Miocene) records in Patagonia are more common (e.g., Carmona et al., 2008, 2009; Le Roux et al., 2008; López Cabrera et al., 2008; Carmona and Ponce, 2011;

* Corresponding author. IDEAN-CONICET, Intendente Güiraldes 2160, Pabellón 2, Ciudad Universitaria, C1428EGA, Buenos Aires, Argentina.
E-mail addresses: elizabeth@gl.fcen.uba.ar, arkhamdryad@gmail.com (D.E. Fernández), marcoscomerio@gmail.com (M. Comerio), pazos@gl.fcen.uba.ar (P.J. Pazos).

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Pearson et al., 2013). In the South Shetland Islands, *Nereites* occurs in Miocene outer shelf to offshore settings (Uchman and Gaździcki, 2010). These southernmost South American and Antarctic records do not comprise a great morphological variability in bedding-plane view such as the ones presented in this work and do not include transitional forms.

Within the Neuquén basin, *Nereites* has been found in fluvial-dominated deltaic deposits of the Middle Jurassic Lajas Formation (Canale et al., 2013); those specimens have not yet been illustrated so, for the moment, no further comparison is possible with other specimens found in the same basin. The marine Mesozoic successions of the Neuquén Basin contain abundant trace fossils, mostly in normal marine settings (e.g., Spalletti et al., 2001a; Lazo et al., 2005; Ballent et al., 2006; Bressan and Palma, 2009; Kietzmann et al., 2010). Fewer studies referred to marginal-marine paleoenvironments (e.g., McIlroy et al., 2005; Schwarz et al., 2006; Rodríguez et al., 2007; Canale et al., 2015). While recent contributions have increased the ichnological information about Cretaceous marginal-marine successions in the basin, particularly in siliciclastic levels of the Agrio Formation (e.g., Fernández et al., 2010; Pazos and Fernández, 2010; Fernández and Pazos, 2012, 2013, 2015; Pazos et al., 2012), the record of trace fossils assignable to *Nereites* in the Cretaceous of the basin has not yet been described in detail.

Nereites is usually considered to be a locomotion/feeding (grazing) trace formed within the substrate by a worm-like organism (e.g., Seilacher, 1986). Based on neoichnological observations some studies have considered arthropods as possible producers of *Nereites*-like traces in the fossil record, and the question of the biological affinities of the tracemaker remains open (Martin and Rindsberg, 2007 and references therein).

The purpose of this work is fourfold: i) to present a more detailed examination of *Nereites* than researchers have generally provided; ii) to provide an examination of this ichnogenus in the Cretaceous of one of the most relevant basins in southernmost South America; iii) to analyse the processes when the shallow-marine host sediment accumulated; iv) to discuss ichnotaxonomic and ethological implications of these new findings with respect to the understanding of this ichnogenus.

2. Study area and geological setting

The Neuquén Basin (Fig. 1A) is located in west-central Argentina between 34° and 41°S. It contains more than 7000 m thick marine and continental deposits of Late Triassic to Paleogene age (Vergani et al., 1995; Legarreta and Uliana, 1999). Most of the Jurassic and Lower Cretaceous deposits are composed of diverse and highly fossiliferous marine facies associated with marine transgressions (Howell et al., 2005). During the Early Cretaceous, the Neuquén Basin was connected to the paleo-Pacific Ocean to the west by a gateway accentuated by a roughly N-S oriented island arc chain and the basin was affected by eustatic variations in sea level (Zapata and Folguera, 2005).

The Mulichinco Formation of the Mendoza Group (Weaver, 1931; Fig. 1B) comprises continental, transitional and marine deposits (Schwarz, 2002, 2003; Schwarz and Howell, 2005; Schwarz et al., 2006, 2011) of early Valanginian age (Aguirre-Urreta et al., 2005) exposed in Neuquén Province in the area between the Agrio River to the south and the southern portion of Mendoza Province to the north. The studied outcrops of interest here are located near National Road 40 (see Fig. 1A) at the localities known as Puerta Curaco (37° 22′ S, 69° 56′ W) and Vega de Escalone (37° 11′ S, 69° 47′ W). In the study area, the Mulichinco Formation is of marine origin and has been informally divided into lower, middle and upper members (Schwarz et al., 2011). Previous facies analyses indicate deposition in an open marine environment, including, amongst others, shoreface deposits with some tidal influence (Schwarz, 2003; Schwarz et al., 2006).

The Agrio Formation is the youngest unit of the Mendoza Group exposed in Neuquén Province (Weaver, 1931; Fig. 1B). The upper member, or Agua de la Mula Member (Leanza et al., 2001), of the Agrio Formation is late Hauterivian to early Barremian in age (Aguirre-Urreta et al., 2007, 2008, 2015; Aguirre-Urreta and Rawson, 2012). It comprises mixed carbonate-siliciclastic marine and marginal-marine deposits (Spalletti et al., 2001a; Lazo et al., 2005; Pazos and Fernández, 2010; Fernández and Pazos, 2012). The material presented here corresponding to this unit comes from the locality known as Bajada del Agrio (38° 25′ S, 70° 00′ W; Fig. 1A). The Agua de la Mula Member presents a remarkable cyclicity (e.g., Archuby and Fürsich, 2010) and four stratigraphic sequences (Guler et al., 2013). This marine setting was tidally influenced as suggested, for instance, by the presence of bipolar structures and reactivation surfaces and underwent variations in depth and exposure (see also Pazos et al., 2012; Fernández and Pazos, 2013).

3. Materials and methods

The logged sections included here (Sections A, B and C; Fig. 1B) are partial; they only comprise the intervals where the trace fossils of interest were found. In each case, a stratigraphical reference to previous works is made to permit future comparisons. Over 65 trace-fossil specimens were analysed. Samples are housed in the Collection of the Área de Paleontología (Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires) under the prefix CPBA. Morphological terms and names follow the discussions in Rindsberg (1994), Uchman (1995), Orr and Pickerill (1995) and Mángano et al. (2000). Measurements of the elements of different morphologies were performed at the bed surface. Relative burrowing depth was estimated using as reference the sand-mud interface, together with the height of some positive elements of the trace fossils, cross-sections of specimens and the cross-cutting relationships with associated trace fossils.

4. Sedimentology and environmental framework of the *Nereites*-bearing beds

4.1. Mulichinco Formation

Vega de Escalone: (Section A, Fig. 1B).

Observations. In this locality, *Nereites* is present in a sandstone bed with combined-flow ripples covered by massive mudstone, approximately 68 m above the contact with the underlying unit. These *Nereites* are associated with *Asteriacites lumbricalis* von Schlotheim, 1820 and *Gyrochorte comosa* Heer, 1865. This bed is located within the uppermost part of the "Lower Member" *sensu* Schwarz et al. (2011) within an interval that consists of coarsening-upward successions. Each one starts with up to 3 m thick massive amalgamated siltstone and grades upward to fine- to medium-grained 0.15–0.5 m thick sandstone beds exhibiting symmetrical and asymmetrical ripple lamination, combined-flow ripples (Fig. 2A), horizontal lamination and hummocky cross-stratification. Stoss-side mud drapes are present in some rippled levels.

Interpretation. Hummocky cross-stratification implies storm events. Mud drapes originated in a very shallow depositional setting when traction and suspension fallout of fine-grained sediments from unidirectional currents alternated (e.g., Kreisa and Moiola, 1986). The sandstone beds with wave and combined-flow ripples were deposited in shallow depths probably related to offshore sediment transport (Reineck and Singh, 1980; Myrow and Southard, 1991, 1996). In nearby localities the "Lower Member" was interpreted as shoreface deposits with some tidal influence (Schwarz, 2003; Schwarz et al.,

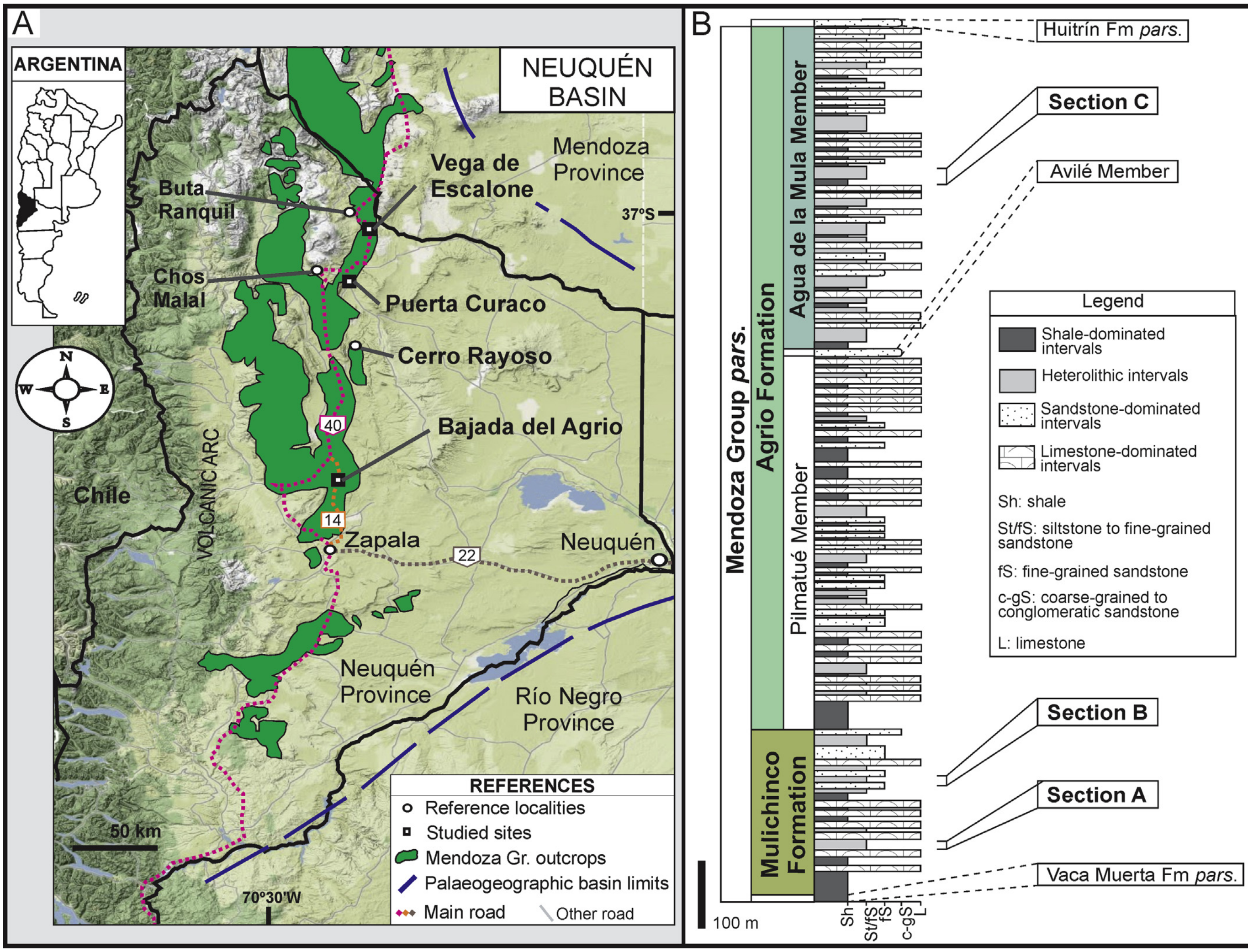

Fig. 1. Neuquén Basin and stratigraphic column of the Mendoza Group. A. Map of the Neuquén Basin and its location in Argentina. Note the location of the Mendoza Group outcrops and the study sites. B. Partial stratigraphic column of the Mendoza Group with location of the logged sections of relevance in this work. The material presented here comes from levels of the Mulichinco Formation and the Agua de la Mula Member (Agrio Formation). Sections A and B correspond to deposits of the Mulichinco Formation in Vega de Escalone and Puerta Curaco, respectively. Section A is the interval located approximately between 60 m and 75 m above the contact with the underlying Vaca Muerta Formation, while section B spans the interval from 177 m to 202 m above that contact. Section C consists of deposits of the Agua de la Mula Member (Agrio Formation) in Bajada del Agrio, being the interval approximately 247 m–271 m above the contact with the underlying Avilé Member (Agrio Formation).

2006). In Vega de Escalone section storm deposits decrease upward while wave-and-current shoreface deposits become more frequent. At the top of the "Lower Member" a subtidal to intertidal depositional setting is evidenced by tidal features such as opposite current directions (herringbone), mud drapes and downlap terminations (Rodríguez et al., 2007). Because of this context, plus the presence of mud drapes and absence of subaerial exposure, the section A is also interpreted as a subtidal setting.

Puerta Curaco: (Section B, Fig. 1B).
Observations. In this locality, *Nereites* is present in three beds: i) on top of cross-stratified sandstone approximately 180 m above the contact with the underlying Vaca Muerta Formation; ii) in sandstone beds with symmetrical ripple lamination within heterolithic intervals 191.5 m above the contact; and iii) on top of sandstone beds with small-scale hummocky cross-stratification associated with *Gyrochorte comosa* 201 m above the contact. In the first case, the *Nereites*-bearing surface is followed by a massive sandstone deposit, while in the others it is covered by structureless mudstones.

The interval of the Mulichinco Formation where these three levels are found (section B) partially coincides with the "Upper Member" of Schwarz et al. (2011). The lowest *Nereites*-bearing bed is found above a succession that starts with cross-stratified and massive sandstone up to 0.5 m thick, followed by 1 m of amalgamated, horizontally laminated mudstones. Stratigraphically upwards is a heterolithic succession where the two other *Nereites*-bearing beds are found. This is a thinning-upward succession dominated by heterolithic intervals mostly with symmetrical ripple lamination but also including hummocky cross-stratification (Fig. 2B) and inclined heterolithic stratification (1 m thick; Fig. 2C). Some tabular bioclastic conglomerates from 10 to 50 cm thick interrupt the mainly heterolithic deposits.

Interpretation. Cross-stratification is evidence of megaripple migration; symmetrical ripples are produced by oscillatory flows and indicate deposition above the fair-weather wave base. Hummocky cross-stratification and bioclastic conglomerates evidence storm events. It is more likely to find heterolithic structures in areas with alternating decantation and tractive processes and where there is sand and clay/silt input. Intertidal and subtidal areas exhibit these characteristics (e.g., Reineck, 1963; Reineck and Wunderlich, 1968). Inclined heterolithic stratification (IHS, Thomas et al., 1987) is a distinctive lateral accretion style of bars and is usually considered an

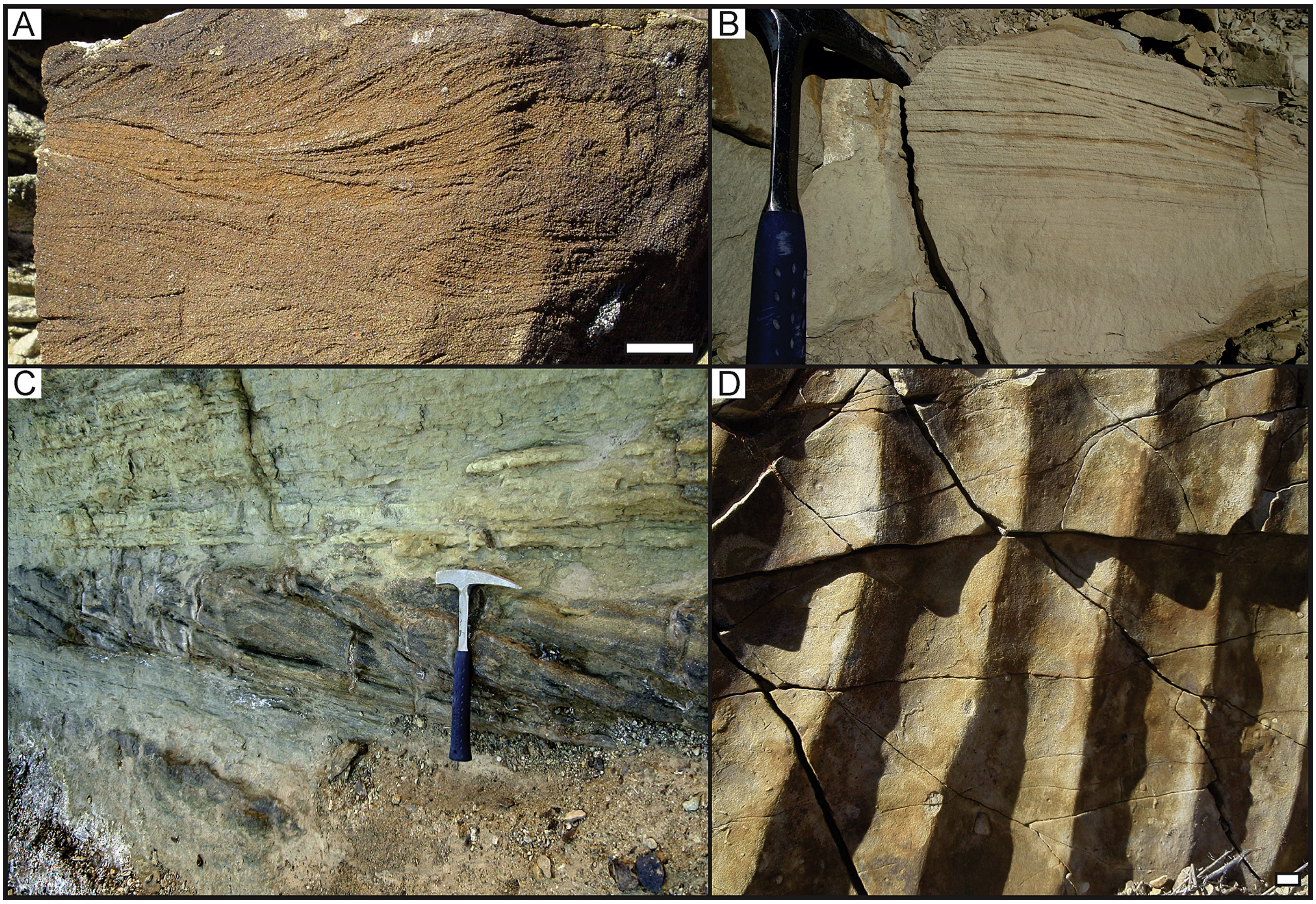

Fig. 2. Examples of sedimentary features of the intervals involved in this work. Rock pick = 33 cm long. Graphic scales = 1 cm. A. Combined-flow ripples, Mulichinco Formation. B. Hummocky cross-stratification, Mulichinco Formation. C. Inclined heterolithic stratification, Mulichinco Formation. D. Wave ripple lamination, Agua de la Mula Member (Agrio Formation).

important indicator of tidal influence in marginal-marine settings (e.g., Demowbray, 1983; Brownridge and Moslow, 1991). In this locality, the "Upper Member" of this unit has been previously interpreted as shoreface platform deposits (Schwarz, 2003; Schwarz et al., 2006). Regarding section B, we concur with the previous interpretations, but report a greater tidal influence.

4.2. Agua de la Mula Member (Agrio Formation)

Bajada del Agrio: (Section C, Fig. 1B).
Observations. Here *Nereites* is present in three beds at approximately 250 m, 256.5 m and 269 m above the contact with the underlying Avilé Member. The trace fossils occur on top of sandstone beds with symmetrical ripple lamination covered by massive or horizontally laminated mudstones (Fig. 1B). *Nereites* is found in association with *Gyrochorte comosa*, *Bolonia lata* Meunier, 1886 and *Chondrites* von Sternberg, 1833 or only with *G. comosa.*

Section C represents coarsening- and thickening-upward heterolithic deposits having up to 3 m thick amalgamated and horizontally laminated mudstones and continue with 4 cm to 0.3 m thick sandstone beds, mostly with symmetrical ripple lamination (Fig. 2D). Primary current lineation, interference ripples or shell debris are present in some levels.

In this locality the unit has been interpreted as an open marine ramp from offshore to subtidal subenvironments and with storm influence (Spalletti et al., 2001b; Lazo et al., 2005; Archuby, 2009). The uppermost levels of the Agua de la Mula Member were interpreted as deposited in an environment that evolved from marine to marginal-marine. Storm and fluvial deposits are present in a tidal-flat setting with evidence of meandering channels documented by IHS and salinity fluctuations (Fernández and Pazos, 2012). Section C is located within the uppermost part of sequence 2 of the sequence stratigraphic framework by Guler et al. (2013; HST 2 of Seq. 2). The general stacking pattern for this highstand systems tract is coarsening- and thickening-upward (shallowing). In the sandstone beds, lags of reworked concretions, valve stacking, massive or horizontal lamination, hummocky cross-stratification and current and wave ripples were all documented. The tops of most of these beds exhibit a diverse trace fossil assemblage belonging to the *Cruziana* ichnofacies (Guler et al., 2013).

Interpretation. Section C is interpreted as shoreface deposits, probably upper shoreface given the presence of primary current lineation indicating high-energy flow conditions.

5. Trace fossil description

5.1. General characteristics

The studied trace fossils occur as shallow endichnial, horizontal to subhorizontal, irregularly winding and only rarely meandering, unbranched structures (Figs. 3–6). An inner area formed by a

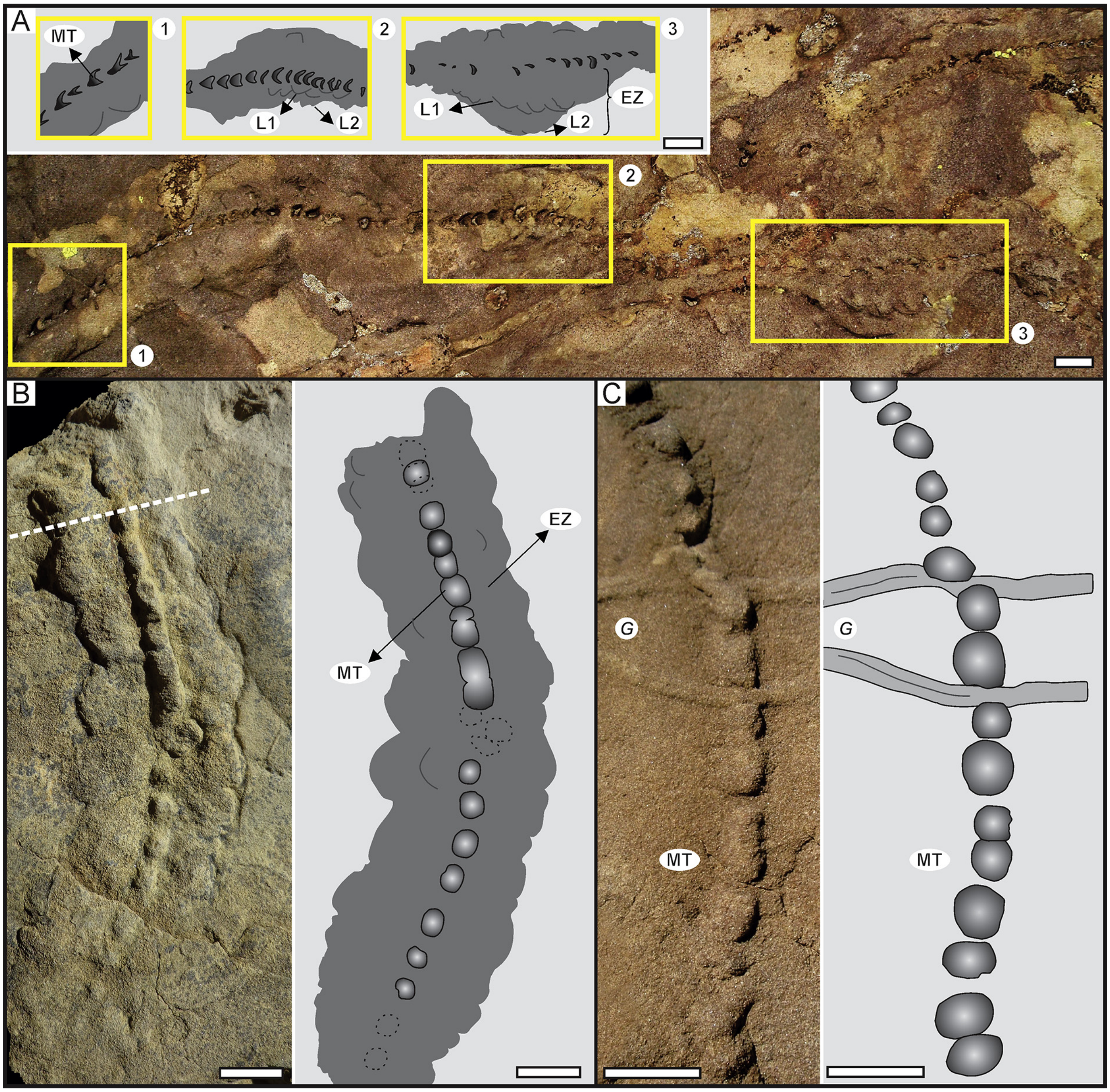

Fig. 3. Photographs and line drawings of examples of *Nereites* found in the studied intervals. The line drawings are included to enhance the features; the colours black, dark grey and light grey indicate negative, neutral and positive structures, respectively. The black dotted lines indicate poor preservation and/or undefined borders. MT = median tunnel. EZ = enveloping zone. Graphic scales = 1 cm. A. Field photograph of *Nereites* specimens where the proportions of the width of the median tunnel with respect to the reworked zone vary along the same specimen from those expected for *N. missouriensis* to those attributed to "other *Nereites*" (*sensu* Uchman, 1995; text-fig. 8). (1), (2) and (3) are line drawings of selected areas of the material (the structures within each rectangle). Note the morphology of the elements of the median tunnel and the two proximal and distal series of lobes. The proximal series (L1) is marked with grey lines; the distal series (L2) is the edge of the enveloping zone. B. CPBA 20457, photograph and line drawing of a specimen with a median tunnel of uniserial, dome-shaped bulges that are sometimes partially convergent and a lobate enveloping zone. The white dotted line indicates where the cross section of Fig. 6, in particular, was cut. C. Field photograph and line drawing of a specimen resembling *N. missouriensis* var. "pearl chain form" cross-cutting weathered *Gyrochorte* specimens (G).

median tunnel is present. In most specimens the tunnel is enveloped by an outer zone of disturbed or reworked sediment (e.g., Fig. 3A,B). The most common total diameter of the structures is 20–24 mm, but this can range between 6 (when only the median tunnel is present) and 44 mm. The maximum length measured is 40 cm. Most of each specimen is preserved as a positive epirelief, which is uncommon in many documented *Nereites*, but some of the tunnels are negative (see below) and the relief of the enveloping zone is sometimes nearly planar (e.g., Fig. 3A).

The tunnel is a shallow burrow which is either: i) uniform (smooth and continuous), ii) consisting of negative menisci or V-shaped and W-shaped elements, or iii) composed of small, uniserial, dome-shaped bulges. The diameter of the tunnel is between 6 and 12 mm, usually approximately 8 mm. Some specimens document the passage from negative elements to positive bulges as the width of the tunnel diminishes (e.g., Fig. 4C). When present, the enveloping outer zone may be lobate, with well-developed lobes with different degrees of incision between them, sometimes overlapping. Each side of the enveloping zone is usually 8–9 mm wide, but can be up to 16 mm.

The median tunnel enveloped by a reworked zone is diagnostic for *Nereites* (Uchman, 1995; Mángano et al., 2000). In some cases the widths of the tunnel and the outer enveloping zone are similar, allowing part of this material to be assigned to *Nereites missouriensis* following the latest emended diagnosis of this ichnospecies by Uchman (1995). According to the characteristics of the inner and

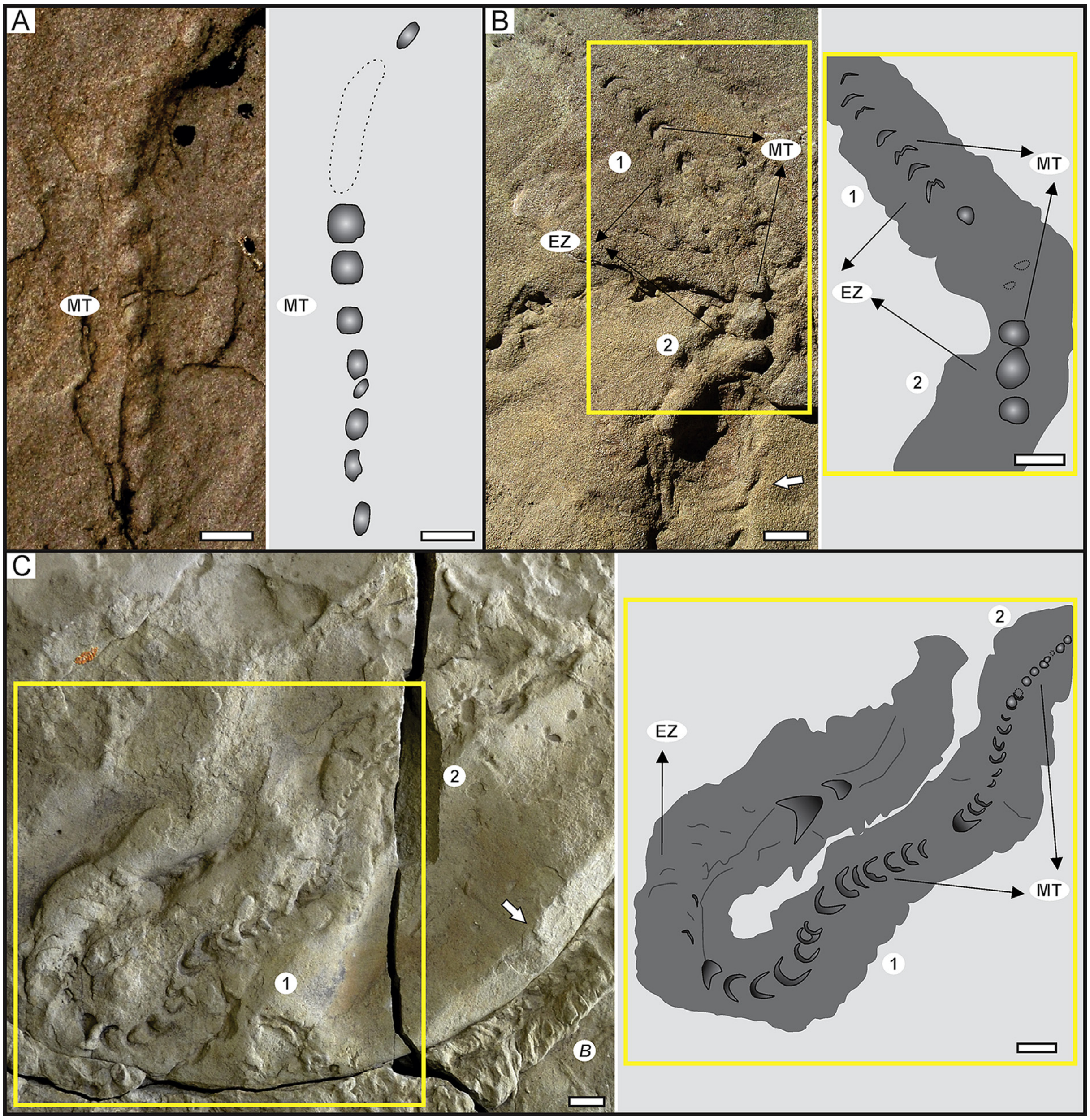

Fig. 4. *Nereites* photographs and line drawings of the structures within each rectangle. The line drawings are included to enhance the features and the colours black, dark grey and light grey indicate negative, neutral and positive structures, respectively. The dotted lines indicate poor preservation and/or undefined borders. In both 4B and 4C morphological transitions within the same specimen are observed: (1) marks the area where the tunnel is composed of negative elements and (2) where it is formed by bulges. MT = median tunnel. EZ = enveloping zone. Graphic scales = 1 cm. A. Field photograph and line drawing of a specimen resembling *N. missouriensis* var. "pearl chain form". B. Example (field photograph) of specimens where some median elements are lunate (menisci) and others are V-shaped and W-shaped. The white arrow points to an area where only the outline of the structure is observed, and poorly preserved, faint menisci appear to occupy the median most part of the enveloping zone. C. CPBA 20456, photograph and line drawing of a *Nereites* specimen that, as the one figured in 4B, presents variation in the median elements and resembles *N. missouriensis* var. "thick-meniscate form" (*sensu* Uchman, 1995) when the enveloping reworked zone is narrower. The white arrow marks a ripple crest and (B) points to an associated specimen of *Bolonia lata*.

outer areas, these structures display preservational variants (Uchman, 1995; Mángano et al., 2000), which are only mentioned as such in this work to facilitate comparisons with other material. Some morphological transitions along specimens are present and some emerging issues are discussed below in sections 5.2 and 6.1.

The relationships among the *Nereites* documented in this work, other ichnotaxa and sedimentary processes are summarized in Fig. 6, which are further discussed in section 6.2. *Nereites* are abundant (approximately 7–9 specimens per square metre) in sections B and C and are scarce in Section A. However, this could be biased by the difference in exposure between the three sections; widely exposed stratification planes that favour the observation of epichnial traces are present in sections B and C but not in A.

5.2. Different morphologies

Specimens such as those in Fig. 3A present a median tunnel and an enveloping reworked zone with well or poorly defined and sometimes overlapping lobes. The maximum observed length is approximately 60 cm. The tunnel is 2–4 mm wide. Most median elements are lunate (menisci) while others are V-shaped. The enveloping zone is complex; each side is variable in width from

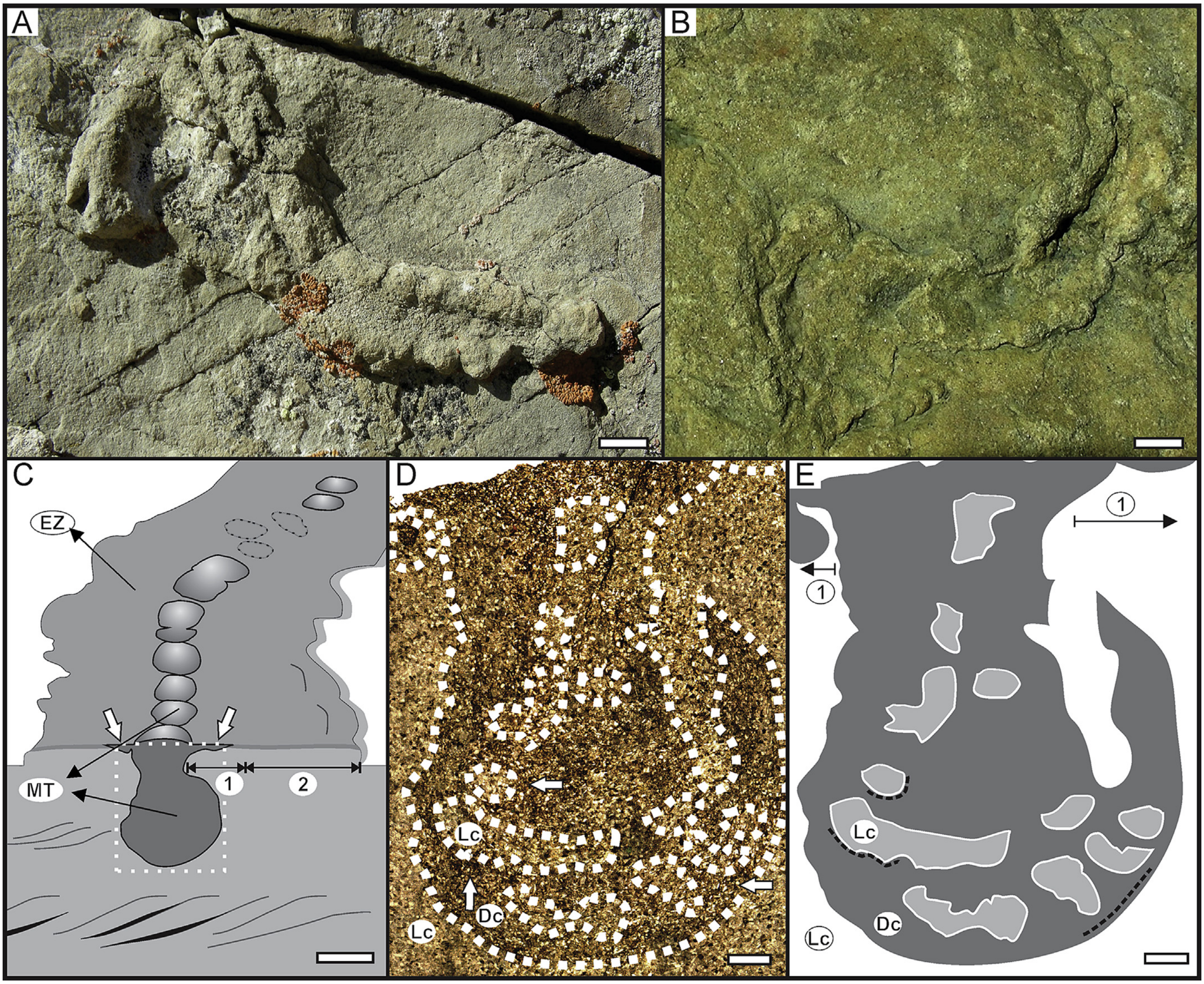

Fig. 5. Other specimens that present an enveloping zone composed of circular to ovate lobes and a poorly preserved median tunnel, and cross section of *Nereites*. MT = median tunnel. EZ = enveloping zone. 1 = inner third of the enveloping zone. 2 = outer two-thirds of the enveloping zone. Graphic scales = 1 cm in A and B, 5 mm in C, 1 mm in D and E. A. Field photograph of specimen with circular lobes in the enveloping zone and undefined median area. B. Field photograph of specimen with an enveloping zone composed of circular to ovate lobes or pads and poorly preserved median area. C. Schematic line drawing of cross section of *Nereites* (specimen of Fig. 3B). The white dotted rectangle shows the thin section area micro-photographed in D. Note the width of the median tunnel on the surface and in cross section. The white arrows point to the area rich in organic matter that extends below what corresponds to the immediate subsurface (uppermost 3 mm) of the inner third of the enveloping zone on each side of the tunnel. On the surface, the poorly delineated proximal series of lobes is marked with grey lines. Below the trace are unidirectional ripples with mud drapes. D. Thin section of the area enclosed in the rectangle in C. The white dotted lines separate dark-coloured (Dc) from light-coloured (Lc) areas. The first ones are rich in organic matter and clay minerals. The second ones are dominated by silt size quartz, bioclasts, lithoclasts and calcite spar cement; scarce peloids are also observed. The white arrows point to zones where reorientation of the grains is more noticeable. E. Schematic line drawing of D. The black dotted lines show some zones of strongly reoriented grains marked with white arrows in C.

4 mm up to 16 mm. The proportions of the width of the median tunnel with respect to the reworked zone sometimes vary along the same specimen from those expected for *N. missouriensis* to those attributed to "other *Nereites*" (*sensu* Uchman, 1995; text-fig. 8). In the first case, the material resembles *N. missouriensis* var. "thick-meniscate form" (*sensu* Uchman, 1995). In the latter case, the reworked outer zone is composed of proximal and distal "series" of lobes, similar to those figured in the line drawings of Orr and Pickerill (1995; fig. 8) for *Nereites jacksoni* Emmons, 1844, but the rest of the characteristics are not typical of this ichnospecies (e.g., the central furrow of *N. jacksoni*, Orr and Pickerill, 1995).

Some specimens exhibit a median tunnel of usually discrete, uniserial, dome-shaped bulges that are sometimes partially convergent (Fig. 3B). The tunnel is typically 6 mm wide. The enveloping zone is lobate and between 8 and 15 mm in width. The maximum observed length is 20 cm. The median tunnel resembles that of *N. missouriensis* var. "*phyllodocites*" (*sensu* Uchman, 1995, text-fig. 8A), but the width proportions of the median tunnel with respect to the enveloping zone vary along the same specimen. The outer reworked zone is usually wider than the tunnel and could be attributed to "other *Nereites*" (*sensu* Uchman, 1995, text-fig. 8C). The marginal areas in some parts show poorly delineated proximal and distal "series" of lobes described for *N. jacksoni* by Orr and Pickerill (1995; fig. 8), but as in the examples of Fig. 3A, the median tunnel characteristics differ from those expected for *N. jacksoni* (see Orr and Pickerill, 1995; Uchman, 1995).

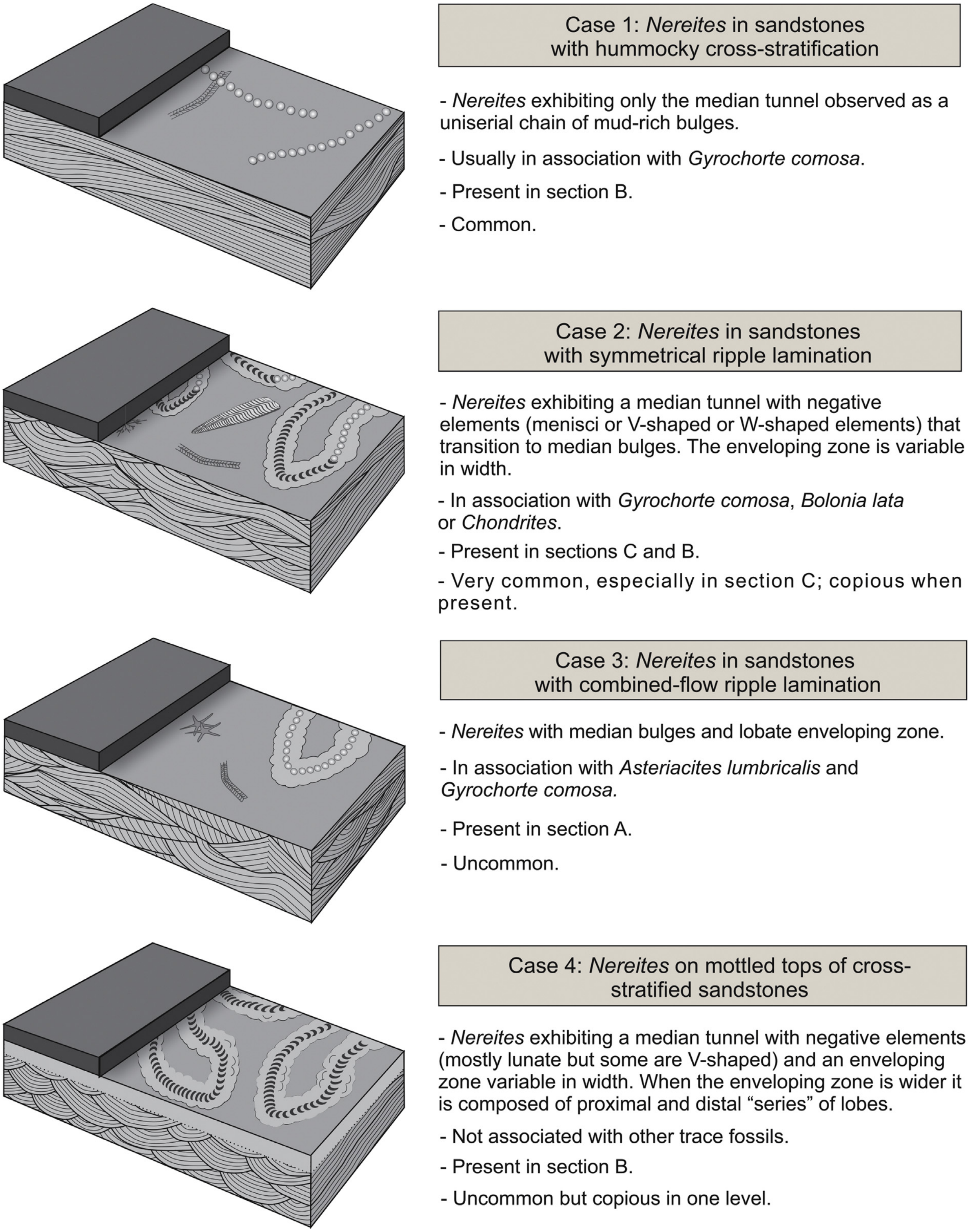

Fig. 6. Diagrams summarizing the relationship between *Nereites* documented in this work and sedimentary processes, with emphasis on the different morphologies and associated trace fossils. Some sedimentary structures were modified from Reineck and Singh (1980).

In other specimens only the median tunnel is observed as a uniserial chain of bulges usually 5 mm in width; they are most commonly not in contact with each other (Figs. 3C, 4A). The maximum observed length is 15 cm. The lack of a connecting string precludes an assignment to *Hormosiroidea* Schaffer, 1928. Given its epichnial to shallow endichnial preservation, it resembles *N. missouriensis* var. "pearl chain form" (*sensu* Uchman, 1995).

More complex specimens were also found (Fig. 4B,C). Firstly, in addition to being lunate (menisci) other median elements are V-shaped and W-shaped. Secondly, along the same specimen a meniscate tunnel (similar to those of Fig. 3A) transitions to a section where the tunnel is composed of bulges (such as that in Fig. 3B). Also the enveloping zone is complex; each side is variable in width. These structures could be *N. missouriensis* (*N. missouriensis* var. "thick-meniscate form" *sensu* Uchman, 1995) when the enveloping reworked zone is narrower. When the enveloping reworked zone is wider, it is similar to the one in *N. jacksoni*, but the tunnel characteristics do not match those typical of *N. jacksoni*.

A few other specimens present an enveloping zone composed of circular to ovate lobes and a poorly preserved median tunnel (e.g., Fig. 5A,B). While the shape of the lobes is similar to that of *Nereites macleayii* (Murchison, 1839) shown by Orr and Pickerill (1995, fig. 8), these specimens are not guided meanders as the typical *N. macleayii* (e.g. Orr and Pickerill, 1995, fig. 4D–F). The preservation of specimens such as the one in Fig. 5B is similar to the example referred to as *Nereites missouriensis* by Schlirf (2000, pl. 11 fig. 6). The specimens of Fig. 5A and B also resemble the epichnial structures pictured by Rindsberg and Martin (2003, figs 7.A,B) as "*Nereites biserialis*" and "*Arthrophycus* with *Nereites*-like morphology". Further discussion on the names used for similar structures can be found in Rindsberg and Martin (2003) and Uchman and Pervesler (2006).

In thin section, the median tunnel with bulges (cross-section, Fig. 5C–E) shows dark-coloured areas rich in organic matter and phyllosilicates, and light-coloured areas, dominated by terrigenous grains (e.g., quartz and feldspars), bioclasts and lithoclasts with calcite spar cement; scarce peloids are also observed (Fig. 5D,E). Particle size increases towards the base. Although these areas richer in organic matter are clearly definable, no indisputable faecal pellets were observed. The maximum width of the median tunnel in cross-section is twice the one observed on the surface of the sample (Fig. 5C). Thus, although the median tunnel on the surface is composed of bulges, internally it shows reorientation or reworking of the detrital grains (in both the light- and dark-coloured areas), which, particularly towards the base, form concave-up laminae. In the uppermost part of the cross section, organic matter extends below what corresponds to the immediate subsurface (the uppermost 3 mm) of the inner third (*1* in Fig. 5C,E) of the enveloping zone on each side of the tunnel. In the outer two-thirds (*2* in Fig. 5C) of the enveloping zone, the uppermost 1 mm is richer in pelitic material than the rest of the sandstone but is without organic matter. Below, the remaining subsurface area corresponding to the enveloping zone is light-coloured with calcite spar cement and some evidence of grain dissolution, but with no reorientation of the grains. This difference within the enveloping zone observed in cross-section (the inner third rich in organic matter extending from the median tunnel and the outer two-thirds without organic matter) is not noticeable on the surface of the trace. There the only sculpture are the poorly delineated "series" of lobes, which are close to the external border of the enveloping zone and do not coincide with the division observed in cross-section. Below the trace are unidirectional ripples with mud drapes (Fig. 5C).

6. Discussion

6.1. Ethology, substrate and names

The absence of relatively sophisticated patterns (e.g., tight meanders) in their grazing path is common for shallow marine representatives of *Nereites*, particularly in the Palaeozoic (Seilacher, 2007 and references therein). The different patterns found in continuity are not compound trace fossils because no change in behaviour is envisaged. In agreement with previous authors (e.g., Chamberlain, 1971; Uchman, 1995; Mángano et al., 2000; Uchman and Pervesler, 2006), the preserved variants of *N. missouriensis* probably originated as a result of different toponomic and taphonomic conditions. However, in this material, some morphological transitions along the same specimen are not attributable to those factors. In particular, the strong variation in the width of the enveloping zone (and the consequent change in the name) along the same specimen is found in both the rippled (e.g., Fig. 4C; cases 2–3 of Fig. 6) and the strongly mottled surfaces (e.g., Fig. 3A; case 4 of Fig. 6). The width of the enveloping zone varies independently of the characteristics of the median tunnel; these do not change significantly when the width of the enveloping area changes, similarly to what Pazos et al. (2015) reported for *N. jacksoni* (reworked lobes of variable width while the tunnel remained constant in width). Given the heterogeneity of sedimentary processes (e.g., Figs 3A (3), 4C, 6) and the good preservation of the outline of the enveloping zone, erosion and differential weathering are discarded as causes of this change in morphology. Additionally, along the same trace there is no variation in substrate properties which might affect preservation (Uchman and Pervesler, 2006). A significant change in the proportion of the enveloping zone with respect to the median tunnel is implicit in the emended diagnosis of *N. missouriensis* by Rindsberg (1994), but not in that of Uchman (1995). In summary, the change in width of the enveloping area is not always due to variation in the burrowing depth of the producer; neither is the proportion of the width of the median tunnel with respect to the enveloping zone. For this material, using the proportion of the width of the central tunnel to the enveloping zone as an ichnotaxobase at the ichnospecific level seems questionable.

However, the characteristics of the median tunnel seem to be affected by the level of exposure. The bearing levels were already covered by some mud when *Nereites* was produced (for details see section 6.2). The exact thickness of the mud layer at that time was not determined, so the burrowing depth is here related to the sand-mud interface (see section 3). There is a clear contrast between negative elements (menisci or V-shaped and W-shaped elements) and positive bulges (e.g., Fig. 4B). Specimens such as the one depicted in Fig. 4C clearly document the passage (left to right) in the median tunnel from negative elements (*1* in Fig. 4C) to positive bulges (2 in Fig. 4C) as the burrowing depth gradually changes and the width of the tunnel diminishes. The position of the bulges coincides with the concave side of the menisci and both even co-occur.

The concave-up laminae observed in cross-section appear to be the perpendicular expression of the menisci observed in other specimens. This is further evidence that the morphological expression of the median tunnel changes with the level of exposure. The increase in particle size towards the base of the structure indicates a grain-size selection. The characteristics of the uppermost sector of the cross-section provide evidence that the inner third of the enveloping zone and the area of the median tunnel were reworked first and thereafter material was deposited in the median tunnel. The rest of the subsurface enveloping zone presents no such connection with the activity of the median tunnel, indicating that it either remained untouched by the producer or that any evidence of direct reworking in that area was lost. In the first case, the outer two-thirds of the lobes could be pressure-release structures made by legs, instead of excavated cavities (Martin and Rindsberg, 2007), while fluidization of the sandy substrate resulting from water circulation/pumping cannot be ruled out. In the second case, some type of fabric alteration (e.g., a displacive spar cement stage) should have taken place, but there is only evidence of some partial dissolution of detrital grains, which by itself could not have destroyed evidence of reworking.

Nereites is usually considered a locomotion/feeding (grazing) trace formed within the substrate (e.g., Wetzel, 2002; Rindsberg, 2012). Chamberlain (1971, text-fig. 5.A–I) presented two possibilities about how this trace could be formed differing in how the mantle lobes are generated, but in his interpretation these were always actively filled. The previously proposed producers have been mainly ascribed to worm-like organisms (e.g., Seilacher, 1986), in which case the core would be composed of faecal pellets. Martin and Rindsberg (2007) found that juvenile *Limulus polyphemus* (Linnaeus, 1758), a modern xiphosurid, leave *Nereites*-like traces on tidal flats. These traces show that juvenile limulids were capable of making furrows, burrows and trackways along the same pathway, and transitions from epibenthic locomotion traces to shallow endobenthic burrows are observed (Martin and Rindsberg, 2007, p. 485–486). This, together with older studies (see Rindsberg and Martin, 2003 and references therein) led to the consideration of burrowing arthropods as possible producers of *Nereites* in the fossil record (Martin and Rindsberg, 2007; Neto de Carvalho and Baucon, 2010). When the bioprint ("characters that allow recognition of the maker", Rindsberg and Kopaska-Merkel, 2005) of burrowing arthropods is taken into account, some *Nereites* are again considered as possibly produced by arthropods (Rindsberg and Martin, 2010). The most common features associated with bioprint of arthropod burrows (Rindsberg and Martin, 2010) are not found in our material. However, if the trace fossils were produced in substrate having special properties (see, for instance, Uchman and Pervesler, 2006, cases B–D of fig. 7), such features might have had no chance to be preserved. Regardless, the median tunnel is a shallow burrow and sorting out and reorientation of the particles as well as and the concentric internal morphology (Fig. 5C–E) all point to a subsurface deposit-feeding strategy, which matches the previously mentioned classical interpretation for *Nereites*. However, the subsurface characteristics of the lobes contradict Chamberlain's (1971) interpretation about how these were constructed; as mentioned above, in his interpretation the lobes were actively filled but in this material the outer two-thirds of the lobes remained untouched by the burrower, but affected by its activity. Additionally, the morphology of the median tunnel indicates a downward- and forward-probing movement and some "concentric exploration of the sediment" as proposed by Mángano et al. (2000). In the case of *Nereites*, and in order not to discard an entire model, it would be appropriate to decouple interpretation of the basic feeding strategy from that of the construction method and the affinities of the producers. For instance, the studied material records that the producers of *Nereites* were shallow infaunal deposit-feeding organisms. The feeding strategy is mentioned in studies of this ichnogenus as matching a worm-like tracemaker, but the subsurface characteristics (particularly of the enveloping zone) support an interpretation of burrowing arthropod as tracemaker.

6.2. Sedimentation and surface colonization

Nereites is found in a mainly tidal setting, but is also associated with sedimentary structures such as symmetrical and combined-flow ripple lamination and cross stratification (Fig. 6). The *Nereites*-bearing beds exhibit a clear dominance of oscillatory flows (mainly wave action) as sedimentary processes, and fine-grained sandstones as a substrate. The sandstone beds are always covered by massive (or rarely horizontally laminated) mudstone, which reflect a decrease in energy. In most *Nereites*-bearing beds (cases 1 to 3, Fig. 6), burrowing was relatively shallow and the primary sedimentary structures are well preserved. This means the bioturbation itself was short-lived and restricted to the top of the level, probably associated with a pause in sedimentation. In case 4, however, *Nereites* are found on the mottled tops of cross-stratified sandstones. In this case, bioturbation occurred while sandy sedimentation continued and a significant part of the upper surface is mottled. The overlying bed is a fine-grained massive sandstone and mudstone appears above this sandstone. This interval is transitional to the overlying heterolithic deposits, while in cases 1 to 3, *Nereites*-bearing beds are found within heterolithic intervals.

The order of colonization is evidenced by the cross-cutting relationship between *Nereites* and *Gyrochorte* and between *Nereites* and *Bolonia*. In cases 1, 2 and 3, *Gyrochorte* makers appeared first, followed by the *Nereites* producers (e.g., Fig. 6). In case 2, the very edge of the enveloping zone of *Nereites* is at least sometimes cross-cut by *Bolonia* (e.g., Fig. 4C, bottom left), while in other cases the order cannot be determined. Also in case 2, the assemblage is later completed by the appearance of *Chondrites* entering from above through the overlying mud (the preservation of these *Chondrites* is similar to the case figured by Fernández and Pazos, 2015, fig. 4.c) and then spreading out mostly upon but also above and below the mud-sand interface. This type of succession matches that described by Wetzel and Uchman (2001) for deep marine event beds. In case 3, the *Asteriacites* specimens show no interaction with *Nereites* or *Gyrochorte*, so their order cannot be determined. In case 4, *Nereites* is the only trace fossil present.

In cases 1 to 3, given the ethological characteristics of the trace fossils involved, once the first thin layer of mud covered the sandy substrate, the order of colonization was probably controlled by the amount of organic matter and oxygen. When *Gyrochorte* makers appeared, the tops of the rippled sands were already covered by mud and these organisms fed on the freshly formed mud-sand interface. This is supported by their construction and ethological characteristics (Gibert and Benner, 2002) and also the good preservation of steep features (Seilacher, 2007). Organic matter must have still been abundant when *Nereites* was produced, given the feeding strategy of its producers. This is also supported by the areas rich in organic matter found in the cross-section of the median tunnel (Fig. 5D,E). The deposit-feeding *Nereites* makers fed near the sediment-water interface or after blooms on the sediment surface where the amount of organic matter is highest (Mángano and Buatois, 1999; Wetzel, 2010; Buatois and Mángano, 2011), and on still well-oxygenated interfaces, while the deeper-tier *Chondrites* makers appeared in this level after the sedimentation of the overlying mud layer was complete, probably under less oxygenated conditions (Seilacher, 2007).

7. Conclusions

In this work *Nereites* specimens are thoroughly described for the first time in the Cretaceous of the Neuquén Basin. They are epichnial/shallow-endichnial, horizontal to subhorizontal, mostly open-path structures. These specimens, observed in bedding-plane view, present a great morphological variety which, together with the shallow marine setting, make this a unique record for *Nereites*. The different morphologies of these *Nereites* allow a possible referral of part of this material to *N. missouriensis*, but some cases of morphological transitions within specimens remain problematic. Unlike some preservational variants of *N. missouriensis*, which (in agreement with previous authors) probably originated from toponomic and taphonomic conditions, the transitional forms are not attributable to such factors. The ratio between width of the median tunnel to that of the enveloping zone is not always due to variation in the burrowing depth of the producer; the same individual was able to produce wider or narrower enveloping areas in the same level along its course. The detailed analysis of the studied material suggests that the use of the ratio between width of the central tunnel to the enveloping zone as an ichnotaxobase even at the ichnospecific level seems questionable.

When *Nereites* is found in association with other trace fossils (*Gyrochorte*, *Bolonia*, *Chondrites*, *Asteriacites*), the order of colonization of the sediment was probably controlled by the amount of organic matter and oxygen availability because already a thin mud layer covered the sandy substrate. Organic matter was still abundant at the time *Nereites* was produced. The deposit-feeding *Nereites* makers fed near the sediment-water interface along relatively well-oxygenated surfaces. Within the studied intervals in the Mulichinco Formation, we mostly concur with previous interpretations, but found a stronger tidal signature in the Puerta Curaco section (B). Within a tidally influenced environmental context the *Nereites*-bearing beds show a dominance of oscillatory flow as a sedimentary process and fine-grained sand as a substrate.

Cross-sections indicate the producer reworked both the median tunnel, where digested material was deposited, and also the immediate subsurface of the inner third of the enveloping zone. The rest of the subsurface enveloping zone representing about 2/3 of it exhibits characteristics being suggestive to be interpreted as pressure-release structures. This domain was not touched by the burrower, but affected by its activity. This is consistent with a burrowing arthropod as producer, but no arthropod bioprints were found in our material possibly because of the sandy nature of the host sediment. Moreover, the subsurface characteristics of the lobes contradict Chamberlain's (1971) interpretation concerning how these were constructed, and the morphology of the median tunnel indicates a downward- and forward-probing movement. The exploration of the sediment points to a subsurface deposit-feeding strategy, which concurs with the classical interpretation for *Nereites*. This material shares similarities with both proposed tracemakers, but for the moment the producers of these *Nereites* can only be described as shallow infaunal deposit-feeding organisms whose affinities remain unknown. It is suggested that future discussions of the tracemakers should differentiate the basic feeding strategy from the construction methods and neither should be automatically linked with one particular tracemaker.

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References

Aguirre-Urreta, M.B., Rawson, P.F., 2012. Lower Cretaceous ammonites from the Neuquén Basin, Argentina: a new heteromorph fauna from the uppermost Agrio Formation. Cretaceous Research 35, 208–216. http://dx.doi.org/10.1016/j.cretres.2012.01.001.

Aguirre-Urreta, M.B., Rawson, P.F., Concheyro, G.A., Bown, P.R., Ottone, E.G., 2005. Lower Cretaceous (Berriasian-Aptian) biostratigraphy of the Neuquén Basin. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwarz, E. (Eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics. Geological Society of London, Special Publication 252, pp. 57–81. http://dx.doi.org/10.1144/GSL.SP.2005.252.01.04.

Aguirre-Urreta, M.B., Mourgues, F.A., Rawson, P.F., Bulot, L.G., Jaillard, E., 2007. The Lower Cretaceous Chañarcillo and Neuquén Andean basins: ammonoid biostratigraphy and correlations. Geological Journal 42, 143–173. http://dx.doi.org/10.1002/gj.1068.

Aguirre-Urreta, M.B., Pazos, P.J., Lazo, D.G., Fanning, C.M., Litvak, V.D., 2008. First U–Pb SHRIMP age of the Hauterivian stage, Neuquén Basin, Argentina. Journal of South American Earth Sciences 26, 91–99. http://dx.doi.org/10.1016/j.jsames.2008.01.001.

Aguirre-Urreta, M.B., Lescano, M., Schmitz, M.D., Tunik, M., Concheyro, A., Rawson, P.F., Ramos, V.A., 2015. Filling the gap: new precise Early Cretaceous radioisotopic ages from the Andes. Geological Magazine 152 (3), 91–99. http://dx.doi.org/10.1017/S001675681400082X.

Archuby, F., 2009. Taphonomy and Palaeoecology of Benthic Macroinvertebrates from the Agua de la Mula Member of the Agrio Formation, Neuquén Basin (Neuquén province, Argentina): sequence stratigraphic significance (Unpubl. PhD Thesis). Universität Würzburg, 349 pp.

Archuby, F., Fürsich, F., 2010. Facies analysis of a highly cyclic sedimentary unit: the late Hauterivian to early Barremian Agua de la Mula Member of the Agrio Formation, Neuquén basin, Argentina. Beringeria 4, 1–54.

Ballent, S., Concheyro, A., Sagasti, G., 2006. Bioestratigrafía y paleoambiente de la Formación Agrio (Cretácico Inferior), en la Provincia de Mendoza, Cuenca Neuquina, Argentina. Revista Geológica de Chile 33, 47–79. http://dx.doi.org/10.4067/S0716-02082006000100003.

Bressan, G.S., Palma, R.M., 2009. Trace fossils from the Lower–Middle Jurassic Bardas Blancas Formation, Neuquén Basin, Mendoza Province, Argentina. Acta Geologica Polonica 59, 201–220.

Brownridge, S.V., Moslow, T.F., 1991. Tidal estuary and marine facies of the Glauconitic Member, Drayton Valley, central Alberta. In: Smith, D.G., Reinson, G.E., Zaitlian, B.A., Rahmani, R.A. (Eds.), Clastic Tidal Sedimentology. Canadian Society of Petroleum Geologists, Memoir 16, pp. 107–122.

Buatois, L.A., Mángano, M.G., 2011. Ichnology: Organism-Substrate Interactions in Space and Time. Cambridge University, Cambridge.

Buatois, L.A., MacSotay, O., Quiroz, L.I., 2009. *Sinusichnus*, a trace fossil from Antarctica and Venezuela: expanding the dataset of crustacean burrows. Lethaia 42, 511–518. http://dx.doi.org/10.1111/j.1502-3931.2009.00156.x.

Callow, R.H.T., McIlroy, D., 2011. Ichnofabrics and ichnofabric-forming trace fossils in Phanerozoic turbidites. Bulletin of Canadian Petroleum Geology 59, 103–111. http://dx.doi.org/10.2113/gscpgbull.59.2.103.

Canale, N., Ponce, J.J., Bournod, C.N., Martinez, M.A., Carmona, N.B., 2013. Ondas de sedimento de grano fino generadas por Corrientes hiperpícnicas en deltas fluvio-dominados de la Formación Lajas (Jurásico Medio), cuenca Neuquina, Argentina. V Simposio Argentino Jurásico Libro de Resúmenes 15.

Canale, N., Ponce, J.J., Carmona, N.B., Drittanti, D.I., Olivera, D.E., Martínez, M.A., Bournod, C.N., 2015. Sedimentología e icnología de deltas fluvio-dominados afectados por descargas hiperpícnicas de la Formación Lajas (Jurásico Medio), Cuenca Neuquina, Argentina. Andean Geology 42, 114–138. http://dx.doi.org/10.5027/andgeoV42n1-a07.

Carmona, N.B., Ponce, J.J., 2011. Ichnology and sedimentology of Miocene hyperpycnites of the Austral foreland Basin (Tierra del Fuego, Argentina): trace fossil distribution and paleoecological implications. In: Slatt, R.M., Zavala, C. (Eds.), Sediment Transfer from Shelf to Deep Water – Revisiting the Delivery System. AAPG Studies in Geology, 61, pp. 171–192.

Carmona, N.B., Buatois, L.A., Mángano, M.G., Bromley, R.G., 2008. Ichnology of the lower Miocene Chenque Formation, Patagonia, Argentina: animal-substrate interactions and the Modern Evolutionary Fauna. Ameghiniana 45, 93–122.

Carmona, N.B., Buatois, L.A., Ponce, J.J., Mángano, M.G., 2009. Ichnology and sedimentology of a tide-influenced delta, lower Miocene Chenque Formation, Patagonia, Argentina: Trace-fossil distribution and response to environmental stresses. Palaeogeography, Palaeoclimatology, Palaeoecology 273, 75–86. http://dx.doi.org/10.1016/j.palaeo.2008.12.003.

Chamberlain, C.K., 1971. Morphology and ethology of trace fossils from the Ouachita Mountains, southeast Oklahoma. Journal of Paleontology 45, 212–246.

Conkin, J.E., Conkin, B.M., 1968. *Scalarituba missouriensis* and its stratigraphic distribution. Paleontological Contributions, University of Kansas, Paper 31.

Demowbray, T., 1983. The genesis of lateral accretion deposits in recent intertidal mudflat channels, Solway Firth, Scotland. Sedimentology 30, 425–435. http://dx.doi.org/10.1111/j.1365-3091.1983.tb00681.x.

Emmons, E., 1844. The Taconic System Based on Observations in New York, Massachusetts, Maine, Vermont and Rhode Island. Carroll and Cook Printers, Albany.

Fernández, D.E., Pazos, P.J., 2012. Ichnology of marginal marine facies of the Agrio Formation (Lower Cretaceous, Neuquén Basin, Argentina) in its type locality. Ameghiniana 49, 505–524.

Fernández, D.E., Pazos, P.J., 2013. Xiphosurid trackways in a Lower Cretaceous tidal flat in Patagonia: palaeoecological implications and the involvement of microbial mats in trace-fossil preservation. Palaeogeography, Palaeoclimatology, Palaeoecology 375, 16–29. http://dx.doi.org/10.1016/j.palaeo.2013.02.008.

Fernández, D.E., Pazos, P.J., 2015. Ichnological research in Lower Cretaceous marginal-marine facies from Patagonia: outcrop studies, SEM examinations and paleontological/sedimentological integration. Neues Jahrbuch für Geologie und Paläontologie 277/2, 177–188.

Fernández, D.E., Pazos, P.J., Aguirre-Urreta, M.B., 2010. *Protovirgularia dichotoma* – *Protovirgularia rugosa*: an example of a compound trace fossil from the Cretaceous (Agrio Formation) of the Neuquén Basin, Argentina. Ichnos 17, 40–47. http://dx.doi.org/10.1080/10420941003659436.

Fillion, D., Pickerill, R.K., 1984. Systematic ichnology of the Middle Ordovician Trenton Group, St. Lawrence Lowland, eastern Canada. Maritime Sediments and Atlantic Geology 20, 1–41.

Gibert, J.M. de, Benner, J.S., 2002. The trace fossil *Gyrochorte*: ethology and paleoecology. Revista Española de Paleontología 17, 1–12.
Guler, M.V., Lazo, D.G., Pazos, P.J., Borel, C.M., Ottone, E.G., Tyson, R.V., Cesaretti, N., Aguirre-Urreta, M.B., 2013. Palynofacies analysis and palynology of the Agua de la Mula Member (Agrio Formation) in a sequence stratigraphy framework, Lower Cretaceous, Neuquén Basin, Argentina. Cretaceous Research 41, 65–81.
Heer, O., 1865. Die Urwelt der Schweiz. Friedrich Schultze, Zürich.
Howell, J.A., Schwarz, E., Spalletti, L.A., Veiga, G.D., 2005. The Neuquén Basin: an overview. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwarz, E. (Eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics. Geological Society of London, Special Publications 252, pp. 1–14.
Kietzmann, D.A., Blau, J., Fernández, D.E., Palma, R.M., 2010. Crustacean microcoprolites from the Upper Jurassic–Lower Cretaceous of the Neuquén Basin, Argentina: systematics and biostratigraphic implications. Acta Palaeontologica Polonica 55, 277–284.
Kreisa, R.D., Moiola, R.J., 1986. Sigmoidal tidal bundles and other tide-generated sedimentary structures of the Curtis Formation, Utah. Geological Society of America Bulletin 97, 381–387.
Lazo, D.G., Cichowolski, M., Rodríguez, D.L., Aguirre-Urreta, M.B., 2005. Lithofacies, palaeoecology and palaeoenvironments of the Agrio Formation, Lower Cretaceous of the Neuquén Basin, Argentina. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwarz, E. (Eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics. Geological Society of London, Special Publication 252, pp. 295–315.
Leanza, H.A., Hugo, C.A., Repol, D., 2001. Hoja geológica 3969-I, Zapala, provincia del Neuquén. Instituto de Geología y Recursos Minerales. Boletín del Servicio Geológico Minero Argentino 275, 1–128.
Legarreta, L., Uliana, M.A., 1999. El Jurásico y Cretácico de la Cordillera Principal y la Cuenca Neuquina. I, Facies sedimentarias. In: Caminos, R. (Ed.), Geología Argentina. Segemar, Buenos Aires, pp. 399–416.
Le Roux, J.P., Nielsen, S.N., Henriquez, A., 2008. Depositional environment of *Stelloglyphus llicoensis* isp. nov.: a new radial trace fossil from the Neogene Ranquil Formation, south-central Chile. Revista Geológica de Chile 35, 307–319.
Linnaeus, C., 1758. Systema Naturae, vol. 1 ed. 10, Stockholm.
López Cabrera, M.I., Olivero, E.B., Carmona, N.B., Ponce, J.J., 2008. Cenozoic trace fossils of the *Cruziana, Zoophycos*, and *Nereites* ichnofacies from the Fuegian Andes, Argentina. Ameghiniana 45, 377–392.
MacLeay, W.S., 1839. Note on the Annelida. In: Murchison, R.I. (main author). The Silurian System, part II, Organic remains. Murray, London, 699–701.
Mángano, M.G., Buatois, L.A., 1999. Feeding adaptations. In: Singer, R. (Ed.), Encyclopedia of Paleontology, vol. 1. Fitzroy Dearborn Publishers, Chicago, pp. 458–465.
Mángano, M.G., Buatois, L.A., Maples, C.G., West, R.R., 2000. A new ichnospecies of *Nereites* from Carboniferous tidal-flat facies of eastern Kansas, USA: implications for the *Nereites-Neonereites* debate. Journal of Paleontology 74, 149–157.
Martin, A.J., Rindsberg, A.K., 2007. Arthropod tracemakers of *Nereites*? Neoichnological observations of juvenile limulids and their paleoichnological applications. In: Miller III, W. (Ed.), Trace Fossils, Concepts, Problems, Prospects. Elsevier, Amsterdam, pp. 478–491.
McIlroy, D., Flint, S., Howell, J.A., Timms, N., 2005. Sedimentology of the tide-dominated Jurassic Lajas Formation, Neuquén Basin, Argentina. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwarz, E. (Eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics. Geological Society of London, Special Publication 252, pp. 83–107.
Meunier, S., 1886. Sur quelques empreintes problématiques des couches boloniennes du Pas-de-Calais. Bulletin de la Société Géologique de France 3 (14), 564–568.
Murchison, R.I., 1839. The Silurian System. John Murray, London.
Myrow, P.M., Southard, J.B., 1991. Combined-flow model for vertical stratification sequences in shallow marine storm-deposited beds. Journal of Sedimentary Research 61, 202–210.
Myrow, P.M., Southard, J.B., 1996. Tempestite deposition. Journal of Sedimentary Research 66, 875–887.
Neto de Carvalho, C., Baucon, A., 2010. *Nereites* trails and other sand flat trace fossils from Portas de Almourão geomonument (Lower Ordovician, Naturtejo Geopark). e-Terra 17 (18), 1–4.
Olivero, E.B., López Cabrera, M.I., 2016. A footnote to Dolf Seilacher's study on Neonereites biserialis based on new evidence from the Upper Cretaceous of Antarctica. Ichnos 23, 25–32.
Olivero, E.B., Medina, F.A., López, M.I., 2009. The stratigraphy of Cretaceous mudstones in the Eastern Fuegian Andes: new data from body and trace fossils. Revista de la Asociación Geológica Argentina 64, 60–69.
Orr, P., Pickerill, R.K., 1995. Trace fossils from Early Silurian flysch of the Waterville Formation, Maine, U.S.A. Northeastern Geology and Environmental Sciences 17, 394–414.
Pazos, P.J., Fernández, D.E., 2010. Three-dimensionally integrated trace-fossils from shallow marine deposits in the Lower Cretaceous of the Neuquén Basin: *Hillichnus agrioensis* isp. nov. Acta Geologica Polonica 60, 105–118.
Pazos, P.J., Lazo, D.G., Tunik, M.A., Marsicano, C.A., Fernández, D.E., Aguirre-Urreta, M.B., 2012. Paleoenvironmental framework of dinosaur track-sites and other ichnofossils in Early Cretaceous mixed siliciclastic–carbonate deposits in the Neuquén Basin, northern Patagonia (Argentina). Gondwana Research 22, 1125–1140.
Pazos, P.J., Gutiérrez, C., Fernández, D.E., Heredia, A., Comerio, M., 2015. The unusual record of *Nereites*, wrinkle marks and undermat mining trace fossils in the late Silurian-earliest Devonian of central-western margin of Gondwana (Argentina). Palaeogeography, Palaeoclimatology, Palaeoecology 439, 27–37.
Pearson, N.J., Mángano, G., Buatois, L.A., Casadío, S., Raising, M.R., 2013. Environmental variability of Macaronichnus ichnofabrics in Eocene tidal-embayments deposits of Southern Patagonia, Argentina. Lethaia 46, 341–354.
Reineck, H.E., 1963. Sedimentgefüge im Bereich der südlichen Nordsee. *Abhandlungen* Senckenbergischen Naturforsche Gesellschaft 505, 1–138.
Reineck, H.E., Singh, I.B., 1980. Depositional Sedimentary Environments. Springer, Berlin.
Reineck, H.E., Wunderlich, F., 1968. Classification and origin of flaser and lenticular bedding. Sedimentology 11, 99–104.
Rindsberg, A.K., 1994. Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous formations. Geological Survey of Alabama, Bulletin 158, 1–107.
Rindsberg, A.K., 2012. Ichnotaxonomy: finding patterns in a welter of information. In: Knaust, D., Bromley, R.G. (Eds.), Trace Fossils as Indicators of Sedimentary Environments. Elsevier, Developments in Sedimentology, 64, pp. 45–78.
Rindsberg, A.K., Kopaska Merkel, D.C., 2005. *Treptichnus* and *Arenicolites* from the Steven C. Minkin Paleozoic footprint site (Langsettian, Alabama, USA). In: Buta, R.J., Rindsberg, A.K., Kopaska-Merkel, D.C. (Eds.), Pennsylvanian Footprints in the Black Warrior Basin of Alabama. Alabama Paleontological Society Monograph 1, pp. 121–141.
Rindsberg, A.K., Martin, A.J., 2003. *Arthrophycus* in the Silurian of Alabama (USA) and the problem of compound trace fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 192, 187–219.
Rindsberg, A.K., Martin, A.J., 2010. The bioprint of burrowing Paleozoic arthropods. Geological Society of America Abstracts with Programs 42 (1), 105.
Rodríguez, D.L., Pazos, P.J., Aguirre-Urreta, M.B., 2007. Cretaceous ophiuroid trace fossils from the Neuquén Basin. In: Bromley, R.G., Buatois, L.A., Mángano, M.G., Genise, J.F., Melchor, R.N. (Eds.), Ichnology at the Crossroads: A Multidimensional Approach to the Science of Organism-substrate Interactions. SEPM Special Publication 88, pp. 7–105.
Schaffer, F.X., 1928. *Hormosiroidea florentina* n.g., n.sp., ein Fucus aus der Kreide der Umgebung vom Florenz. Paläontologische Zeitschrift 10, 212–215.
Schlirf, M., 2000. Upper Jurassic trace fossils from the Boulonnais (northern France). Geologica et Palaeontologica 34, 145–213.
Schlotheim, E.F. von, 1820. Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreiches der Vorwelt erläutert. Becker, Gotha.
Schwarz, E., 2002. Estratigrafía, bioestratigrafía y secuencias de la Formación Mulichinco, Cuenca Neuquina, Argentina. ¿Nuevos enfoques? XV Congreso Geológico Argentino Actas I 806–811.
Schwarz, E., 2003. Análisis paleoambiental y estratigrafía secuencial de la Formación Mulichinco en el sector septentrional de la provincia del Neuquén, cuenca Neuquina, Argentina (Unpubl. PhD thesis). Universidad Nacional de La Plata, La Plata, 303 pp.
Schwarz, E., Howell, J.A., 2005. Sedimentary evolution and depositional architecture of a lowstand sequence set: the Lower Cretaceous Mulichinco Formation, Neuquén Basin, Argentina. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwarz, E. (Eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics. Geological Society of London, Special Publications 252, pp. 109–138.
Schwarz, E., Spalletti, L.A., Howell, J.A., 2006. Sedimentary response to a tectonically induced sea-level fall in a shallow back-arc basin: the Mulichinco Formation (Lower Cretaceous), Neuquén Basin, Argentina. Sedimentology 53, 55–81.
Schwarz, E., Spalletti, L.A., Veiga, G.D., 2011. La Formación Mulichinco (Cretácico temprano) en la cuenca Neuquina. XVIII Congreso Geológico Argentino Relatorio 131–144.
Seilacher, A., 1986. Evolution of behavior as expressed in marine trace fossils. In: Nitecki, M.H., Kitchell, J.A. (Eds.), Evolution of Animal Behavior. Oxford University Press, New York, pp. 67–87.
Seilacher, A., 2007. Trace Fossil Analysis. Springer-Verlag, Berlin Heidelberg.
Seilacher, A., Meischner, D., 1965. Fazies-Analyse im Palälozoikum des Oslo-Gebietes. Geologische Rundschau 54, 596–619.
Spalletti, L.A., Poiré, D.G., Schwarz, E., Veiga, G.D., 2001a. Sedimentologic and sequence stratigraphic model of a Neocomian marine carbonate-siliciclastic ramp: Neuquén basin, Argentina. Journal of South American Earth Sciences 14, 609–624.
Spalletti, L.A., Poiré, D., Pirrie, D., Matheos, S., Doyle, P., 2001b. Respuesta sedimentológica a cambios en el nivel de base en una secuencia mixta clástica-carbonática del Cretácico de la cuenca Neuquina, Argentina. Revista de la Sociedad Geológica de España 14, 57–74.
Sternberg, G.K. von, 1833. Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt, IV Heft. C.E. Brenck. Regensburg.
Thomas, R.G., Smith, D.G., Wood, J.M., Visser, J., Calverly-Range, E., Koster, E.H., 1987. Inclined heterolithic stratification: terminology, description, interpretation and significance. Sedimentary Geology 53, 123–179.
Uchman, A., 1995. Taxonomy and palaeoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). Beringeria 15, 3–115.
Uchman, A., Gaździcki, A., 2010. *Phymatoderma melvillensis* isp. nov. and other trace fossils from the Cape Melville Formation (lower Miocene) of King George Island, Antarctica. Polish Polar Research 31, 83–99.
Uchman, A., Pervesler, P., 2006. Surface Lebensspuren produced by amphipods and isopods (crustaceans) from the Isonzo Delta tidal flat, Italy. Palaios 21, 384–390.

Vergani, G.D., Tankard, A.J., Belotti, J., Welsink, H.J., 1995. Tectonic evolution and paleogeography of the Neuquén Basin, Argentina. In: Tankar, A.J., Suárez, R., Welsink, H.J. (Eds.), Petroleum Basins of South America. American Association of Petroleum Geologists, Memoir 62, pp. 383–402.
Weaver, C.E., 1931. Paleontology of the Jurassic and Cretaceous of west central Argentina. Memoir of the University of Washington 1 1–469.
Wetzel, A., 2002. Modern *Nereites* in the South China Sea – ecological association with redox conditions in the sediment. Palaios 17, 507–515.
Wetzel, A., 2010. Deep-sea ichnology: observations in modern sediments to interpret fossil counterparts. Acta Geologica Polonica 60, 125–138.
Wetzel, A., Uchman, A., 2001. Sequential colonization of muddy turbidites in the Eocene Beloveza Formation, Carpathians. Palaeogeography, Palaeoclimatology, Palaeoecology 168, 171–186.
Zapata, T., Folguera, A., 2005. Tectonic evolution of the Andean Fold and thrust belt of the southern Neuquén Basin, Argentina. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwarz, E. (Eds.), The Neuquén Basin, Argentina: A Case S tudy in Sequence Stratigraphy and Basin Dynamics. Geological Society of London, Special Publications 252, pp. 37–56.