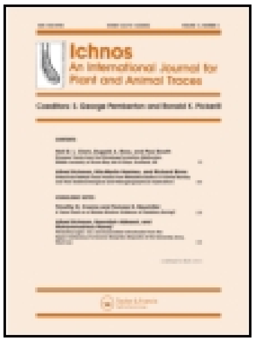

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A Footnote to Dolf Seilacher's Study on *Neonereites biserialis* Based on New Evidence from the Upper Cretaceous of Antarctica

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ABSTRACT
The irregular meandering, endichnial trace fossil *Nereites biserialis* characterized by alternating biserial row of dimples flanked by even to lobate laminae of sediment, best observed in weathered exposures of tidal sandy siltstones and silty sandstones, are extremely abundant in the outcrops at the base of the Maastrichtian López de Bertodano Formation in Antarctica. Polished sections, perpendicular to bedding, show that the dimples represent voids left by eroded terminal backfilled muddy globular fecal masses inside the central tunnel of the burrow and that the globular fecal masses are totally surrounded by a terminal-radial backfill of lobate, crescentic laminae of the enveloping zone. While uniserial to multiserial pustules of the external hyporelief are known in several ichnospecies of *Nereites*, the alternating biserial row of fecal masses inside the central tunnel is a diagnostic ichnospecific feature, accordingly *Nereites biserialis* (Seilacher) is considered a valid ichnospecies.

KEYWORDS
Nereites biserialis; Cretaceous; Antarctica; Ichnotaxonomy

Introduction

The ichnogenus *Nereites*, a name derived from the similarity with the body impression of the extant polychaete *Nereis*, is understood as representing the behavior of a worm-like animal that moved inside the sediment searching for food. While moving, the animal reworked and sorted the sediment extracting nutritious components adhering to fine-grained particles and, after digesting the nutritious components, eliminated the fecal residues inside the burrow (Seilacher, 1986, 2007). This particular behavior is documented in the trace fossil by two distinct architectural elements: an outer enveloping zone or halo reworked by the animal, where subsequently sorted-out material was stored, and an inner central tunnel, where the animal discarded the digested particles.

Neonereites was initially erected by Seilacher (1960) as a new ichnogenus with *N. biserialis* from the Jurassic of Germany as the type ichnospecies. In epirelief *Neonereites* forms an irregularly curved chain composed of deep, smooth dimples. The chains are restricted in length and can be flanked at either side by a reworked halo. Associated hyporeliefs occurs as indistinct rows of pustules having the width of the reworked halo. In their median part there are muddy globular fecal masses that correspond to the small dimples of the epirelief (Seilacher, 1960). Later on, Seilacher and Meischner (1965; see also Seilacher, 1986, 2007) considered *Neonereites* as a variant of *Nereites*, departing only from the general program of the latter by the architecture of the central tunnel, which is characterized by a single row (*N. uniserialis*) or by an alternating biserial row (*N. biserialis*) of bead-shaped fecal masses, which are normally preserved as dimples in epirelief preservation. Leaving aside the taxonomy of *N. uniserialis*, whose single string of bead-shaped fecal masses are in occasions difficult to distinguish from the scalariform menisci of the central tunnel of *N. missouriensis* (= *Scalarituba*), the double row of alternating beads in the central tunnel of *N. biserialis* seems to be highly diagnostic, as originally stated by Seilacher (1960).

However, different interpretations of the double row of dimples and/or the occasionally accompanying external pustules in *N. biserialis*, and other species of *Nereites*, have resulted in the so-called *Nereites-Neonereites* debate (cf. Mangano et al., 2000). The "debate" expresses three opposite views regarding the origin and position of the double row of dimples and of the double or multiple rows of external pustules.

First, in the original interpretation of Seilacher (1960), the double row of alternating dimples in epirelief preservation are the molds of muddy globular fecal masses that

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represent digested sediments filling the central tunnel of the structure, whereas associated hyporelief occurs as indistinct rows of external pustules having the width of the reworked enveloping zone.

Second, in the interpretation of Chamberlain (1971), the alternating row of dimples represents either the enveloping zone seen in epirelief, analogous to the alternating meniscate lobes in the *Phyllodocytes* preservation or the multiserial or biserial row of external pustules in the hyporelief.

Third, in the interpretation of Uchman (1995; see also Pickerill, 1991), the alternating pustules, ordered in biserial or multiple rows, represent the structure observed occasionally in the external part of the positive hyporelief of *Nereites*.

As a consequence, the type material of *Neonereites biserialis* has been considered either as a valid ichnospecies (Seilacher, 1960; D'Alessandro, 1980; Olivero and López-Cabrera, 2013) or as a junior synonym of *Nereites missouriensis* (Chamberlain, 1971; Uchman, 1995, and the bibliography cited therein).

In Upper Cretaceous tidal-influenced deposits of Antarctica, *Nereites* structures bearing a biserial row of dimples preserved in full relief are extremely abundant. The aim of this paper is to document and discus this new material that bear important evidence on the origin of the double rows of alternating muddy globular fecal masses in the central tunnel of *Nereites*.

Material and methods

The studied material includes hundreds of specimens preserved in full relief and observed in the field during several Antarctic research seasons to Snow Hill and Seymour islands by one of the authors (EBO). Selected samples of cemented slabs of fine-grained silty sandstones and sandy siltstones, most of them containing several specimens of *N. biserialis*, were collected and are currently deposited in the paleontological collections of the Centro Austral de Investigaciones Científicas (CADIC-CONICET), Ushuaia, Tierra del Fuego, under the numbers CADIC PI 311 to 317.

The collected material includes 40 samples: CADIC PI 311 and 311–1 are from the early Maastrichtian Haslum Crag Sandstone exposed in Snow Hill Island; CADIC PI 312, 314, 315, 316, 317 and 317–1 to 317–19 from the early Maastrichtian López de Bertodano Formation exposed in Snow Hill Island; and CADIC PI 313 and 313–1 from outcrops of the same Formation exposed in Seymour Island.

Selected samples were cut and polished to analyze the internal structure of the *N. biserialis* in detail. However, only those burrows preserved in silty very fine-grained sandstones and siltstones rendered some internal details on the polished surfaces. Trace fossils preserved in fine-grained, homogeneous clean sandstones generally do not show any internal detail on the polished surfaces because of the lack of grain-size differences.

Nereites biserialis from Antarctica

Location and depositional settings

The studied material of *Nereites biserialis* (Seilacher) was recorded in the upper part of the Santonian-Danian Marambio Group cropping out on NE Snow Hill Island and SW Seymour Island, located to the NE of the Antarctic Peninsula (Fig. 1). The Marambio Group includes three depositional sequences (Olivero, 2012), of which only the uppermost part of the NG Sequence (Haslum Crag Sandstone) and the lowermost part of the MG Sequence (basal López de Bertodano Formation) bear *N. biserialis* (Fig. 1). A few specimens of *N. biserialis* were observed in the early Maastrichtian sandy siltstones and very fine-grained silty sandstones of the Haslum Crag Sandstone, on the contrary *N. missouriensis* can be very abundant in certain horizons of this Sandstone (Fig. 2A). Conversely, *N. biserialis* is extremely abundant in the overlying basal part of the López de Bertodano Formation (Fig. 2B).

The Haslum Crag Sandstone is interpreted as forced regressive, cross-bedded tidal deposits, which records the incision, migration, and filling of relatively large and deep subtidal channels (Olivero et al., 2008).The upper, fine-grained part of the channel fill is generally strongly bioturbated. The most conspicuous trace fossils are *N. missouriensis* (Fig. 2A), *Patagonichnus stratiformis, Schaubcylindrichnus coronus, Ophiomorpha nodosa, Teichichnus rectus*, and *Rhizocorallium* isp. *Nereites biserialis* is occasionally observed, whereas *Euflabella* isp. is rare (Olivero and López-Cabrera, 2013).

The López de Bertodano Formation is interpreted as a transgressive system, which includes at its base shallow marine and estuarine mudstones and sandstones, transitionally covered by transgressive, glauconite-rich sandstones and mudstones (Olivero et al., 2008; Olivero, 2012). The basal shallow marine and estuarine tidal-channel deposits rest on a high-relief unconformity deeply incised into the Haslum Crag Sandstone (Pirrie et al., 1997; Olivero et al., 2008). Trace fossil abundance and composition of the trace fossil association are highly variable in these deposits, with ichnofossils being more abundant and diverse toward the axial, subtidal portion of the estuary (Olivero et al., 2008). These deposits include large subtidal channels filled with thin alternation of mudstone and muddy very fine-grained

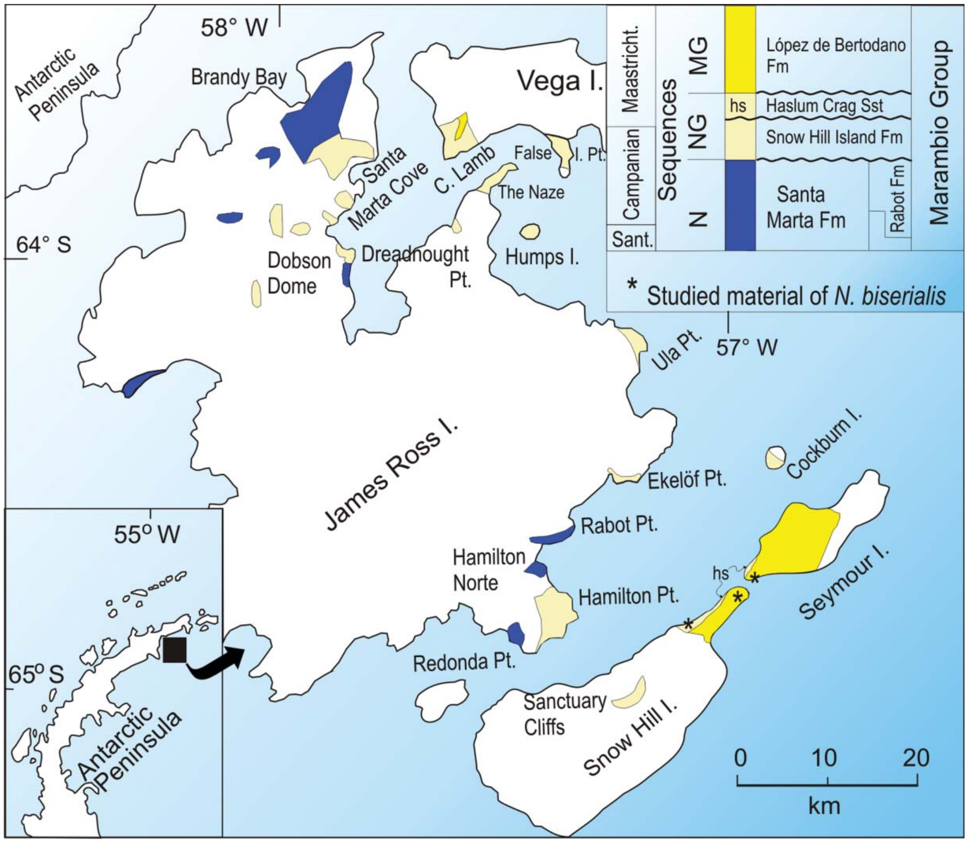

Figure 1. Location and geological map of the Upper Cretaceous Marambio Group in the James Ross Archipelago. The asterisks indicate the provenance of the studied material of *Nereites biserialis* in Snow Hill and Seymour islands. The geographic coordinates of the most prolific horizons with *N. biserialis* in the López de Bertodano Formation are: Snow Hill Island 64° 22′14.6″S; 56° 57′12.3″;W; Seymour Island 64°19′18.42″S; 56°52′3.18″W.

sandstones. Dominant trace fossils are *Nereites biserialis* (Figs. 2B–D, 3, and 4)—abundant at certain levels (Fig. 2B) where it is rarely found in association with *N. missouriensis* (Fig. 2C), *Phycosiphon incertum, Schaubcylindrichnus coronus, Thalassinoides suevicus* and *Euflabella radiata* (Olivero and López-Cabrera, 2013).

Description

In the most common type of preservation, generally on the exposed weathered surface of siltstones and silty very fine-grained sandstones, the trace fossil consists of a alternating biserial row of dimples flanked on both sides by a diffuse, even to lobate halo, defining an enveloping zone of reworked sediments (Figs. 2B–D, 3, and 4A, E). The width of the whole structure (enveloping zone plus biserial row) ranges between 2 and 3.7 cm, of which 1–1.4 cm corresponds to the width of the biserial row of dimples. The diameter of individual dimples varies between 0.5 and 0.8 cm. The whole structure is up to 20–25 cm long and forms irregular and open meanders, which are oriented parallel or slightly oblique to the bedding plane. Along the curve of tight meanders some specimens bear only uniserial dimples for a short distance. In these cases the size of the uniserial dimples are up to nearly two times larger than the usual biserial dimples (Fig. 2D).

On weathered surfaces, the dimples represent voids separated by asymmetric elevated ridges having a steep concave margin on one side and a gently inclined, truncated and deformed one on the opposite side (Figs. 2D and 3C). The material originally filling the voids is generally not preserved but in occasions a thin film of mud having a color differing from the rest of the structure, is observed at the bottom (Figs. 2C, 4A) and patches of mud are occasionally preserved within the dimples of *N. biserialis* (Figs. 3A, B). The corresponding halo of reworked sediments forms a slightly elevate enveloping zone flanking the double row of dimples. The internal structure of the enveloping zone consists of diffuse and dense, even to lobate laminae, which are hardly visible on most weathered surfaces except for some relatively well preserved specimens (e.g. Fig. 3A–B).

N. biserialis is commonly preserved in dense aggregation of closely spaced specimens characterizing a very distinctive ichnofabrics (Figs. 2B, 2D, 4). In well-preserved specimens, polished surfaces cut normal to bedding show

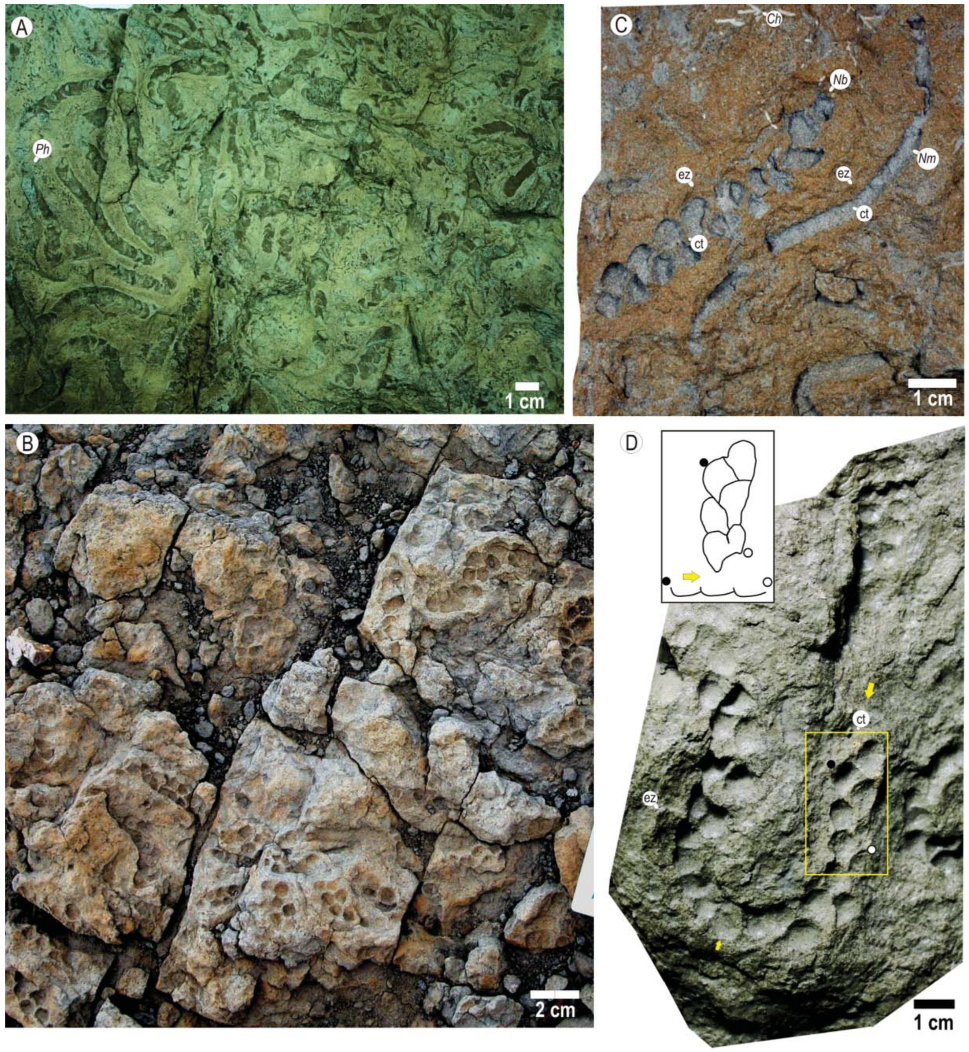

Figure 2. *Nereites missouriensis* (Weller) and *N. biserialis* (Seilacher) in upper bedding plane view, Upper Cretaceous, Antarctica. **A**. Dense aggregation of *N. missouriensis*. Note *Phycosiphon* (*Ph*) producers having reworked the enveloping zone of *N. missouriensis*, Haslum Crag Sandstone, Snow Hill Island, CADIC PI 311. **B**. Dense aggregation of *N. biserialis*, López de Bertodano Formation, Snow Hill Island, field photograph. **C**. Rare association of *N. biserialis* (*Nb*) and *N. missouriensis* (*Nm*) reworked by *Chondrites* (*Ch*) producers. Note the diffuse lobate laminae of the enveloping zone (ez) and the darker central tunnel (ct) covered with a film of mud in both ichnospecies of *Nereites*. López de Bertodano Formation, Snow Hill Island, CADIC PI 312. **D**. Three specimens of *N. biserialis*; the largest one shows a short transition to uniserial and larger dimples (small arrow) in the central tunnel (ct); the asymmetry and concavity of the ridges in biserial dimples indicates the movement of the producer (large arrow), the enveloping zone (ez) is indicated by diffuse laminae. The rectangle indicates the location of the sketch and corresponding cross—section shown in the upper left; the direction of movement of the producer is indicated by the asymmetry of the margins of the dimples. López de Bertodano Formation, Seymour Island, CADIC PI 313.

the details of this distinctive ichnofabrics (Fig. 4). Transversal sections of the trace fossil depict an oval central tunnel filled with mud and an enveloping zone of disturbed sediments completely surrounding the central tunnel. The finer material of the central tunnel appears to be structureless. Patches of very diffuse short laminae were observed in some cases, but it is unclear if this is part of the original structure of the trace fossil. On the contrary, the coarser material of the enveloping zone is characterized by crescentic, irregular and distorted laminae disposed all around the central tunnel (Figs. 4C, D). Similar elemental components are also seen in longitudinal sections, where the central tunnel is denoted by a longitudinal string of mud with irregular margins, partly preserving the intervening elevated ridge of coarser material between muddy globular fecal masses, and the enveloping zone is defined by an elongate area with crescentic laminae of coarser sediments (Figs. 4B, D, F).

Interpretation

In the most common preservation, the dimples and the flanking halo of reworked sediment observed on the upper surface of silty and sandy beds are interpreted as

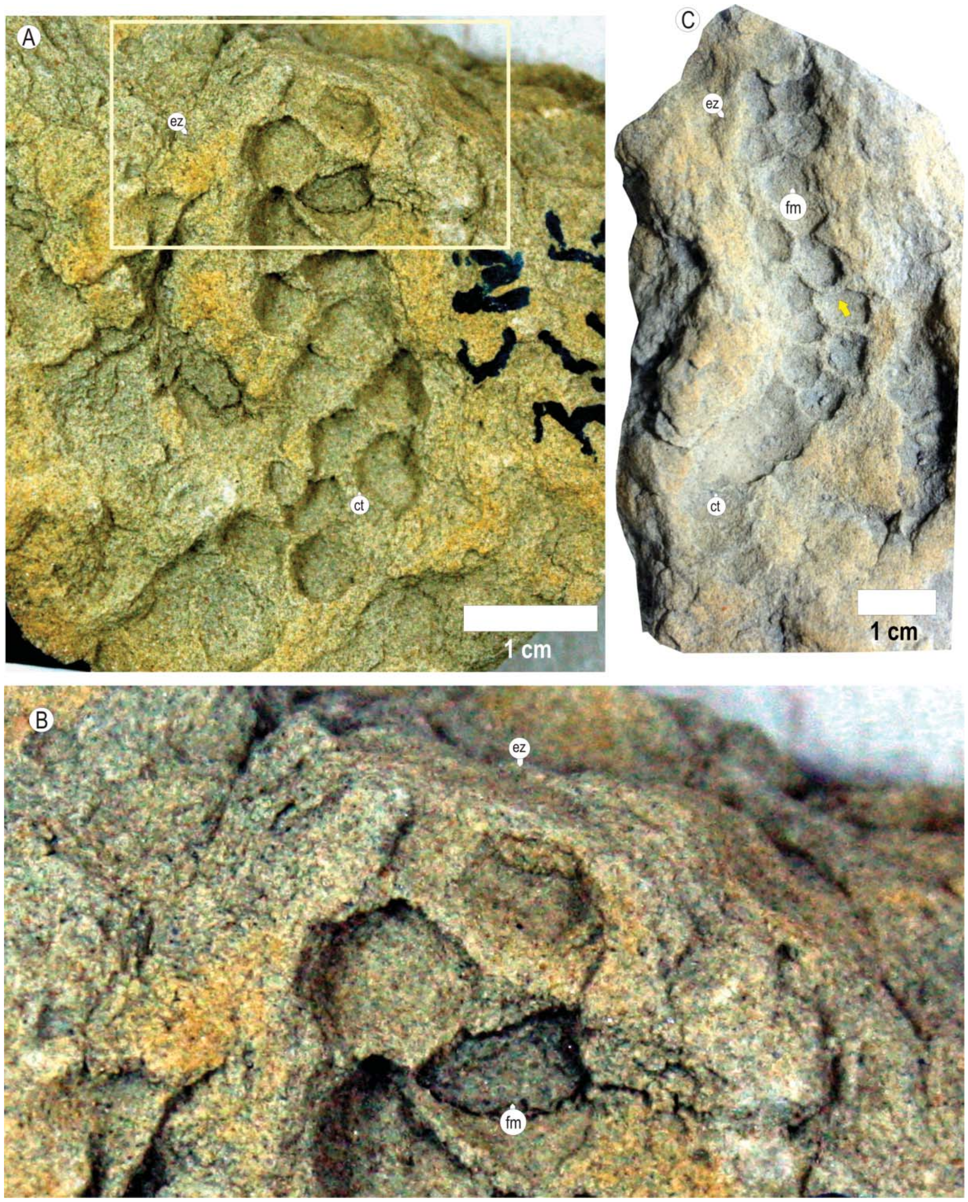

Figure 3. *N. biserialis* (Seilacher) in upper bedding plane view, Upper Cretaceous, López de Bertodano Formation, Snow Hill Island, Antarctica. **A**, **B**. Well preserved specimen with even to lobate laminae in the enveloping zone (ez) and dimples of the central tunnel (ct) preserving part of the original muddy fecal mass (fm). Rectangle in (A) indicates the location of close-up in (B), CADIC PI 314. **C**. Specimen with slightly elevated enveloping zone (ez) flanking a depressed central tunnel (ct) with dimples preserving part of the muddy fecal masses (fm). Note the asymmetry of the pushing ridges indicating the movement direction of the trace maker (arrow), CADIC PI 315.

representing the central tunnel and the enveloping zone, respectively. The dimples represent the void left after erosion of the terminal backfilled muddy fecal masses stuffed inside the central tunnel of the burrow. This is evident by the preservation of relict mud films (Fig. 2C) or patches of mud (Fig. 3) within the dimples. In the rare case of joint preservation of *N. missouriensis* and *N. biserialis*, both ichnospecies preserve the same muddy film of similar color along the central tunnel (Fig. 2C), strengthening the argument that the alternating dimples of *N. biserialis* are part of the central tunnel. Moreover, polished sections of the trace preserved in full relief leave no doubts that the central tunnel of *N. biserialis* is composed of a biserial row of muddy globular fecal masses completely surrounded by distorted, crescentic laminae of the enveloping zone (Figs. 4B, D). Both, transverse and longitudinal sections of *N. biserialis* show oval-shaped, generally compressed during diagenesis, bipartite muddy fecal masses separated by a low ridge composed of coarser sediment (Figs. 4C, D).

Even though the laminae of the enveloping zone exhibit a complex pattern and are only partly preserved, they always

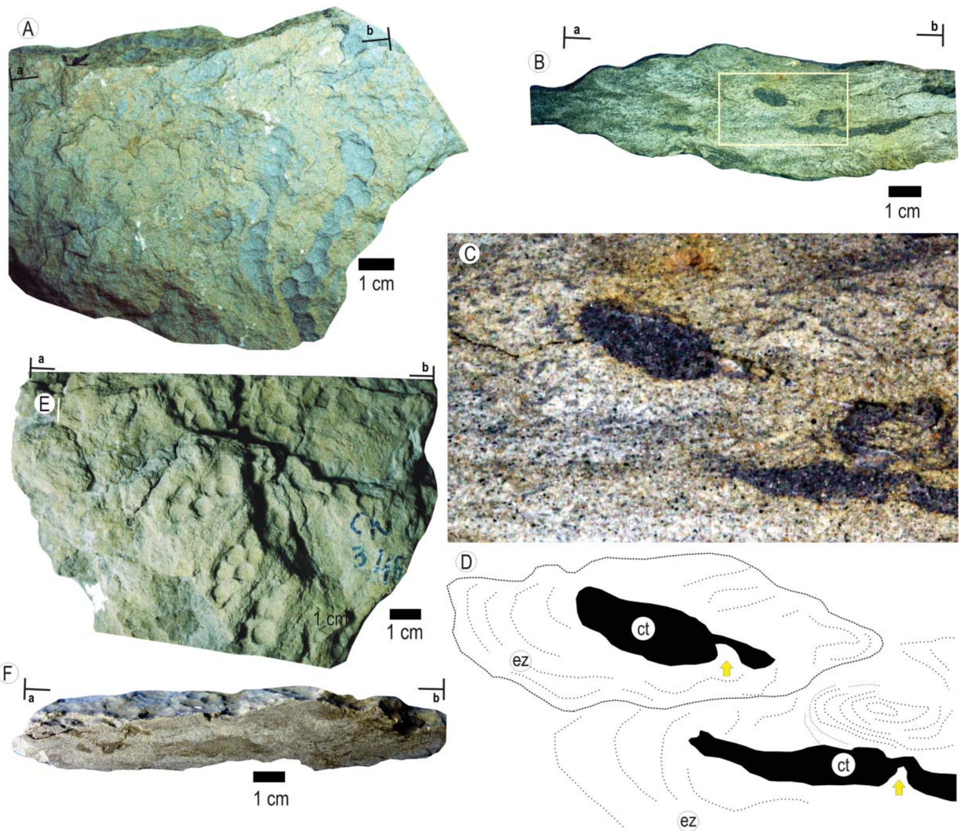

Figure 4. Polished cross sections of *N. biserialis* (Seilacher), Upper Cretaceous, López de Bertodano Formation, Snow Hill Island, Antarctica. **A-D**. CADIC PI 316, **A**. original slab with several specimens of *N. biserialis*, upper bedding plane view, a-b indicates the position of cross-section in (B); **B**. polished cross-section showing a dense *N. biserialis* ichnofabric, rectangle shows location of close-up in (C) and (D); **C-D**. close-up and sketch showing a transverse section of *N. biserialis*(upper-central part) with its central tunnel (ct) filled with two muddy fecal masses, the large one (left) is separated from the smaller one (right) by an asymmetric ridge of coarser material (arrow) and the enveloping zone (ez) made of lighter crescentic laminae that surrounds completely the central tunnel; and a longitudinal to oblique partial section of *N. biserialis*(lower right), note the complex geometry of the enveloping zone (ez) and the ridge of coarser material at the base (arrow) separating the biserial muddy fecal masses of the central tunnel (ct). **E-F**. CADIC PI 317, **E**. the original slab with several specimens of *N. biserialis*, upper bedding plane view, a-b indicates the position of crosssection in (F); **F**. polished cross-section preserving a dense *N. biserialis* ichnofabric.

show an inward concave surface that faces the central tunnel (Figs. 3B, 4C, 4D). As the curved laminae of the enveloping zone surround the central tunnel, it seems that the trace maker reworked the sediments radially with respect to the central tunnel (Fig. 4C). This is consistent with the terminal-radial backfill structure in the enveloping zone made by the trace maker while reworking and sorting out the sediments (Seilacher, 1986).

The biserial row of muddy globular fecal masses are interpreted as the terminal backfill structure of the central tunnel. The asymmetric pattern of the ridges between adjacent dimples suggests the movement direction of the trace maker. This asymmetry is interpreted as reflecting the strongest pushing of the sediments produced by the trace maker on its posterior end, hence the steeply inclined and concave ridge indicates the backward position and the opposite gently inclined ridge the forward position (Figs. 2D, 3C).

Discussion

Different taphonomic effects and stratinomic positions (epichnial, endichnial, hypichnial) introduce preservational modifications in *Nereites*, which in the past were recognized as different ichnogenera. However, several seemingly distinct trace fossils, such as *Helminthoida, Phyllodocites, Scalarituba*, and *Neonereites*, represent only different types of preservation and/or stratinomic position of typical architectural elements of *Nereites* (see Seilacher and Meischner, 1965; Chamberlain, 1971; Seilacher, 1986; Uchman, 1995; Mángano et al., 2000).

In line with these concepts, Chamberlain (1971) and Uchman (1995) offered alternative explanation for the biserial dimples and pustules of *N. biserialis*, which in the original interpretation of Seilacher (1960) are thought to represent the central tunnel (epirelief) or the enveloping zone (hyporelief), respectively. Chamberlain

(1971) interpreted that the dimples of *N. biserialis* do not represent the fecal masses of the central tunnel (median crawlway or median gallery in Chamberlain's terminology) but alternating lobes of the enveloping zone in epirelief preservation, i.e. a structure similar to that of *Phyllodocites*. According to Chamberlain (1971), the central tunnel was not preserved because the tracemaker of *N. biserialis* was working in a mud horizon just above an underlying sand horizon and only the marginal lobes of the enveloping zone were preserved in epirelief. The pustules on the hyporelief of *N. biserialis* were interpreted as possible partial preservation of the multiserial pustules that Chamberlain (1971, plate 31, fig. 2) found at the base of *N. missouriensis* (at that time still recognized as *Scalarituba missouriensis*).

Uchman (1995) interpreted the apparent uniserial (*Neonereites uniserialis* preservation), biserial (*N. biserialis* preservation), or multiserial (*N. multiserialis* preservation) characteristics of the external pustules to represent consecutive higher levels of exposition of the external margin of the hyporelief of *Nereites*. Hence, the uniserial row represents the outermost part, the biserial row an intermediate part, and the multiserial row a more complete exposure of the concave margin of the hyporelief (see also Chamberlain, 1971; Pickerill, 1991).

As a consequence of their interpretations, both Chamberlain (1971) and Uchman (1995) considered *Neonereites biserialis* Seilacher as a junior synonym of *Nereites missouriensis*. Although these interpretation may be valid in some cases, particularly when only the hyporelief is preserved (e.g., in the case of *N. multiserialis*, see Pickerill, 1991) they do not satisfactorily explain the origin of the biserial row of dimples in the central tunnel of the specimens of *N. biserialis* from the Jurassic of Germany (Seilacher, 1960) and the Cretaceous of Antarctica.

The biserial dimples observed in the exposed weathered surfaces of endichnial *Nereites* in Antarctica are clearly part of the stuffed central tunnel. In most cases the original muddy fecal masses were eroded, but a thin film of mud or patches of mud still remains inside the dimples in some specimens. Furthermore, as on upper plane view the dimples are flanked by the complex laminae of the enveloping zone and in endichnial view (crosssections) the enveloping zone totally surrounds the muddy globular fecal masses. Therefore, the dimples cannot be simply explained either as the biserial lobes of the enveloping zone (epichnial intepretation of Chamberlain, 1971) or as the external pustules of the hyporelief (Uchman, 1995).

The new findings are in agreement with the original interpretation of *N. biserialis* (Seilacher, 1960). Following the conceptual guide of ichnotaxobases for ichnogenus and ichnospecies (Fürsich, 1974; Bertling et al., 2006), *Neonereites* has the typical diagnostic features of *Nereites* (a central tunnel stuffed with muddy fecal masses surrounded by an enveloping zone of reworked sediments) and thus, *Neonereites* should be considered a synonym of *Nereites*. The biserial row of alternating muddy fecal masses in the central tunnel, however, reflects a specific behavior not known in any other ichnospecies of *Nereites*. Consequently, *Nereites biserialis* (Seilacher) has to be considered as a valid ichnospecies.

Nereites missouriensis and *N. biserialis* differ in the dominant arrangement of muddy fecal masses within the central tunnel; otherwise the general pattern characterized by open and irregular meanders is similar. In the emended diagnosis of *N. missouriensis*, Uchman (1995) indicates that "…the interior may be preserved as a row of at least uniserial closely packed sediment depressions…" As the central tunnel of *N. biserialis* may have segments, albeit very short ones with respect to the total length of the burrow, bearing uniserial fecal masses or depressions, it is necessary to rephrase the diagnosis of *N. missouriensis* to "…the interior may be preserved as a row of dominantly uniserial closely packed sediment depressions…" While *N. missouriensis* is a relatively common trace fossil, *N. biserialis* is apparently only known from the Jurassic of Germany (Seilacher, 1960) and the Cretaceous of Antarctica, suggesting that it is a relatively rare trace fossil. *N. missouriensis* and *N. biserialis* rarely occur together in the same bed, perhaps reflecting the expression of different behaviors in different environmental conditions. We have not reached a convincing explanation for the particular arrangement of biserial muddy fecal masses in the central tunnel of *N. biserialis* yet, but it seems plausible that this particular behavior would be beneficial for the producer while feeding in highly nutritious sediments. In that case, the animal would stay for a longer time in a nearly stationary position and the disposal of an increased volume of digested sediments would require an excess of space in the central tunnel. It is hypothesized that the need of an extra space can be solved by the disposal of the fecal masses in a biserial, alternating fashion within the central tunnel. Furthermore, the sideward shifting of the posterior end could have enhanced the pumping of water along the body of the producer that takes its respiration water from the pore water.

Conclusions

The abundant specimens preserved in full relief in the Upper Cretaceous siltstones and silty very fine-grained sandstones from Antarctica indicate that *Nereites biserialis* (Seilacher) is a valid ichnospecies. Contrary to alternative interpretations (e.g., Chamberlain, 1971; Uchman, 1995), the new findings fully support the original interpretation of Seilacher (1960) on the origin of the alternating biserial dimples as fecal masses filling the central tunnel of the *N. biserialis* structure.

The number and arrangement of pustules in the hyporelief seem to be a variable feature; that is, the presence/absence of uniserial, biserial or multiserial pustules may be controlled in part by partial or complete preservation of the outer margin of the enveloping zone. However, the dominant biserial alternating arrangement of fecal masses in the central tunnel is a diagnostic character of *N. biserialis*.

Similarly to the type material from the Jurassic of Germany, the biserial row of dimples observed in endichnial Antarctic material represents the voids left by erosion of the fecal masses originally discarded by the producer in the central tunnel of *N. biserialis*. Supporting evidence for this interpretation of the Antarctic material are:

- On weathered upper surfaces of siltstones and fine-grained sandstones, the biserial dimples are flanked by even to lobate laminae of the enveloping zone and thin films of mud or partial preservation of patches of mud are observed within the dimples.
- Aassociated traces of *N. missouriensis* display similar preservational features, that is, a central tunnel with simple, scalariform menisci flanked by even to lobate laminae of the enveloping zone.
- Polished crosssections of endichnial structures of *N. biserialis* show that the central tunnel is made of biserial muddy fecal masses totally surrounded by laminae of the enveloping zone.

Acknowledgments

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