# Environmental variability of *Macaronichnus* ichnofabrics in Eocene tidal-embayment deposits of southern Patagonia, Argentina

NADINE J. PEARSON, M. GABRIELA MÁNGANO, LUIS A. BUATOIS, SILVIO CASADÍO  AND MARTIN R. RAISING

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The Middle Eocene Man Aike Formation of southern Patagonia, Argentina, offers the opportunity to study the palaeoecological and palaeoenvironmental significance of *Macaronichnus* ichnofabrics in a tide-dominated, coastal embayment compound-dune complex. Four recurrent *Macaronichnus* ichnofabrics are recognized: *Macaronichnus* IF-1 characterized by *Macaronichnus segregatis segregatis*; *Macaronichnus* IF-2 with *M. segregatis segregatis*, *Ophiomorpha nodosa*, *Skolithos linearis* and rare *Palaeophycus tubularis*; *Macaronichnus* IF-3 typified by *M. segregatis segregatis*, *O. nodosa*, *Asterosoma radiciforme* and rare *S. linearis*; and *Macaronichnus* IF-4 consisting of *M. segregatis segregatis*, *Nereites missouriensis*, *A. radiciforme*, *O. nodosa*, *Rosselia socialis*, *S. linearis*, *P. tubularis*, *Planolites* isp. and *Chondrites* isp. Variations in these ichnofabrics are linked to changes in local hydraulic conditions in the upper and lower trough areas of the compound dunes. In high-energy, shallow and marginal marine environments, the *Macaronichnus* tracemaker is commonly the first to colonize the shifting, sandy substrates. Overprinting by other ichnoguilds occurs only after the physiochemical conditions became favourable and the colonization window length increases. □ *Eocene, ichnofabrics,* Macaronichnus, *Man Aike formation, tidal embayment.*

*Nadine J. Pearson [nadinepearson@gmail.com], M. Gabriela Mángano [gabriela.mangano@usask.ca], and Luis A. Buatois [luis.buatois@usask.ca], Department of Geological Sciences, University of Saskatchewan, 114 Science Place, Saskatoon, SK S7N 5E2, UK; Silvio Casadío [scasadio@unrn.edu.ar], Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Roca, Río Negro, Argentina; Martin R. Raising [martin_rodriguezraising@yahoo.com.ar], XR-GEOMAP, R. Durand Av. N 397, Grand Bourg Salta, Argentina; manuscript received on 20/01/2012; manuscript accepted on 01/10/2012.*

Ichnofabric analysis provides an excellent tool for understanding the ecology of a palaeocommunity and documenting the endobenthic response to physiochemical controls within that community (Droser & Bottjer 1993; Pollard *et al.* 1993; McIlroy 2008; Knaust 2009; Aguirre *et al.* 2010). The variety of environmental parameters influencing ichnofabric generation include – but are not limited to – sedimentation rate, hydraulic energy, salinity and oxygenation. Unravelling the physiochemical controls within a depositional environment can be challenging, even with the aid of ichnofabric analysis. *Macaronichnus* is unique because it occurs under a very specific set of depositional conditions. These controls are well documented in previous *Macaronichnus* studies of the foreshore (Clifton & Thompson 1978; Saunders & Pemberton 1988; Seike 2008, Seike 2009; Quiroz *et al.* 2010), but are largely overlooked in other shallow and marginal marine settings (e.g. sub-tidal sand bodies), in which this ichnogenus may be present as well (e.g.

Savrda & Uddin 2005; Olariu *et al.* 2012). As well, secondary colonization and its controls are rarely explored in these studies. Tidal-embayment deposits from the Middle Eocene Man Aike Formation, in southwestern Patagonia, Argentina, elucidate the primary and secondary ecological controls resulting in variations in *Macaronichnus* ichnofabrics.

The objectives of this article are to: (1) characterize the *Macaronichnus* ichnofabrics present in the tidal-embayment facies of the Man Aike Formation and (2) establish the relationship between inferred ecological parameters and *Macaronichnus* ichnofabric distribution.

## Concepts and methods

An ichnofabric is the overall texture and internal structure that develops because of bioturbation or bioerosion at all scales (Ekdale & Bromley 1983;

Bromley & Ekdale 1986; Droser & Bottjer 1993; Taylor & Goldring 1993). It is the record of primary depositional conditions, original endobenthic community structure and subsequent taphonomic history (Taylor & Goldring 1993). Different parameters from an endobenthic community are incorporated, such as rates of biogenic activity (bioturbation intensity), burrow ordering, tier profile and the recognition of different ichnoguilds (Taylor & Goldring 1993; Taylor *et al.* 2003; Mángano & Buatois 2004; McIlroy 2004; Desjardins *et al.* 2010; Desjardins *et al.* 2012). Elements of the ichnofabric may be attributed to a number of controls, in particular to the tiering pattern and manner of colonization (Taylor *et al.* 2003). Vertical profiles of modern marine sediments exhibit differences in sediment water content, oxygenation, food content, tiering and preservation of trace fossils (Droser & Bottjer 1993; Bromley 1996). The surface layer, that is, the mixed layer, is generally 3–15 cm thick and does not preserve biogenic structures well because of its high water content (Berger *et al.* 1979; Ekdale 1985; Droser & Bottjer 1993; Savrda 2007). The underlying transition layer, its thickness varying with local environmental factors, has less water content and is characterized by tiers of organisms that live or feed at greater depths in the sediment column; biogenic structures emplaced here have sharper boundaries than those in the mixed layer and are commonly better preserved (Berger *et al.* 1979; Droser & Bottjer 1993; Savrda 2007).

Tiering consists of the vertical partitioning of the habitat (Ausich & Bottjer 1982; Bromley & Ekdale 1986; Buatois & Mángano 2011). A number of tiering styles have been established by Taylor & Gawthorpe (1993), Goldring (1995) and Taylor *et al.* (2003), but only three were documented in this study: (1) single-tier colonization, (2) single, successive-tier colonization with gradual tier replacement and/or delayed resumption with an initial change in colonization; and (3) multiple, successive-tier colonization with gradual tier replacement. Single-tier colonization refers to a single colonization event by an opportunistic or pioneer organism and commonly signifies a temporary environmental shift that allowed this particular colonization (Goldring 1995; Taylor *et al.* 2003). Successive tiering is characterized by colonization by a single ichnotaxon or multiple ichnotaxa in an aggradational depositional environment; it is associated with a relatively stable depositional setting (Goldring 1995; Taylor *et al.* 2003). Tier modification is triggered by changes in ecological conditions (e.g. oxygen content, nutrient supply, hydraulic energy, sedimentation rate, etc.) commonly associated with essentially continuous sedimentation (Taylor *et al.* 2003). Tier replacement

occurs when the initial tier tracemakers are replaced by other taxa using different behavioural strategies, triggered commonly by a change in environmental conditions. Event-bed ichnofabrics commonly differ from those of the pre-event sediments and are regularly characterized by delayed resumption with an initial change in colonization. This slow recolonization may lead to a frozen tier ichnofabric followed by reformation of the pre-event ichnofabric, but often no change in overall palaeogeography is indicated (Taylor *et al.* 2003).

A suite of biogenic structures represents the preserved evidence of the activities of the specific benthic community that inhabited the sediment at one time (Bromley & Ekdale 1986). According to Bromley & Ekdale (1986), ichnofabrics commonly comprise more than one trace fossil suite occurring within the same sediment (i.e. two or more suites of burrows are juxtaposed upon one another to produce a composite ichnofabric). A composite ichnofabric may arise where burrows of organisms in the lower tiers cross-cut burrows of organisms in shallower tiers, as mixed and transition layers migrate upwards with steady sediment accretion (Droser & Bottjer 1993). A composite ichnofabric may originate *in situ* through two processes: a major change in depositional conditions, that is, bathymetry, salinity, hydraulic energy, sedimentation rate, etc, which results in community turnover, or continuous vertical accretion of the seafloor during deposition, accompanied by continuous upward migration of a tiered infaunal community (Bromley & Ekdale 1986). The former situation is exemplified in the sequence of burrowing communities that colonized the sub-tidal compound dunes of the Man Aike Formation. The entire trace fossil assemblage forms an ichnofabric that represents more than one set of environmental conditions (Bromley & Ekdale 1986).

The bioturbation index (BI), ranging from 0 to 6, proposed by Taylor & Goldring (1993) characterizes the amount of biogenic reworking with respect to the original sedimentary fabric. Each grade is based on burrow density, amount of burrow overlap and distinctiveness of the original sedimentary fabric (Taylor & Goldring 1993). A sedimentary fabric characterized by no bioturbation (0%) corresponds to a BI = 0. An ichnofabric that shows sparse to low levels of bioturbation corresponds to a BI = 1 (1–4%) to 2 (5–30%), where physical sedimentary structures dominate over biogenic structures. A BI = 3 (31–60%) describes an ichnofabric with discrete trace fossils, moderate bioturbation and still distinguishable bedding boundaries. BI = 4 (61–90%) is characterized by intense bioturbation, high trace fossil density, common overlap of trace fossils

and primary sedimentary structures that are mostly destroyed. A sediment with completely disturbed bedding and showing intense bioturbation corresponds to a BI = 5 (91–99%) to 6 (100%) and reflects the dominance of biogenic structures (see Buatois & Mángano 2011, Fig. 5.1).

Studying the *Macaronichnus* ichnofabrics of the Man Aike Formation was challenging as: (1) observations were often limited to two-dimensional, vertical to sub-vertical surfaces; (2) sections demonstrating vertical continuity commonly had patchy distributions; and (3) occurrences of weathering and diagenetic haloes often inhibited observations. However, in some cases, bedding-plane views and concretionary horizons revealed the 3-D geometry of the trace fossils in a limited areal extent.

# Geological setting

The specimens of *Macaronichnus* came from an outcrop of the Middle Eocene Man Aike Formation, in the southwestern portion of the Austral Basin, Patagonia, Argentina. Described samples are from outcrop localities in the Calafate River Valley south of the town of El Calafate (Figs 1 and 2). The samples are present in two sandstone facies within an extensive sub-tidal compound-dune complex. This formation was deposited in a broad incised valley system, with a fill comprising lowstand braided-fluvial conglomerate and transgressive tidal-embayment sandstone. The palaeovalley was excavated during the Middle Eocene phase of Patagonian Cordillera uplift and was subsequently infilled during the late Middle Eocene transgressive period (Kraemer *et al.* 2002; Malumián 2002; Marenssi *et al.* 2002; Ramos 2002; Casadío *et al.* 2009). This formation consists of approximately 220 m of pebble conglomerate, very fine- to coarse-grained sandstone, siltstone and shale (Fig. 3).

# Facies characterization of *Macaronichnus*-bearing units

## Facies 1: bioturbated sandstone

This facies encompasses bioturbated, very fine- to coarse-grained sandstone with primary stratification obscured by biogenic reworking. Rare relict medium- to large-scale trough cross-stratification can be discerned. Reactivation surfaces are present and truncate both physical and biogenic sedimentary structures. These surfaces are demarcated by thin lags comprising very coarse-grained sand, pebbles

and fragmented shell debris. Basal contacts are erosive and typically have associated lags comprised of very coarse-grained sand, pebbles and fragmented skeletal debris, for example, brachiopod valves and bryoliths (bryozoans). Bedsets are 0.4–4.9 m thick and form sheet- to wedge-like geometries that persist laterally for several hundred metres.

## Facies 2 – planar-tabular to trough cross-stratified sandstone

Facies 2 comprises 0.2–2.0 m thick sets of small- to large-scale (dominantly medium scale) planar-tabular to trough cross-bedded, fine- to very coarse-grained sandstone. Bedsets have distinct bed boundaries and increase in thickness upwards. Grain size demonstrates a uniform to faintly coarsening upward trend. Deposits display sheet geometries that continue laterally for at least 200 m, foresets that dip westward and multiple reactivation surfaces. Coarse-grained sand, shell hash and mudstone drapes commonly delineate the cross-bed foresets. Reactivation surfaces and rare tidal bundling, that is, recurrent variations in the laminae grain size and thickness, are present. Bedset boundaries and internal stratification are commonly defined by rows of nodules and concreted horizons.

## Facies interpretation

Facies 1 and 2 were formed in a forward-migrating, flow-transverse, sub-tidal compound-dune complex in a tide-dominated coastal embayment. The medium- to large-scale cross-stratification is interpreted as the product of sub-aqueous compound dunes migrating in the regional flood direction, that is, westward (Berné *et al.* 1993; Yoshida *et al.* 2004; Sixsmith *et al.* 2008; Desjardins *et al.* 2012). The textural maturity, the dominance of medium- to large-scale cross-bedding and the scarcity of mudstone drapes imply deposition in a dominantly high-energy, shallow to marginal marine setting characterized by periods of reduced sedimentation and energy (Pollard *et al.* 1993; Yoshida *et al.* 2004). Evidence of tides is not apparent in Facies 1 due to the lack of any preserved primary physical structures, but they are recorded in Facies 2 by reactivation surfaces, rare mudstone drapes and tidal bundling, that is, diurnal thickness variation and neap–spring cyclicity.

## The ichnogenus Macaronichnus: potential producers and ethological significance

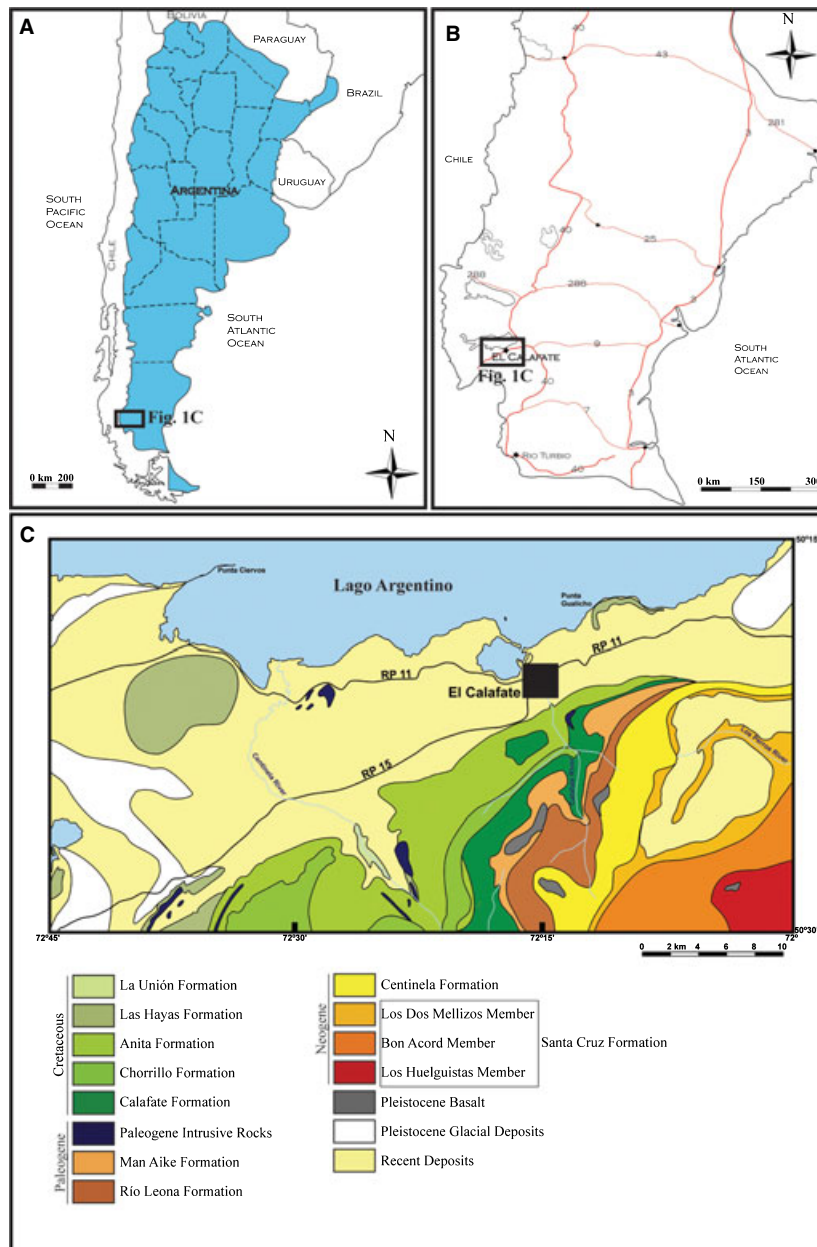*Macaronichnus* is an intrastratal ichnofossil that is cylindrical, straight to winding, unbranched and

*Fig. 1.* Location maps. (A) Argentina with the Santa Cruz Province highlighted. (B) Santa Cruz Province with the town of El Calafate identified. (C) Geology of the Lago Argentino area, southwestern Patagonia. Modified from Furque (1973) and Rodríguez-Raising (2010).

interpenetrates randomly, in some cases displaying false branching. In the Man Aike Formation, this trace fossil commonly displays dense population densities, with a bimodal size distribution, that is, small 1–5 mm and large 5–10 mm diameters. Trace fill has a zoned backfill structure comprising: (1) an outer mantle of darker-coloured, high-density minerals and (2) a central core of pale-coloured, low-density grains. The infill-mantle contact is sharp, while the mantle-host is gradual. *Macaronichnus* is regularly preserved as full relief and/or positive

epirelief. The Man Aike specimens are included in *Macaronichnus segregatis segregatis* (Bromley *et al.* 2009).

Modern polychaetes from the Opheliidae family, for example, *Euzonus* sp., *Ophelia* sp., *Armandia* sp. and *Travisia* sp., produce structures similar to the ichnospecies *Macaronichnus segregatis* (e.g. Clifton & Thompson 1978; Saunders & Pemberton 1988; Pemberton *et al.* 2001; Gingras *et al.* 2002; Nara & Seike 2004; Seike 2007, Seike 2008, Seike 2009; Dafoe *et al.* 2008a,Dafoe et al. 2008b; Seike *et al.* 2011).
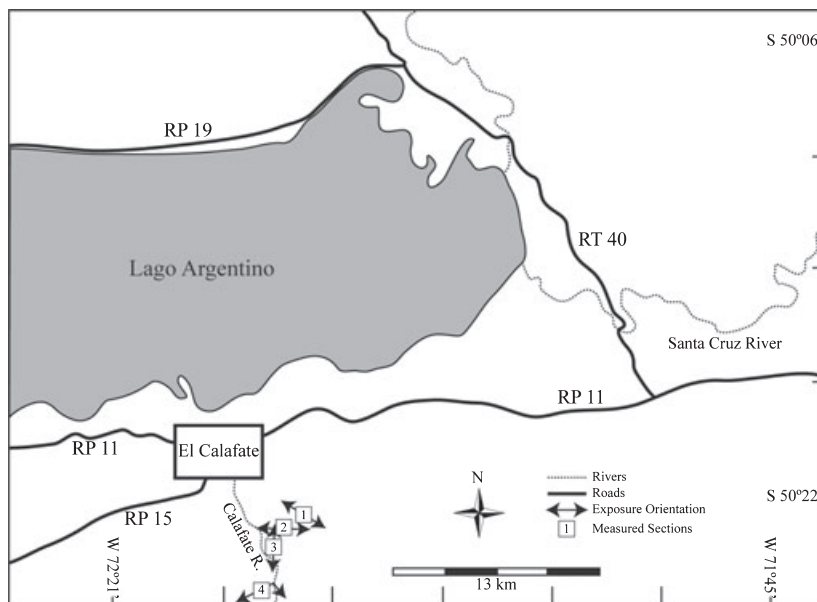
*Fig. 2.* Location map showing study area within the Lago Argentino area and locations of measured sections with exposure orientations. 1–3, Estancia 25 de Mayo Sections 1–3. Sections 1 and 3 were previously referred to as localities 3 and 4 by Marenssi *et al.* (2002) and Casadío *et al.* (2009), respectively. 4, Estancia Huyliche Section. This section was previously described as locality 1 by Marenssi *et al.* (2002) and Casadío *et al.* (2009).

Opheliids are well known for specific substrate distribution patterns and being restricted to substrata with relatively narrow particle size ranges (Harris 1991; Maciolek & Blake 2006). Associated grain sizes commonly are fine and medium sand as these are easily ingested by the tracemaker. They also carry a greater number of bacteria and adsorbed amino acids per unit mass than coarser grains (Clifton & Thompson 1978; Hutchings & Murray 1984; Harris 1991; Maciolek & Blake 2006; Dafoe *et al.* 2008a). Populations commonly feed on an epigranular food source, but they also can ingest free amino acids, bacteria, protozoans and other small organisms associated with the sand (Faulchald & Jumars 1979; Harris 1991). Adults possess low levels of food specialization in comparison with juveniles that display a high level of precision in the selection of substrata (Faulchald & Jumars 1979). Movement of some species through the sediment is controlled by daily differences in oxygen concentration, salinity and temperature (De Souza & Borzone 2007). The presence of haemoglobin in the tissues of some of these polychaetes has been postulated as assisting in aerobic metabolism maintenance during low tide (Dangott & Terwilliger 1986; De Souza & Borzone 2007).

Opheliids perform two primary behaviours, deposit feeding and locomotion, and subsist dominantly on an epigranular food resource (Faulchald & Jumars 1979; Harris 1991; Pemberton *et al.* 2001; Dafoe *et al.* 2008b; Seike 2008). Opheliids burrow through the sands using peristaltic contractions and selectively ingest the sediment with a proboscis to feed from microbes or meiofauna living on grain surfaces or between grains (Savrda & Uddin 2005). This foraging produces a *Macaronichnus*-like trace and involves the collection of felsic (i.e. quartz and feldspar) sand grains, ingestion of the grains through the mouth, nutrient processing in the gut and grain excretions through the pygidium (Dafoe *et al.* 2008a). Under these circumstances, it is improbable that these organisms could feed haphazardly and still obtain the energy required to fulfil metabolic needs (Saunders 1989). It has been hypothesized that the primary behavioural adaptation of these organisms is grain-selective feeding. This is the selective removal of sand grains, prior to ingestion that reduces the organism's net energy gain per unit time feeding (Saunders & Pemberton 1988). Factors, such as geomorphology, sediment dynamics and nutrient distribution, may be highly variable and control the overall distribution of this trace fossil within a depositional environment (Dafoe *et al.* 2008a, Dafoe *et al.* 2008b; Seike 2008, Seike 2009). Moderate- to high-energy regimes (i.e. tide, wave or storm) provide the ideal conditions for interstitial fauna as the sediment contains the maximum input of water, oxygen and nutrients, which are replenished often through subsequent water movement (Harris 1991; Seike 2008, Seike 2009).

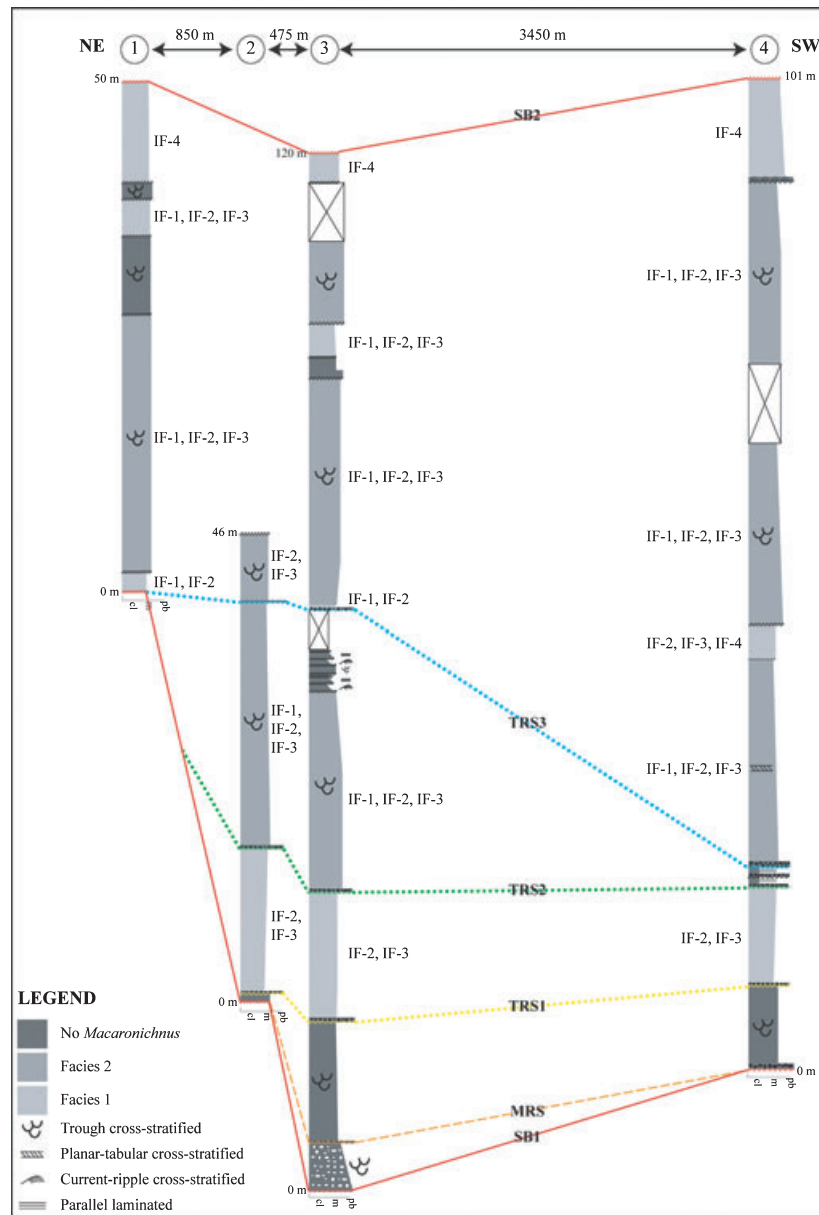Habitat distribution of opheliid polychaetes (e.g. *Euzonus*, *Ophelia*, *Armandia* and *Travisia*) ranges

*Fig. 3.* Measured sections at Estancia 25 de Mayo and Estancia Huyliche showing distribution of *Macaronichnus*-bearing facies and ichnofabrics. IF = ichnofabric; MRS = maximum regressive surface; SB = sequence boundary; TRS = tidal ravinement surface; cl = clay, m = medium sand, pb = pebble.

from polar to sub-tropical, intertidal to sub-tidal and marginal to fully marine settings (e.g. modern protected and exposed foreshore, shallow shoreface, protected embayment and proximal offshore environments) (Dales 1952; Wood 1963; Clifton & Thompson 1978; Britton-Davidian & Amoureux 1982; Gianuca 1983; Hutchings & Murray 1984; Dangott & Terwilliger 1986; Kemp 1988; Harris 1991; Defeo *et al.* 1992; Sicinski & Janowska 1993; Jaramillo 1994; Elías *et al.* 2003; Misaka & Sato 2003; Maciolek & Blake 2006; De Souza & Borzone 2007; Seike 2007, 2008, 2009; Dafoe *et al.* 2008a,b; Rowe 2010; Seike *et al.* 2011). Opheliid polychaetes

have high degrees of mobility and can rapidly shift in the substrate, allowing them to migrate in accordance with shifting environmental circumstances (Dafoe *et al.* 2008a; Seike 2008). The primary controls on infaunal movement in the sediment appear to be fluctuations in hydraulic energy, oxygen content, sedimentation rate and nutrient content (Harris 1991; Dafoe *et al.* 2008a; Seike 2008, 2009).

## *Macaronichnus* ichnofabrics

Four ichnofabrics were identified in the cross-bedded facies of the studied outcrop sections. The

ichnofabrics are defined based on their ichnotaxonomic composition, degree of bioturbation, ichnodiversity, tiering and relation with sedimentary structures. The ichnoguild concept is used to provide information on the adaptive strategies displayed by benthic organisms during ecospace colonization (Bromley 1996; Buatois & Mángano 2011). Some of the ichnofabrics are common and recurrent within the migrating bedforms at different stratigraphic positions, while others occur locally within a single-dune bedform or stratigraphic unit.

## Macaronichnus ichnofabric 1 (IF-1)

This monospecific assemblage of horizontal burrow-fill structures (*Macaronichnus segregatis segregatis*) accounts for almost all of bioturbation in this ichnofabric. Rare occurrences of *Macaronichnus segregatis maeandriformis* and *Macaronichnus segregatis spiriformis* were observed on bedding surfaces (Fig. 4). Ichnofossils are 2–7 mm wide. *Macaronichnus* IF-1 occurs in the trough and planar-tabular

cross-stratified sandstones of Facies 2. This ichnofabric is characterized by low to intense degrees of bioturbation (BI = 2–5), but typically are moderate (BI = 3). The distribution of *Macaronichnus* in the Man Aike Formation is limited to the upper 10–20 cm of the compound dunes. Individual trace fossils include horizontal (dominant), oblique and vertical components. A large portion of the cross-stratification is preserved.

Strong uni-directional currents affected the migrating compound dunes – inferred from grain size and ichnological trends (Allen 1980; Dalrymple 1984; Buck 1987; Berné *et al.* 1991; Pollard *et al.* 1993). As current speeds dropped below the threshold of sediment motion, sub-aqueous compound dunes became inactive and short-term colonization windows developed (Buck 1987; Pollard *et al.* 1993; Desjardins *et al.* 2010). Colonization by the *Macaronichnus* tracemaker is inferred to have occurred shortly after sediment deposition (see also Curran 1985; Saunders & Pemberton 1988; Pollard *et al.* 1993; Dafoe *et al.* 2008a,b;
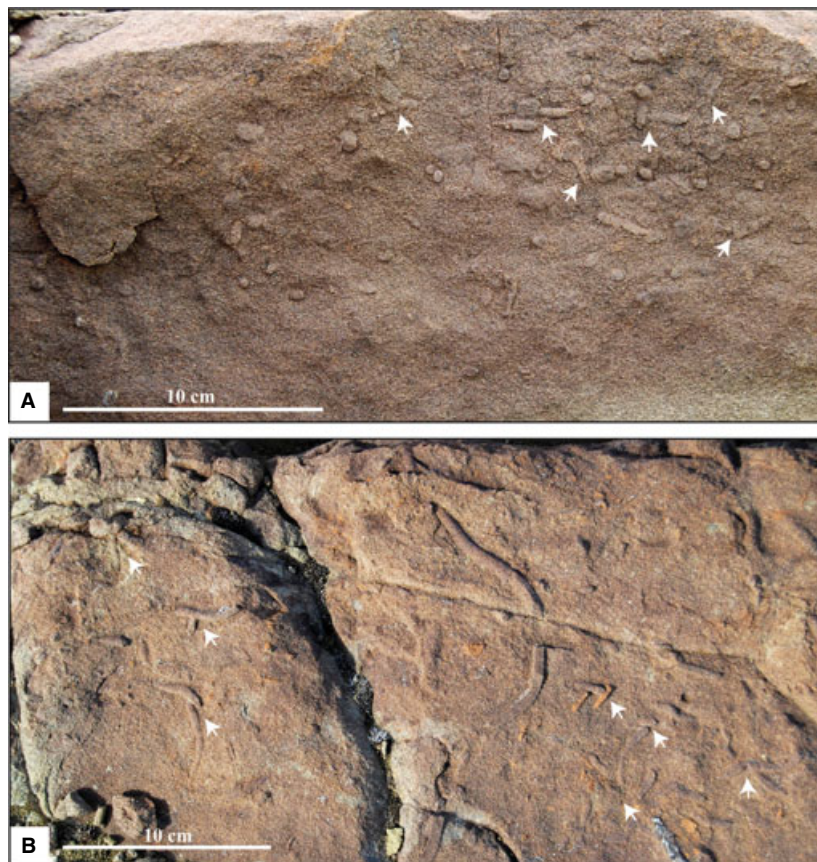


*Fig. 4. Macaronichnus* ichnofabric 1 (IF-1). (A) *Macaronichnus segregatis segregatis* (arrows) in the upper 15–20 cm of the trough cross-stratified sandstone, cross-sectional view. Estancia 25 de Mayo Section 3. (B) Bedding-plane view of *Macaronichnus* structures, showing common interpenetration where mantle material has been removed between intersecting structures (arrows). Estancia 25 de Mayo Section 2.

Seike 2008, 2009; Quiroz *et al.* 2010). This ichnofabric reflects the single, successive-tier colonization (*sensu* Goldring 1995 and Taylor *et al.* 2003), of the substrate by a mid-tier, vagile deposit-feeding ichnoguild. Its occurrence in cross-stratified sands, that is, Facies 2, which are bioturbated almost penecontemporaneously with deposition, confirms a high-energy environment for this ichnofabric (Pollard *et al.* 1993).

## *Macaronichnus Ichnofabric 2 (IF-2)*

*Macaronichnus* IF-2 is dominated by *Macaronichnus segregatis segregatis*, along with *Ophiomorpha nodosa*, *Skolithos linearis* and rare *Palaeophycus tubularis* cross-cutting (Fig. 5). *Macaronichnus segregatis segregatis* is 2–4 mm wide; *O. nodosa* is 7–20 mm wide and up to 230 mm long; *S. linearis* is 4–8 mm wide and 70–80 mm long; and *P. tubularis* is 3.5–5.5 mm wide. This composite ichnofabric occurs in Facies 2, with sediment packages moderately to completely bioturbated (BI = 3–6), but most commonly are highly bioturbated (BI = 4). *Ophiomorpha nodosa* overprints deposits as simple, broad shafts with well-formed, ovoid-shaped pelletoidal linings. Cross-sections vary from circular to elliptical.

Burrow infill comprises structureless sand identical to the host stratum.

Moderate to strong uni-directional currents, inferred from grain size and ichnological trends, influenced the upper trough interdune areas of the migrating compound dunes (Allen 1980; Dalrymple 1984; Buck 1987; Berné *et al.* 1991; Pollard *et al.* 1993). Depositional conditions were initially the same as IF-1, which allowed single, successive-tier colonization by the vagile, mid-tier deposit-feeding *Macaronichnus* ichnoguild. Subsequently, a decrease in sedimentation rate and hydraulic energy permitted tier replacement and multiple, successive-tier colonization by: (1) vagile to stationary, deep-tier mostly suspension-feeding *Ophiomorpha–Skolithos* ichnoguild and (2) rare vagile, shallow-tier suspension-feeding or passive-predatory *Palaeophycus* ichnoguild. Rare occurrences of shallow-tier *Palaeophycus* overprinting the mid-tier *Macaronichnus* ichnoguild most likely represent local zones in the interdune areas within the compound-dune complex where either tidal erosion changed the position of the sediment–water interface or subsequent migration of the interdune area allowed colonization by organisms from the deeper trough without associated erosion.
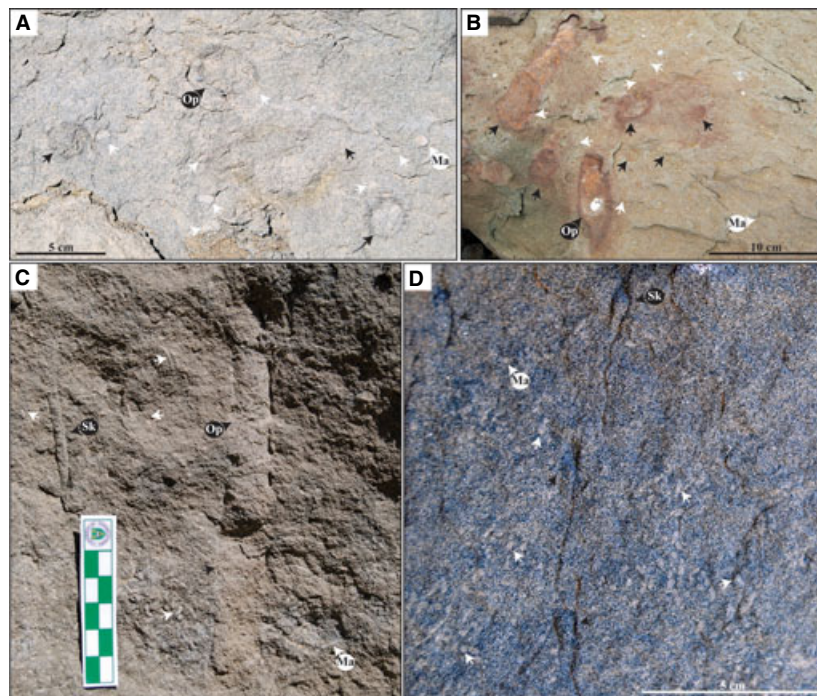


*Fig. 5.* *Macaronichnus* ichnofabric 2 (IF-2). Ms = *Macaronichnus segregatis segregatis* (white arrows), Op = *Ophiomorpha nodosa* (black arrows) and Sk = *Skolithos linearis* (yellow arrows). (A) Highly bioturbated sandstone (BI = 5–6). Cross-sectional view. Estancia 25 de Mayo Section 1. (B) Trough cross-stratified sandstone (BI = 4–6). Bedding-plane view. Estancia 25 de Mayo Section 3. (C) Highly bioturbated sandstone (BI = 5–6). *Ophiomorpha* and *Skolithos* burrows are found in approximately equal numbers, and trace fossils extend down from bedform boundaries. Cross-sectional view. Estancia 25 de Mayo Section 1. D, highly bioturbated sandstone (BI = 5–6). Cross-sectional view. Estancia 25 de Mayo Section 1.

## *Macaronichnus Ichnofabric 3 (IF-3)*

*Macaronichnus* IF-3 comprises *Macaronichnus segregatis segregatis*, with *Ophiomorpha nodosa, Asterosoma radiciforme*, and rare incidences of *Skolithos linearis* overprinting (Fig. 6). *Macaronichnus segregatis segregatis* is 2–10 mm wide; *O. nodosa* shafts are 20–30 mm wide and are at least 250 mm long; *A. radiciforme* have bulbs that are 20–52 mm in diameter, causative burrow widths of 3–8 mm, with lengths between 90 and 290 mm; and *S. linearis* is 5–10 mm wide and up to 160 mm long. This ichnofabric occurs in Facies 1 and 2. Sediment packages are moderately to completely bioturbated (BI = 3–6), but are typically moderate (BI = 3).

Moderate-energy uni-directional currents, inferred from grain size and ichnological trends, influenced the lower trough interdune areas of the migrating compound dunes (Allen 1980; Dalrymple 1984; Buck 1987; Berné *et al.* 1991; Pollard *et al.* 1993). *Macaronichnus* IF-3 represents multiple, successive-tier colonization with gradual tier replacement by: (1) mid-tier, vagile deposit-feeding *Macaronichnus* ichnoguild; (2) mid-tier, stationary detritus-feeding *Asterosoma* ichnoguild; (3) deep-tier, mostly vagile suspension-feeding *Ophiomorpha* ichnoguild, with rare occurrences of a (4) deep-tier, stationary *Skolithos* ichnoguild. Extended lower energy conditions allowed opportunistic colonization by stationary, detritus-feeding infauna (i.e. *Asterosoma*). This style of colonization represents a further decrease in sedimentation rate and hydraulic energy in comparison with IF-2.

## *Macaronichnus Ichnofabric 4 (IF-4)*

*Macaronichnus* IF-4 is characterized by *Nereites missouriensis, Asterosoma radiciforme, Ophiomorpha nodosa, Rosselia socialis, Skolithos linearis, Palaeophycus tubularis, Planolites* isp. and *Chondrites* isp. cross-cutting *Macaronichnus segregatis segregatis* (Fig. 7). *Macaronichnus segregatis segregatis* is 2–5 mm wide. *Asterosoma radiciforme* has a bulb diameter of 30–40 mm and a causative burrow width of 65–75 mm. *Nereites missouriensis* is 6–8 mm wide, with the central faecal string ranging from 4 to
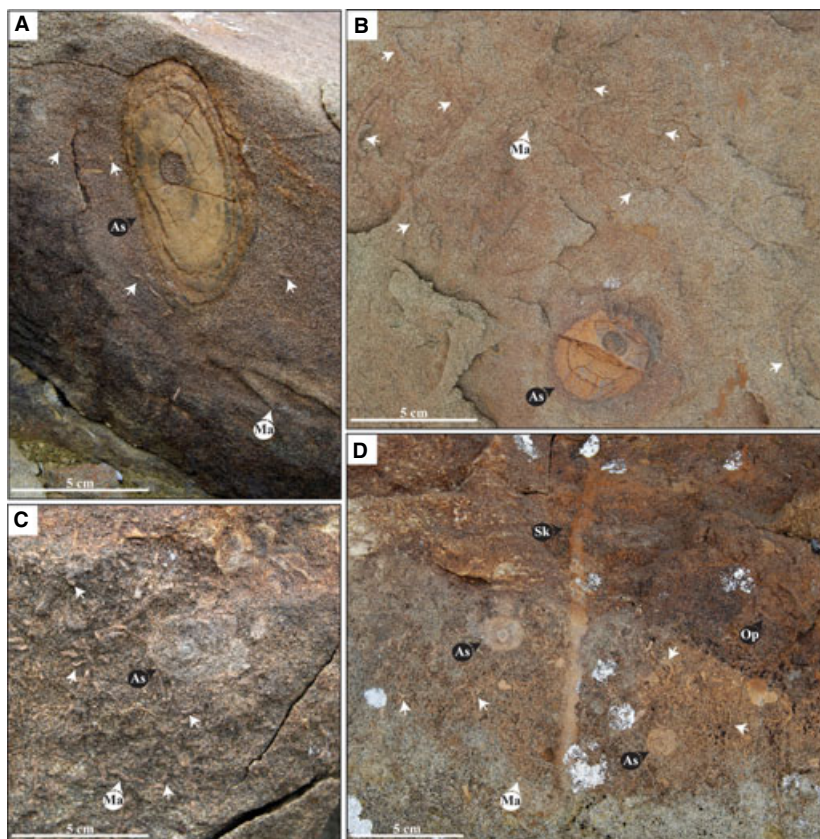


*Fig. 6. Macaronichnus* ichnofabric 3 (IF-3). As = *Asterosoma radiciforme*, Ma = *Macaronichnus segregatis segregatis* (white arrows), Op = *Ophiomorpha nodosa* and Sk = *Skolithos linearis*. (A) Trough cross-stratified sandstone (BI = 3–4). Cross-sectional view. Estancia 25 de Mayo Section 3. (B) Highly bioturbated sandstone (BI = 4–6). Bedding-plane view. Estancia 25 de Mayo Section 3. (C, D) highly bioturbated sandstone (BI = 4–6). Cross-sectional view. Estancia Huyliche Section.
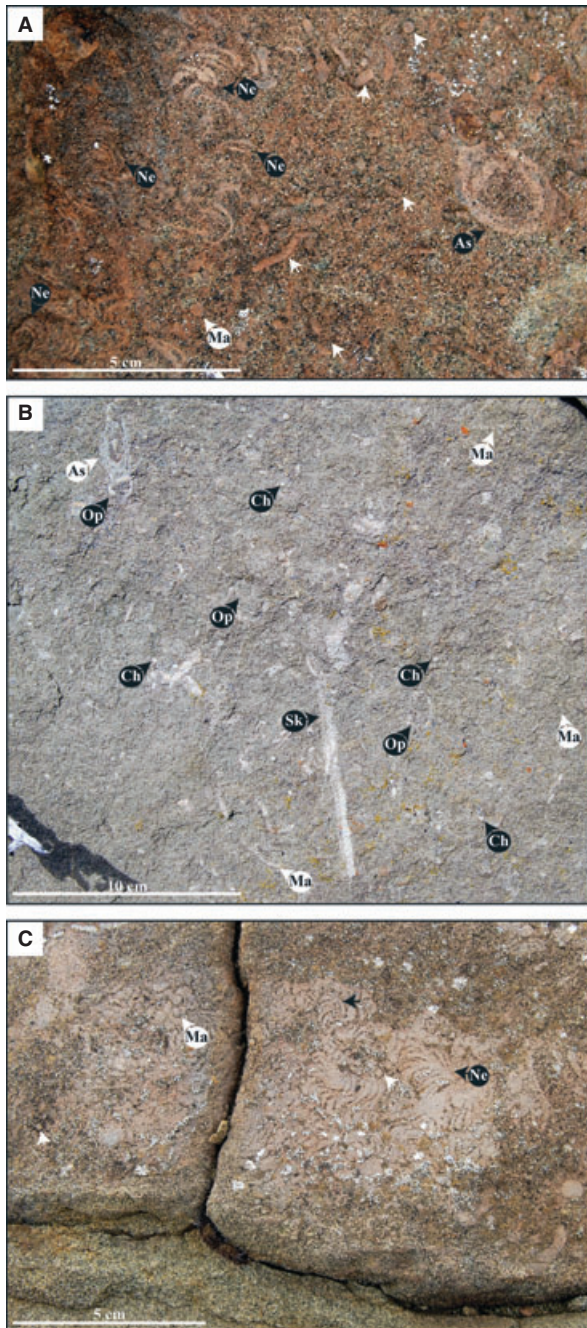
*Fig. 7.* *Macaronichnus* ichnofabric 4 (IF-4). As = *Asterosoma radiciforme*, Ch = *Chondrites* isp. (arrows), Ma = *Macaronichnus segregatis segregatis* (arrows), Ne = *Nereites missouriensis*, Op = *Ophiomorpha nodosa* and Sk = *Skolithos linearis*. (A–C) Highly bioturbated sandstone (BI = 5–6). Estancia 25 de Mayo Section 3. (A) Bedding-plane view. (B) Cross-sectional view. (C) Bedding-plane view.

5 mm in width. *Rosselia socialis* displays a funnel shape with a central burrow 6–10 mm wide, surrounded by concentric sediment composed of mudstone with thin sandstone laminae. *Skolithos linearis* is 4–8 mm wide and 80–150 mm long. *Ophiomorpha nodosa* is 5–10 mm wide and up to 450 mm long

(horizontal). *Palaeophycus tubularis* is 5.5–12 mm wide. *Planolites* isp. is 7.5–10 mm wide. *Chondrites* isp. is 1.5–4.5 mm wide and have branch lengths up to 55 mm (bedding-plane view). This ichnofabric occurs in Facies 1 in the uppermost beds of the formation. These sandstone bedsets are exemplified by extremely high degrees of bioturbation (BI = 4–6; mean 5) and moderate ichnodiversities. *Planolites* isp. overprints *Macaronichnus*, *Asterosoma* and *Rosselia*.

Fluctuating hydraulic conditions affected the trough area of the sub-tidal compound dunes, inferred from grain size and ichnological trends, in the most marine portions of the tidal embayment (Allen 1980; Dalrymple 1984; Berné *et al.* 1991). This ichnofabric represents multiple, successive-tier colonization by a mid-tier, vagile deposit-feeding *Macaronichnus* ichnoguild. Prolonged lower energy conditions furnished the correct conditions for opportunistic colonization and gradual tier replacement by: (1) shallow-tier, vagile deposit-feeding *Nereites–Planolites* ichnoguild; (2) shallow-tier, vagile probably suspension-feeding *Palaeophycus* ichnoguild; (3) mid-tier, stationary detritus-feeding *Asterosoma–Rosselia* ichnoguild; (4) deep-tier, vagile to stationary suspension-feeding *Ophiomorpha–Skolithos* ichnoguild; and (5) deep-tier, vagile deposit-feeding or chemichnion *Chondrites* ichnoguild. Frequent overprinting of the mid-tier (i.e. *Macaronichnus*, *Asterosoma* and *Rosselia* ichnoguilds) by shallow tiers (e.g. *Nereites*, *Planolites* and *Palaeophycus*) suggests that multiple erosion events occurred within the sub-tidal compound-dune field altering the position of the sediment–water interface. Alternatively, subsequent migration of the interdune area may have allowed colonization by organisms from the deeper trough in the absence of erosion.

## Palaeoecological and palaeoenvironmental implications of the Macaronichnus ichnofabrics

The Middle Eocene Man Aike Formation was deposited in a sub-tidal compound-dune field in a tide-dominated coastal embayment. Beds within the compound-dune troughs were initially unbioturbated, but as hydraulic energy decreased, to just below the threshold of sediment transport, they became colonized by vagile, deposit-feeding organisms – *Macaronichnus* (Fig. 8A). *Macaronichnus* represents the activity of vagile, deposit-feeding worms resident in the areas of the sub-tidal compound-dune field with the highest energy. Cross-bedded zones with no or sparse bioturbation reflect energetic periods in which the benthic boundary layer shear stress was
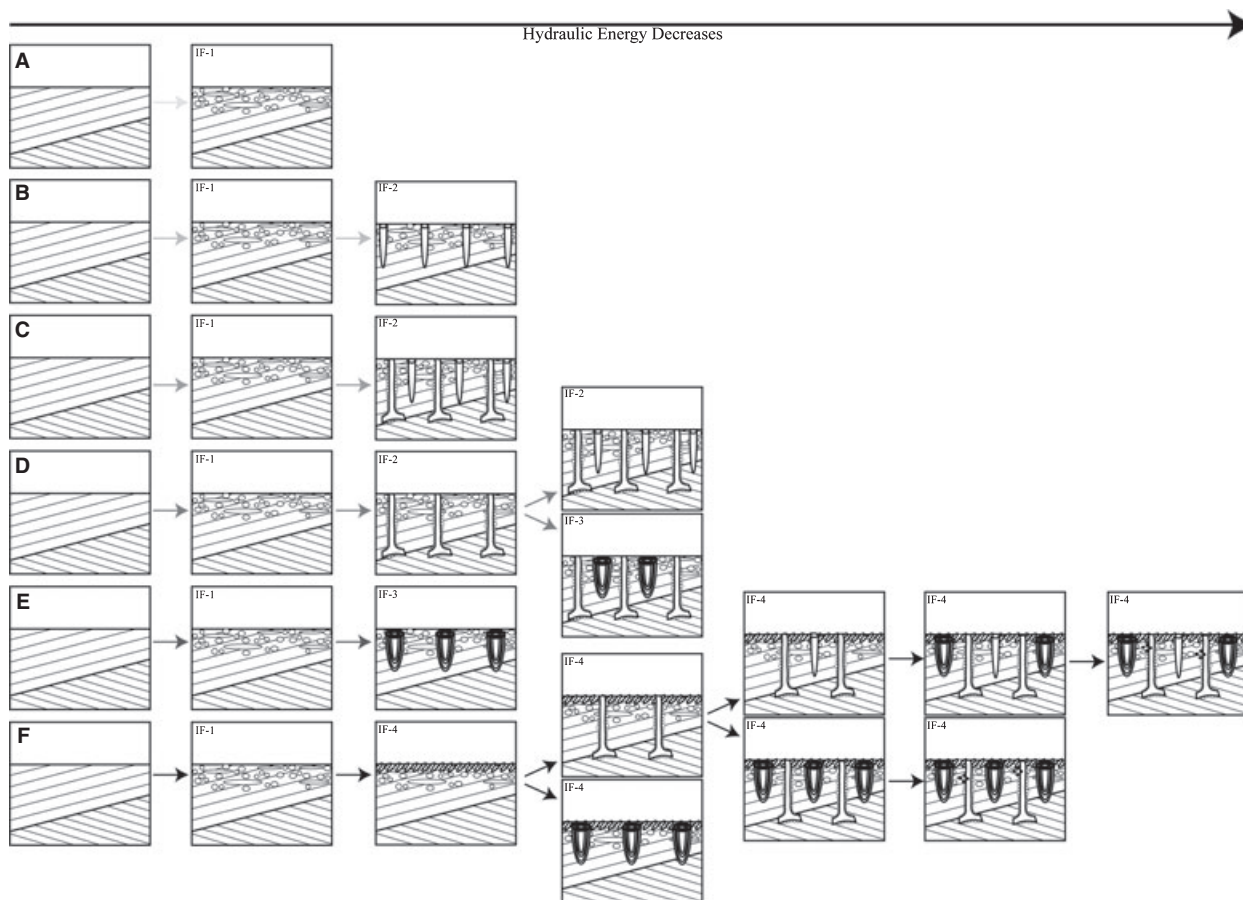
*Fig. 8.* Distribution and dynamics of the different *Macaronichnus* ichnofabrics in the Middle Eocene Man Aike compound-dune field. (A) Compound-dune stabilization with single colonization events by deposit feeders (*Macaronichnus*). (B) Compound-dune stabilization with multiple colonization events by deposit (*Macaronichnus*) and suspension (*Skolithos*) feeders in the upper trough area. (C) Compound-dune stabilization with multiple colonization events by deposit (*Macaronichnus*) and suspension (*Ophiomorpha* and *Skolithos*) feeders in the upper trough area. (D) Compound-dune stabilization with multiple colonization events by deposit (*Macaronichnus*), suspension (*Ophiomorpha*) and detritus (*Asterosoma*) feeders in the upper and lower trough areas. The position of the upper and lower trough areas changes with subsequent compound-dune migration. (E) Compound-dune stabilization with multiple colonization events by deposit (*Macaronichnus*) and detritus (*Asterosoma*) feeders in the lower trough area. (F) Compound-dune stabilization and deactivation, that is, abandonment, with multiple colonization events by deposit (*Macaronichnus*, *Nereites* and *Chondrites*), suspension (*Ophiomorpha* and *Skolithos*) and detritus (*Asterosoma* and *Rosselia*) feeders. Compound-dune migration resumes with a subsequent change in position of the upper and lower trough areas.

intolerable to the infaunal community (Beynon & Pemberton 1992). Initial colonization by the *Macaronichnus* association, that is, IF-1, suggests that the bottom waters were agitated, well oxygenated and nutrient rich (Saunders & Pemberton 1988; Pemberton *et al.* 2001). The overall varying degree of bioturbation in IF-1 most likely reflects fluctuations in the duration of the individual colonization windows.

With the continued reduction in depositional energy, opportunistic vagile to stationary, mostly suspension-feeding (*Ophiomorpha, Skolithos* in IF-2, IF-3 and IF-4) and stationary, detritus-feeding (*Asterosoma* in IF-3 and IF-4) ichnoguilds inhabited the substrate (Fig. 8B–E). Moderate to strong unidirectional currents affected the trough areas of the migrating sub-aqueous compound dunes (Allen 1980; Dalrymple 1984; Buck 1987; Berné *et al.* 1991;

Pollard *et al.* 1993; Desjardins *et al.* 2012). In the upper trough areas, food particles were kept in suspension promoting the opportunistic settlement of these areas by hemi-sessile, suspension-feeding infauna (Fig. 8B–D). As a means of escaping the instability at the sediment–water interface, these organisms construct deeply penetrating, wall re-enforced, vertical domiciles (Pemberton & Frey 1984; Saunders & Pemberton 1988; Pemberton *et al.* 1992, 2001). Because these trace fossils are commonly constructed below the zone of active physical reworking, preservation potential of the resulting association is high. In the lower trough areas, prolonged lower energy conditions allowed opportunistic colonization by stationary, detritus-feeding infauna (Fig. 8D–E). By reconstructing the palaeoecology of the tracemakers, *Asterosoma* producers are

presumed to feed on nutrient-rich, fine-grained material deposited during these low-energy periods. *Asterosoma* is a mid-tier burrow, with the trace-maker sustaining contact with the sediment–water interface to feed and maintain its domicile (Pemberton *et al.* 2001).

*Macaronichnus* IF-4 reflects multiple stages of colonization within the sub-tidal compound-dune field. Increased ichnodiversity in this ichnofabric suggests that conditions within the embayment were close to fully marine. Aggrading dune bedforms underwent fluctuating hydraulic regimes (Fig. 8F). The initial decrease in hydraulic gradient allowed colonization by deep-tier suspension and mid-tier detritus-feeding infauna represented by *Ophiomorpha*, *Skolithos* and *Asterosoma*. Overprinting of deep-to mid-tier ichnoassemblages by shallow-tier suites, for example, *Nereites* and *Planolites*, suggests that subsequent migration of the compound interdune area introduced horizontal trace fossils from the deeper trough without erosion or multiple erosional events occurred within the aggrading sub-tidal compound dunes. *Nereites* represents a grazing structure (pascichnia), in which the organism probed and backfilled sediment laterally around its burrow in various directions at regular intervals (Seilacher 2007). The finer and more nutritious fraction of the excavated sediment would have been selectively ingested, passed through the gut and subsequently backfilled behind the organism (Seilacher 2007). With continued sediment aggradation and burial, a deep-tier, deposit-feeding or chemichnion trace fossil assemblage, that is, *Chondrites*, overprinted the sub-tidal compound dunes. *Chondrites*, a well-known facies-crossing trace fossil, are a common element of the *Cruziana* ichnofacies (Pemberton *et al.* 2001). *Chondrites* may represent tunnels produced by endobenthic, deposit feeders (Bromley & Ekdale 1984; Pemberton *et al.* 2001) or by chemo-symbiotic organisms that utilize $H_2S$ of the interstitial water to feed bacterial endosymbionts (Seilacher 1990, 2007). Its occurrence in these clastic units indicates that the burrow system was produced deep within the sediment partly in the anaerobic zone below the surficial oxidized zone (Bromley & Ekdale 1984). *Nereites* and *Chondrites* represent complex feeding strategies that are generally associated with fully marine conditions.

## Conclusions

Detailed ichnofabric analysis coupled with a comprehensive sedimentological study provided the means of determining the limiting factors present during the accumulation of the Middle Eocene *Macaronichnus*-bearing tidal-embayment deposits. Four recurrent *Macaronichnus* ichnofabrics (IF-1 to IF-4) were documented in the compound-dune complex of the Man Aike Formation. This investigation revealed how colonization trends in a high-energy, tide-dominated coastal embayment are controlled by ecological factors specific to the different sub-environments within the sub-tidal compound-dune field. Differences in the observed *Macaronichnus* ichnofabrics were linked to changes in local hydraulic conditions in the upper to lower trough of the compound interdune areas. Upper trough areas are characterized by trough to planar-tabular cross-stratified, moderate to highly bioturbated (*Macaronichnus* IF-1 to IF-2) sandstone. The combination of high-energy physical sedimentary structures, coarser grain sizes and high-energy resilient ichnofauna (e.g. *Macaronichnus*, *Ophiomorpha*, *Skolithos*) indicates the prevalence of strong to moderate uni-directional tidal currents. Lower trough areas were moderate to completely bioturbated (*Macaronichnus* IF-3 and IF-4), suggesting that prolonged lower energy conditions or dune migration ceased during colonization by the shallow to mid-tier, deposit and detritus-feeding (*Nereites* and *Asterosoma*) ichnoguilds.

In the Man Aike Formation, the *Macaronichnus* tracemaker was the first to colonize the shifting sandy substrates. This tracemaker appears to inhabit an ecological niche, that is, at least temporarily, intolerable for other organisms. Overprinting by other ichnoguilds occurred only after physiochemical conditions become favourable (i.e. fluctuations in hydraulic energy, sedimentation rate and degree of physical reworking) and the colonization window length increased.

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