Geobios xxx (xxxx) xxx

Contents lists available at ScienceDirect

Geobios

journal homepage: www.elsevier.com/locate/geobio

Macaronichnus ‘co-occurrence’ in offshore transition settings: Discussing the role of tidal *versus* fluid muds influence ☆

Francisco J. Rodríguez-Tovar *, Fernando García-García

Departamento de Estratigrafía y Paleontología, Universidad de Granada, 18002 Granada, Spain

A R T I C L E I N F O

Article history:
Received 5 December 2022
Accepted 27 July 2023
Available online xxxx

Keywords:
Trace fossils
Macaronichnus
Ecological segregation
Mud deposition
Tortonian
Betic Cordillera

A B S T R A C T

Macaronichnus is a key trace fossil in palaeoceanographic, palaeoclimatic, and petroleum exploration research. Small ichnosubspecies such as *Macaronichnus segregatis segregatis*, *M. s. lineiformins*, *M. s. maeandriformis* and *M. s. spiriformis*, typically occur in wave-dominated foreshore sands where large *M. s. degiberti* was never found. The latter shows a wide environmental distribution, occurring in sandy deposits of tidal channels, tidal bar sand sandridges, tidal-flat sand sheets, shorefaces, bioturbated sandy shelf, shelf storm-sheets, shelf sand ridges, and upper slopes. Small *M. segregatis* and large *M. s. degiberti* have not been observed to date due the ecological segregation of the tracemakers. An abundant record of large *M. s. degiberti* in a Tortonian (Late Miocene) mixed carbonate-siliciclastic unit from the Betic Cordillera (southern Spain) has been studied. Occurrence of *M. s. degiberti* is the result of the interaction of tidal and waves, storm influenced environment determining high-energy conditions and associated palaeoenvironmental parameters as shifting substrates, organic matter availability, and oxygenated pore and bottom-waters. Locally, associated to *M. s. degiberti* appear small, sinuous traces infilled by light material that were originally assigned to *M. s. maeandriformis*, and very rare *M. s. spiriformis*. However, the absence of the typical rim of *Macaronichnus* avoid a conclusive assignment. The coexistence of both small traces (?*M. s. maeandriformis*) and large *M. s. degiberti* is identified in the deposits underlying mudstone layers, revealing the importance of mud deposition during tidal slack water intervals or linked to fluid mud events favouring the co-occurrence of the trace makers of both *Macaronichnus* ichnosubespecies. This fact would have significant palaeobiological and palaeoecological implications, and could be the first record of both ichnosubspecies in the same intervals.

1. Introduction

A number of recent studies have described the use of ichnology (trace fossils analysis) as an effective tool in sedimentary basin research, and to evaluate the effect of bioturbation on rocks’ flow-media properties. Several ichnotaxa such as *Macaronichnus* can indicate highly specific palaeoenvironmental conditions (Rodríguez-Tovar and Aguirre, 2014; Uchman et al., 2016; Quiroz et al., 2019; Miguez-Salas et al., 2020, 2021) and petroleum potential (Gingras et al., 2002; Dafoe et al., 2008a,b; Gordon et al., 2010; Dorador et al., 2021).

Macaronichnus segregatis (Clifton and Thompson, 1978) is the type ichnospecies of *Macaronichnus*. It consists of an intrastratal, preferentially horizontal trace with a non-branching cylindrical structure spanning 3–5 mm in diameter. It occurs typically in sand-rich, shallow-marine (up to foreshore), high-energy settings at middle to high latitudes. This trace is produced during feeding processes (pascichnial behaviour; Clifton and Thompson, 1978; Pemberton et al., 2001; Gingras et al., 2002; Nara and Seike, 2004; Seike, 2009). Small ichnosubspecies such as *M. s. segregatis* Clifton and Thompson, 1978, *M. s. lineiformins* Bromley and Uchman in Bromley et al., 2009, *M. s. maeandriformis* Bromley and Uchman in Bromley et al., 2009, and *M. s. spiriformis* Bromley and Uchman in Bromley et al., 2009, typically occur in wave-dominated foreshore sands (Seike et al., 2011; Nara and Seike, 2019).

The ichnosubspecies *M. s. degiberti* Rodríguez-Tovar and Aguirre, 2014, was proposed for large *Macaronichnus* (4–12 mm in diameter) with occasional true branching with simultaneous sort (Bromley, 1990) and locally showing obliquely to vertically oriented galleries relative to bedding planes (Rodríguez-Tovar and Aguirre, 2014). Specimens of *M. s. degiberti* occur in deeper, more variable environments from the middle to outer shelf and deep-sea environments including areas affected by

---

☆ Corresponding editor: Emmanuel Fara.

* Corresponding author.

E-mail address: fjrtovar@ugr.es (F.J. Rodríguez-Tovar).

https://doi.org/10.1016/j.geobios.2023.07.001
0016-6995/© 2023 The Author(s). Published by Elsevier Masson SAS.

Please cite this article as: F.J. Rodríguez-Tovar and F. García-García, *Macaronichnus* ‘co-occurrence’ in offshore transition settings: Discussing the role of tidal *versus* fluid muds influence, Geobios, https://doi.org/10.1016/j.geobios.2023.07.001

bottom-currents (Rodríguez-Tovar and Aguirre, 2014; Knaust, 2017; Pérez-Asensio et al., 2017; Nara and Seike, 2019; Miguez-Salas et al., 2020, 2021). *M. s. degiberti* is interpreted as revealing an exploratory behaviour (sequorichnia), aiming for copulation (Nara and Seike, 2019). Thus, *M. s. degiberti* has a wide environmental distribution, occurring in sandy deposits of tidal channels, tidal bar sand sandridges, tidal-flat sand sheets, shorefaces, bioturbated sandy shelf, shelf storm-sheets, shelf sand ridges, and upper slopes (Masuda and Yokokawa, 1988; Nara, 1998, 2014; Tamura and Masuda, 2005; Kotake, 2007; Nara et al., 2007, 2017; Seike et al., 2011; Olariu et al., 2012; Pearson et al., 2013; Rodríguez-Tovar and Aguirre, 2014; Pérez-Asensio et al., 2017). As indicated by Nara and Seike (2019), *M. s. degiberti* has not been found in wave-dominated foreshore sands where small ichnosubspecies (i.e., *M. s. segregatis*, *M. s. lineiformins*, *M. s. maeandriformis*, and *M. s. spiriformis*) typically occur. The absence of co-occurring *Macaronichnus segregatis* (*M. s.*) and *M. s. degiberti* suggests that this could be due to ecological segregation: is it the case?

Here the occurrence of large *M. s. degiberti* in a mixed carbonate-siliciclastic unit embedded into a Tortonian (Late Miocene) planktonic-rich marl-dominated succession in the Betic Cordillera (southern Spain) is presented. Moreover, the presence of small burrows previously assigned to *M. s. maeandriformis* could be the first coetaneous record of both small and large *Macaronichnus*, with significant palaeobiological and palaeoecological implications.

2. Facies associations and *Macaronichnus* distribution

The studied outcrop is located in the central sector of the Betic Cordillera (southern Spain; Fig. 1(A–C)). Selected section belongs to an Upper Miocene unit into the marine infilling of a Neogene-Quaternary Basin in the central part of the Cordillera. This unit consists of a 200 m thick, plankton-rich marls succession alternating with 5–10 m thick, bioclastic sandstone units deposited during the late Tortonian (Soria et al., 2003; Fig. 1(D)). It has been interpreted as representing the transition between shelf to pelagic basin environments (Giannetti et al., 2018). *Macaronichnus* appears in one of the mixed units; a 7 m thick, sharp-based, tabular-shape fining-upward mixed siliciclastic-carbonate unit (Fig. 2(A, B)).

From bottom to top, four facies associations (FA) have been identified in the unit containing *M. s. degiberti* (Fig. 2(C, D))

- FA-1: mixed bioclastic-siliciclastic coarse-grained sandstone dominated by *Ophiomorpha*;
- FA-2: highly-burrowed massive medium-grained mixed sandstones deposits dominated by *M. s. degiberti*;
- FA-3: planar cross-stratified well-segregated mixed bioclastic-siliciclastic sandstones deposits with small traces (?*M. s. maeandriformis*) and *M. s. degiberti*;
- FA-4: highly-burrowed fine-grained sandstone with mudstone layers alternating dominance of *M. s. degiberti* and ?*M. s. maeandriformis.*

FA-1. Mixed bioclastic-siliciclastic coarse-grained sandstone dominated by *Ophiomorpha*. This facies association occurs at the lowermost part of the studied unit. It is represented by massive, poorly-sorted coarse-grained sandstones to granules with scattered pebble clasts (Fig. 3(A)). Scattered organic terrestrial particles are also common (Fig. 3(B)). Disarticulated and broken bivalves and brachiopod shells (see brachiopod classification in Giannetti et al., 2018) appear into coarse (1–2 mm in diameter) and medium-grained (0.2–0.3 mm in diameter) sand matrix (Fig. 3(B)). Other bioclastic remains such as bryozoans, red algae and echinoids are also present. Planktonic and benthic foraminifera are common. Quartz is the main siliciclastic component and common peloids of detrital glauconite are found within the sandy matrix. Irregular, mud-pebble rip-up clasts appear aligned in some stratigraphic horizons (Fig. 3(C, D)). The ichno-assemblage differentiated in these deposits is dominated by *Ophiomorpha* and includes rare *M. s. degiberti* and *Bichordites monastiriensis* (Fig. 3(D)).

FA-2. Highly-burrowed massive medium-grained mixed sandstones deposits dominated by *M. s. degiberti*. It is mainly represented by massive, ungraded, moderately-sorted medium sandstones. Diffuse micro-hummocky cross-stratification (HCS) rarely appears at the top of unsegregated siliciclastic-bioclastic fine- to medium-grained mixed beds (Fig. 3(E)). The ichno-assemblage is dominated by *M. s. degiberti* which is concentrated in some horizons or dispersed into the sandstone beds (Fig. 3(F, G)). They present large forms, 5–15 mm in diameter and segments up to 25 cm long, densely packed, endichnial, cylindrical, straight to slightly sinuous, filled with the same brownish material that the host sediment and showing a darker (greenish) rim. Cross-cutting relationships are frequent. Real branching and regularly spaced mantle lobes (Miguez-Salas et al., 2020) are occasionally observed.

FA-3. Planar cross-stratified, well-segregated mixed sandstones deposits with ?*M. s. maeandriformis* and *M. s. degiberti.* Tractive sedimentary structures as planar cross-lamination and planar-lamination with siliciclastic (dark laminae) and bioclastic (light laminae) segregation are identified at the middle to upper part of the unit in transition to facies association FA-4. Small traces (?*M. s. maeandriformis*; see below) and *M. s. degiberti* occurs in theses cross-laminated mixed sandstones (Fig. 3(H)).

FA-4. Highly-burrowed fine-grained sandstone with mudstone layers in which there is an alternating dominance of *M. s. degiberti* and ?*M. s. maeandriformis*. The small traces (?*M. s. maeandriformis*) and large *M. s. degiberti* only occur together in the upper part of the mixed bioclastic-siliciclastic unit, consisting of 20 cm thick horizontal rhythmic alternations of mixed bioclastic-siliciclastic, fine-grained, burrowed, brownish sandstone beds and single or grouped light grey, thin mudstone layers (up to 1 cm thick; Fig. 4(A)). Thicker mudstone intervals appear in groups of two or three paired-mudstone layers (Fig. 4). Thin, massive sandstone laminae of up to 1 cm thick can appear within the paired-mudstone layers (Fig. 4(E)). Mudstone intervals are commonly homogeneous and structureless (Fig. 4(E)). The lateral continuity of mudstone layers is cut by soft-sediment deformations (i.e., water-escape structures; Fig. 4(F)). Load structures at the sandstone-mudstone boundary can be observed. Traction-driven sedimentary structures (i.e., laminated-deposits) are absent.

As indicated above, sandstone beds are intensively burrowed by small traces and large *M. s. degiberti*. However, the assignment of the small traces to *M. s. maeandriformis*, and very rare *M. s. spiriformis*, as originaly proposed by Giannetti et al. (2018), can be dubious. This refers to unbranched forms, with a prevailing horizontal to slightly oblique development, consisting of very thin tubes, ca. 2 mm in diameter, up to 5–7 cm long, and showing a pale filling with whitish colour, contrasting with the brownish colour of the detritus-rich calcarenites (Giannetti et al., 2018). In thin sections, the filling is clearly more felsic-rich than the surrounding sediment. Our study agrees with the original description, but the typical rim in *Macaronichnus* consisting of high density material (dark coloured mafic sand grains) surrounding the low density material (light-coloured felsic sand) of the burrow core, is not observed. Thus, a conservative position using ?*M. s. maeandriformis* is preferable. According to our observations, small forms mainly show a dense distribution in the uppermost 5 cm of sandstones underlying mudstone layers (Fig. 4(B, C)).?*M. s. maeandriformis* are also abundant in sandstone beds overlying mudstone layers,

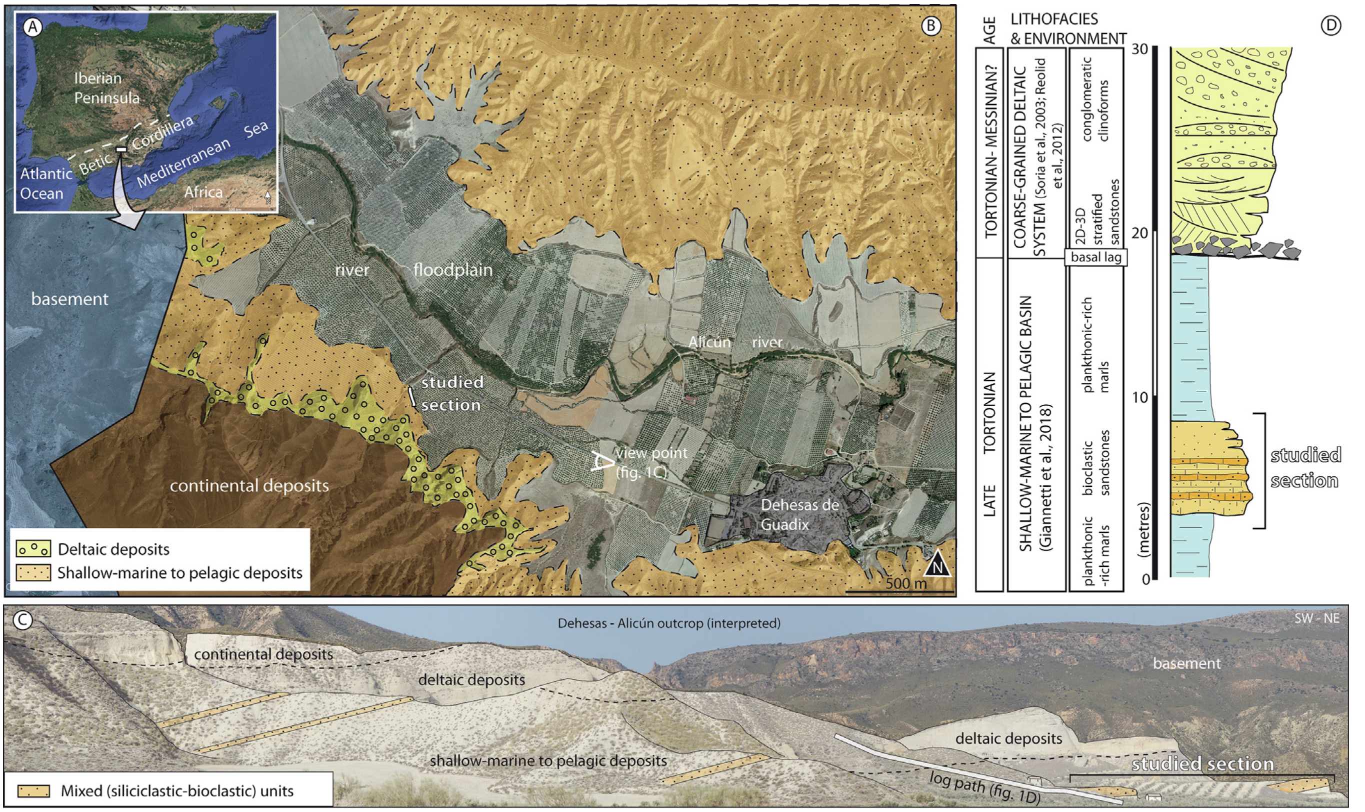


Fig. 1. Stratigraphic setting. **A.** Location map of the study area within the Betic Cordillera at the south of the Iberian Peninsula. **B.** Interpreted satellite image of the study area close to Dehesas de Guadix village (modified from Soria et al., 2003). **C.** Interpreted panoramic view of the Dehesas de Guadix outcrop. The lower mixed unit showed at the lower right corner of the picture is the *Macaronichnus* burrowed unit focus of this study. **D.** Synthetic stratigraphic log (see log path in C).

but are less common and dispersed. Small forms crosscutting large *M. s. degiberti* have been recognized (Fig. 4(D)).

3. Discussion

3.1. Sedimentary processes and environment of *Macaronichnus segregatis degiberti*

The basal clast lag and lowermost poorly-sorted deposits (FA-1) consist of grains reworked by high-energy currents from different more proximal sources such as continental areas (organic terrestrial particles), beach (rounded pebbles), coastal to shallow-water bioclastic-carbonate factory (bioclasts) and underlying marls (detrital glauconite peloids). The abundance of coal grains suggests deposition fairly close to a terrigenous source, indicative of direct river inputs (Mulder and Alexander, 2001). Abundant detrital glauconite peloids are probably reworked from underlying marls by storms (Amorossi, 1995). Fragments and broken shell accumulations of a foramol to bryomol bioclastic association with red algae presumably represent storm beds formed by wave-reworking components of carbonate factory loci in the photic to oligophotic zone (Pomar et al., 2012). Particles from different proximal sources indicate wave reworking from the shoreline to shallow-marine settings. The aligned shale clasts mark repeated erosion and deposition linked to unstable flow. There is no evidence for channel (i.e., incised surfaces, channel-fill sequences); non-channelized, turbulent high-energy currents (i.e., storm-surge currents) are likely at the origin of the aligned rip-up clasts. Non-segregated siliciclastic and bioclastic fractions point to a subenvironment dominated by storm wave activity and lack influence of tide currents (Chiarella et al., 2012). The absence of wave rippled beds indicates water depths below fair-weather wave base. Storm-wave driven currents are indicated by combined flow structures (FA-2) as HCS (Dott and Bourgois, 1982; Duke, 1985; Duke et al., 1991; Cheel and Leckie, 1992; Dumas et al., 2005). The sharp base with significant lithological break (coarser-grained, accumulation of storm-wave-reworked particles from coastal settings and from underlying marls (i.e., detrital peloidal glaucony) have been proposed as criteria for identifying forced-regressive shorefaces (Plint, 1988; Ainsworth et al., 2000; Fitzsimmons and Johnson, 2000; Posamentier and Morris, 2000). Sharp base would represent a regressive surface of marine erosion (RSME). During the regressive stage, a storm-wave dominated shoreface to upper offshore transition (with no tidal influence) was developed (Fig. 5(A)). At the middle part of the unit, segregated siliciclastic and bioclastic fractions in cross-bedded mixed sandstones (FA-3) point to a subenvironment influenced by tide currents (Chiarella and Longhitano, 2012). It is interpreted as a shallow-water setting with wave and tidal influences (Fig. 5(B)). The upper part of the unit is represented by siliciclastic and bioclastic components (FA-4) that are finer than lower deposits (FA-3); the lack of traction-driven (i.e., wave- or tidal-driven currents) sedimentary structures reveal a more distal setting than previous described facies associations.

The vertical change represented in the complete unit is interpreted as a consequence of a progradational to retrogradational evolution (a transgressive to regressive cycle) of a storm wave-dominated (regressive stage), tidal-influenced mixed (transgressive stage) coastal to offshore transition system. *M. s. degiberti* appears together with ?*M. s. maeandriformis* only during the transgressive phase of the cycle, when tidal influence (represented by different signals, i.e., density segregation of siliciclastic and carbonated grains) occurs between storm events. Thus, the origin of mudstones layers is key to understand the environmental conditions favouring the *Macaronichnus* co-occurrence.

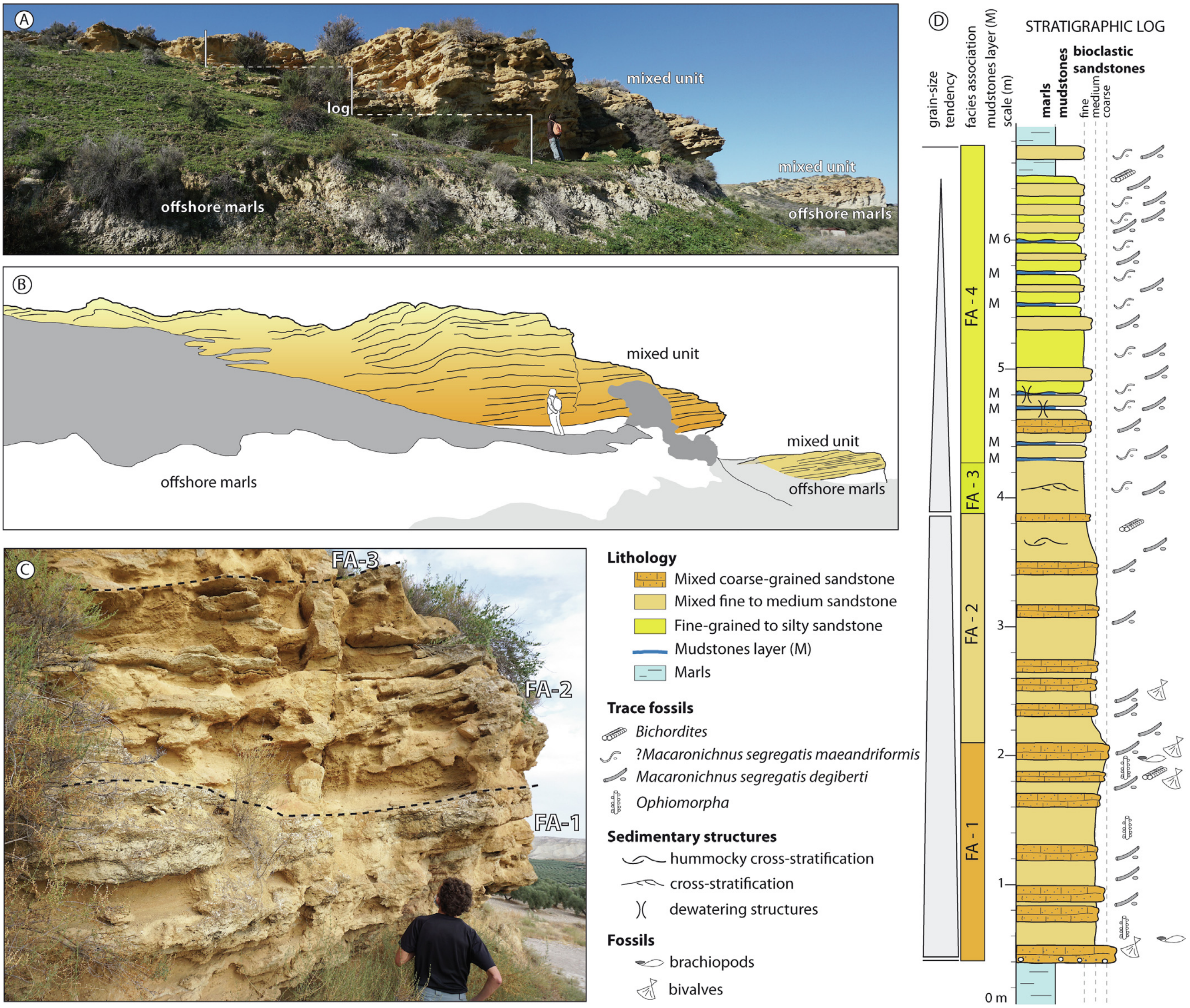
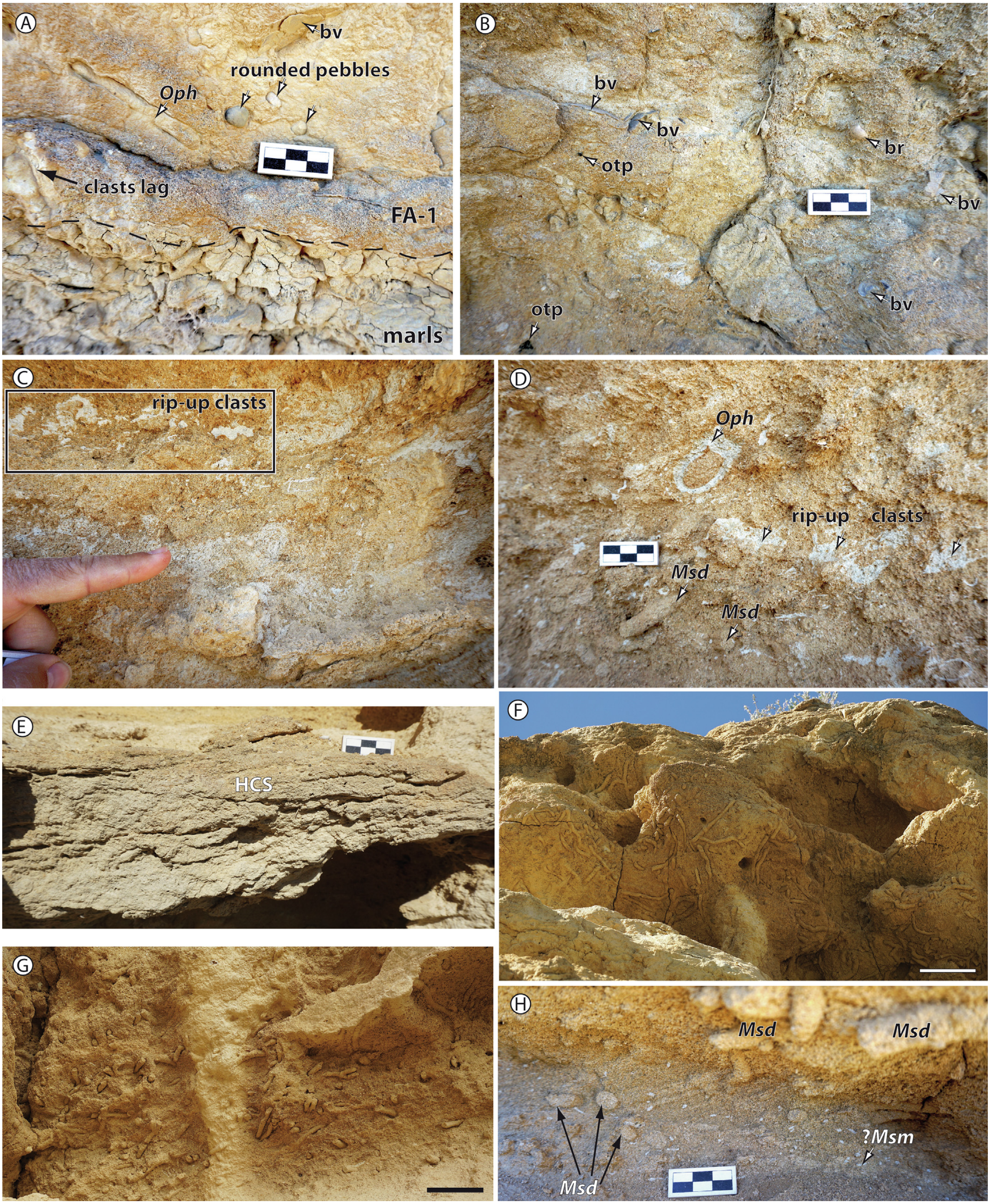


Fig. 2. Stratigraphic log and facies associations of the study section. **A, B.** Panoramic view of the outcrop (log path is marked) and line drawing showing the brownish mixed siliciclastic-carbonate unit embedded into grey marls (a person to scale). **C.** Detail of the lower part of the mixed bioclastic-siliciclastic unit. Bedding is represented by alternating of friable and diagenetic calcite concreted in sandstone beds. Vertical distribution of facies associations is marked (FA-1–3; see text for description) (person to scale). **D.** Stratigraphic log of the *Macaronichnus* burrowed mixed unit. FA-1–4: Facies associations (see text for description).

3.2. Palaeoecological conditions and the Macaronichnus 'co-occurrence'

In the last years two main controlling factors have been invoked to affect the distribution of *Macaronichnus* trace makers: high-energy conditions, and food availability. Quiroz et al. (2010, 2019) invoked upwelling and primary productivity as major controls for the occurrence of *Macaronichnus*. Traditionally, this occurrence was exclusively related to the environmental physical conditions. Release of nutrients from bottom sediments and their diffusion into the water column is an important mechanism of nutrient loading reported in fluid muds (Mehta, 1991). The record

Fig. 3. Main sedimentary and ichnological features in outcrop of the facies association FA-1 (A–D), facies association FA-2 (E–G) and facies association FA-3 (H). **A.** Erosive, sharp-based (dashed line) mixed deposits represented by a basal lag of rounded pebble clasts overlain by coarse-grained siliciclasts and bioclasts (bv: broken bibalve) with *Ophiomorpha* (*Oph*) overlying planktonic-rich marls. **B.** Poorly-sorted, massive matrix-supported granules to coarse siliciclastic sands with broken bioclastic assemblage (bv: bivalves; br: brachiopods) and organic terrestrial particles (otp) occurring at the lower part of the mixed unit. **C, D.** Massive, unsegregated, burrowed (*Oph*: *Ophiomorpha*; *Msd*: *Macaronichnus segregatis degiberti*) medium-grained mixed deposits alternating with light-coloured rip-up clasts layers. **E.** Microhummocky cross-stratification (HCS) at the top of a non-burrowed, unsegregated, fine-grained mixed bed. It appears at the transition of facies associations FA-1–2 in the middle part of the unit. **F, G.** Abundant horizontally-oriented *Macaronichnus segregatis degiberti* bearing basal horizons (F) or into sandstone beds (G). **H.** Planar cross-laminated mixed deposits (at the middle part of the photograph, over the scale bar) with siliciclastic (dark laminae) and bioclastic (light laminae) segregation showing transversal sections of ?*Macaronichnus segregatis maendriformis* (?*Msm*: white smallest trace fossils) and *Macaronichnus segregatis degiberti* (*Msd*). Cross-laminae are dipping toward the southwest (to the left). Non-stratified, unsegregated deposits at the top are dominated by *Msd*. Scale bars: 3 cm (A, B, D, E, H), 25 cm (F), 10 cm (G).


A
bv
rounded pebbles
Oph
clasts lag
FA-1
marls
B
bv
bv
otp
br
bv
otp
bv
C
rip-up clasts
D
Oph
rip-up clasts
Msd
Msd
E
HCS
F
G
H
Msd
Msd
?Msm
Msd

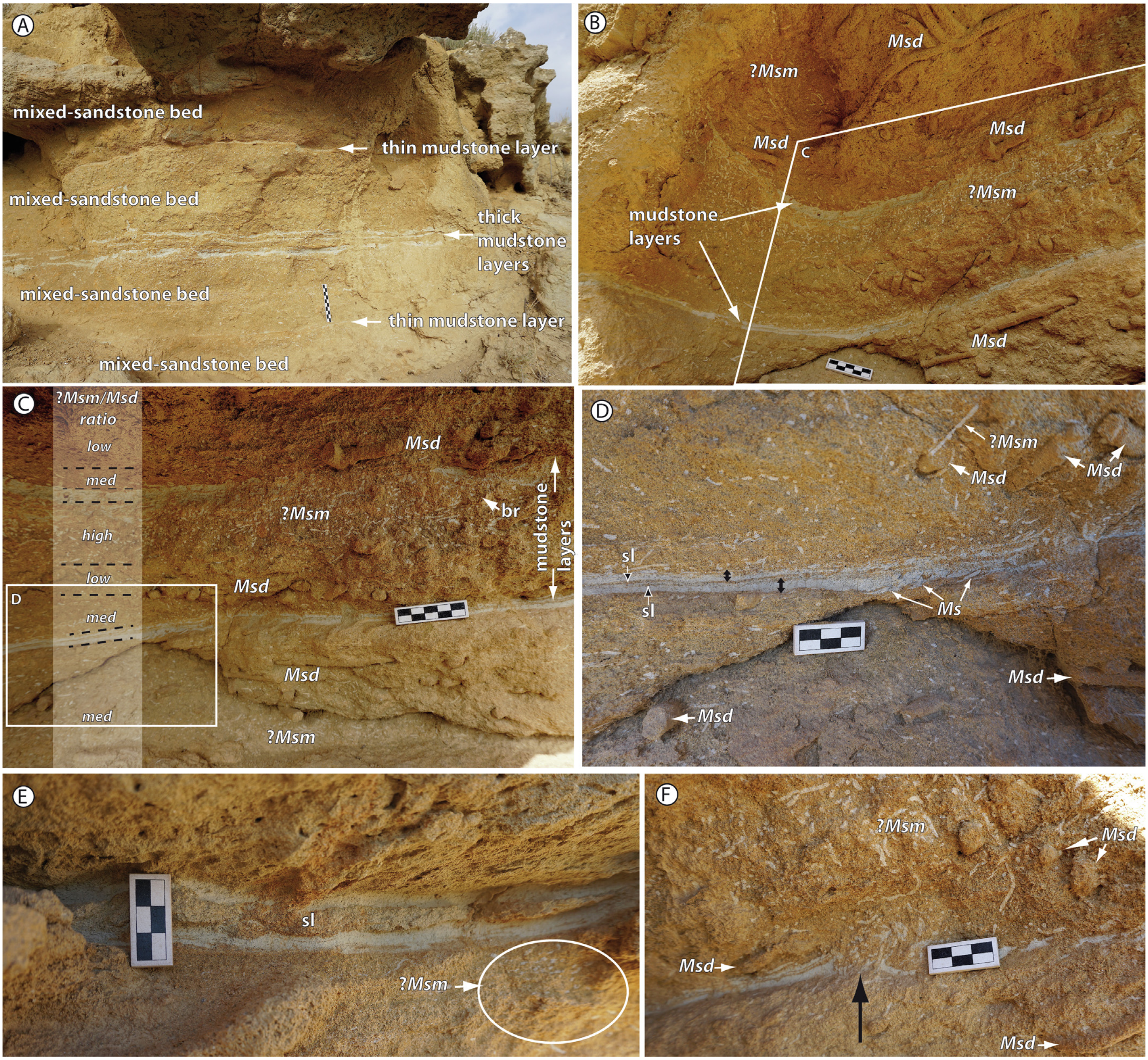


Fig. 4. Main sedimentary and ichnological features in outcrop of the facies association FA-4. **A.** Horizontal rhythmites with thick mixed-sandstone (brownish beds) and thin light grey mudstone layers alternation. The alternating of sandstone-dominated (with a single <1 cm-thick mudstone layer) and a thick grouped mudstone-layers dominated middle part of the succession presumably represents a spring-neap-spring tidal succession. Look at the discontinuous character of the mudstone layers at the left side of the photograph. **B.** ?*Macaronichnus segregatis meandriformis* (?*Msm*) and *Macaronichnus segregatis degiberti* (*Msd*) in horizontal tidal rhythmites with 10 cm-thick sandstone beds and above 1 cm-thick light grey mudstone layers alternations. **C.** Detail of B showing a qualitative vertical distribution of ?*Msm* and *Msd* ratio. Lower mudstone layer is a double-paired interval separated by thin sandstone laminae interpreted as a subordinate-tide deposit. Look at the discontinuous character of the upper mudstone layer (br: brachiopod). **D.** Detail of C showing a 1 cm-thick group of mudstone layers consisting of couple of paired mudstones intervals (black arrows) separated by thin a sandstone laminae (sl) interpreted as a subordinate-tide deposit. Abundant ?*Msm* close to mudstone layers group, three traces (arrows) coming down from the lower mud interval. Look also at a long ?*Msm* cross-cutting *Msd* at the upper-right part of the picture. **E.** A detail of a 2.5 cm-thick couple of mudstone layers with an interlayer of a thin undulated (rippled) sandstone laminae (sl). Look at diffuse internal lamination into the lower mudstone layer. **F.** Soft-sediment deformation structure (i.e., water-escape; black arrow) cutting a group of paired mudstones layers. Scale bars: 10 cm (A), 5 cm (B, C), 3 cm (D-F).

of abundant *M. s. degiberti* in sandy contourite deposits has been related to increase food supply within bottom current outflow (Miguez-Salas et al., 2020, 2021).

The original assignment of the small traces to *M. s. maeandriformis* and to very rare *M. s. spiriformis* by Giannetti et al. (2018) must be considered with caution. Even if *Macaronichnus* has been profusely studied, several fundamental questions on palaeoenvironmental and palaeobiological aspects remain unanswered, especially the reciprocal exclusion of the small *M. segregatis* and the large *M. s. degiberti*. Small together with large *Macaronichnus* have not been observed to date probably due ecological segregation: small *M. s.* and *M. s. degiberti* have been related to different trace makers showing a variable behavior and living in incompatible habitats. Occurrence of the large *M. s. degiberti* in the fossil record is in agreement with continental shelf sea-floor environments (i.e., middle to outer ramp) from where they have been identified (Seike et al., 2011; Rodríguez-Tovar and Aguirre, 2014; Pérez-Asensio et al., 2017). Nevertheless, ichnosubspecies of small *M. s.* are

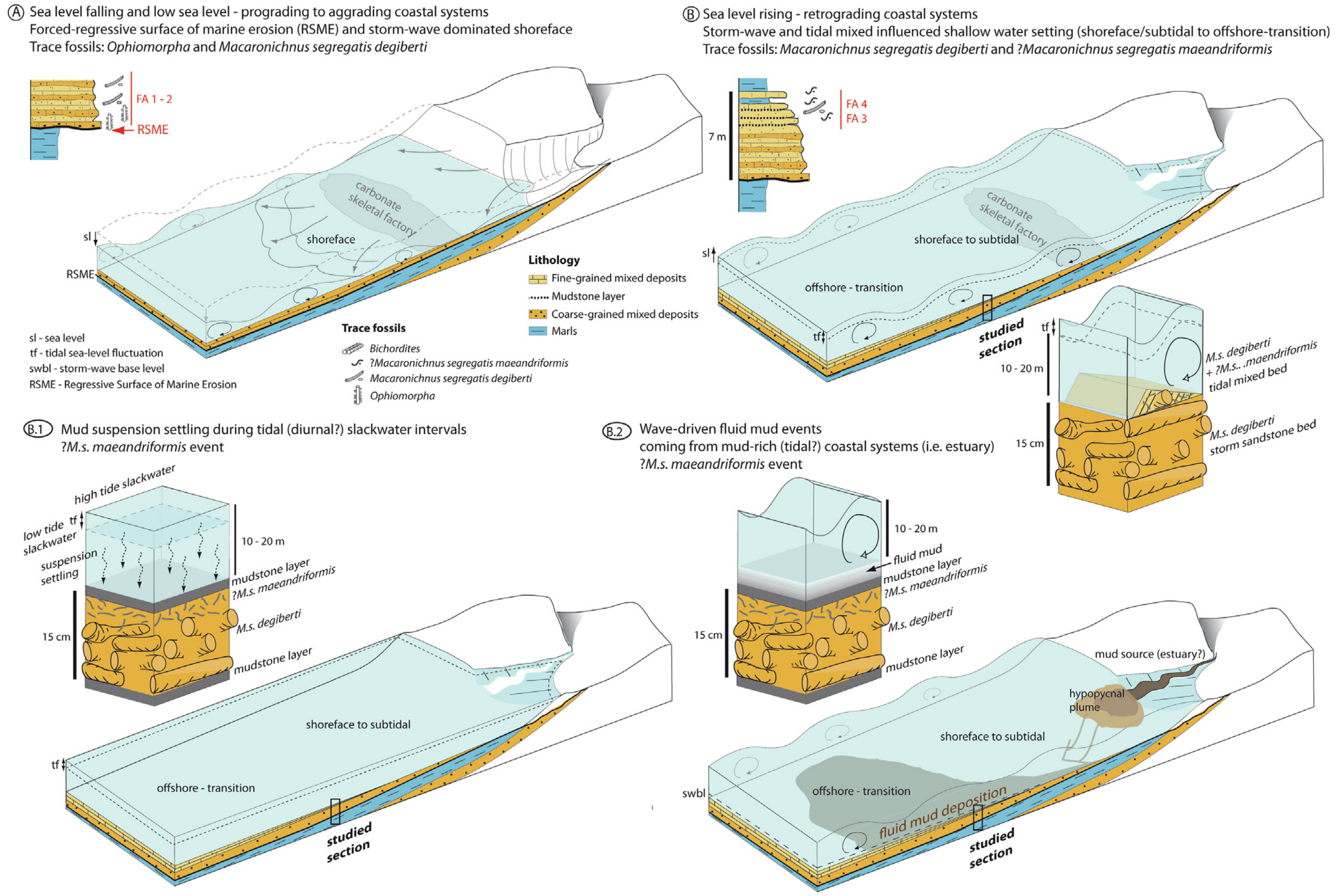


Fig. 5. Depositional model evolution from a regressive storm-wave dominated shoreface to offshore transition with *Ophiomorpha* and *M. s. degiberti* (*Msd*) **(A)**, to a transgressive storm-wave dominated and tidally-influenced mixed shoreface/subtidal to offshore transition with *M. s. d.* and ?*M. s. maeandriformis* (?*Msm*) **(B)**. *M. s. d.* and ?*M. s. m.* appear together in storm/tidal influenced mixed dunes. Two hypothetical patterns for ?*M. s. m.* events linked to mud deposition are proposed, as tidal slack water intervals (**B.1**) or fluid mud events (**B.2**).

mainly associated to the coastal, foreshore environment of high-energy beaches. The record of discrete intervals with abundant *M. s.* (the *Macaronichnus* Assemblage) has been mainly located into the foreshore but also in the upper shoreface-foreshore transition, and in reflective shoreline it may occur down in the upper shoreface (Pemberton et al., 2001, 2012: Hobbs, 2003; Uchman and Krenmayr, 2004; MacEarchern and Bann, 2008; Buatois and Mángano, 2011). According to this, the *Macaronichnus* Assemblage is usually integrated as part of the *Skolithos* ichnofacies, but is also assigned to the *Skolithos-Cruziana* assemblage. The punctual presence of small *Macaronichnus* in shoreface deposits was explained by the occurrence of a few species of *Euzonus* inhabiting subtidal (shoreface) settings and because juvenile forms of the polychaetes *Travisia* in shoreface environments are possibly the producers of the small-burrow (Seike et al., 2011). Thus, densely packed occurrences of *M. s.* are certainly diagnostic of a foreshore environment, while these dense records are not observed in shoreface settings (Seike et al., 2011).

Here, the co-occurrence, if confirmed, of both *Macaronichnus* ichnosubespecies is linked with mudstone layers. The latter could be deposited during slack water periods in between tidal currents (Fig. 5(B.1)) or they could represent fluid muds as recognized in high-energy tidal coastal environments with high concentrations of suspended-sediment (Fig. 5(B.2)). This can occur in distributary/tidal channels in tidal-dominated delta plains, middle-reach of estuaries and tidal flat (Dalrymple and Choi, 2007; Longhitano et al., 2012; Yu et al., 2017). Most of mudstone layers in the study section appear as double-mud (paired) drapes which are suggestive of shallow tidal settings where slack water deposition took place. Horizontal rhythmites appearing within the upper part of the unit record tidal cycles as described in modern tidal-dominated coasts (Dalrymple et al., 2003). Grouped mudstone layers may reflect neap-tide slack water conditions. Thin sandstone laminae separating paired mudstones are interpreted as a subordinate-tidal deposit. Most single layers analysed in our example are less than 1 cm thick. Nevertheless, fluid mud origin is not discarded for thicker mudstone layers. Ichaso and Dalrymple (2009) proposed a minimum thickness of 1 cm (0.5 cm after compaction) as a criterion for distinguishing fluid-mud layers from mudstone layers accumulated by slow, particle-by-particle settling from suspension. Fluid muds have been also reported in shallow-water offshore environments, such as the Amazon continental shelf (Kineke, et al., 1996; Traykovski et al., 2000; Puig et al., 2001; Hale and Ogston, 2015). Fluid-muds in coastal and continental shelves can be generated in both tidal- and wave-dominated environments (Ichaso and Dalrymple, 2009). From the nearshore, fluid muds can rapidly travel across continental margins as wave stress maintains highly suspended-sediment concentrations near the seafloor (Hale and Ogston, 2015). Then fluid muds coming from nearshore would trigger ephemeral environmental and biological changes in offshore seabed (i.e., bringing allochthonous organisms from coastal environments or provoking changes in behaviour among shelf organisms that adapt rapidly to the new environmental conditions). Nevertheless, the rhythmic and paired character of the mudstone layers strongly favours the hypothesis of a tidal origin for this possible co-occurrence. After mud depositions, and returning to palaeoenvironmental conditions before fluid mud event, community of small ?*M. s. maeandriformis* decreases and then disappears. The coetaneous presence of ?*M. s. maeandriformis* and *M. s. degiberti* supports the influence of palaeoenvironmental conditions favouring colonization at the same time by different trace makers. *Macaronichnus* occurrence will be the result of the interaction of tides and waves, determining high-energy conditions, and associated palaeoenvironmental parameters as shifting substrates, organic matter availability, and oxygenated pore and bottom-waters.

The discussion about the sedimentary processes (tide slack water periods *vs.* fluid mud events) and environmental conditions encouraging the *Macaronichnus* ‘co-occurrence’ is still open. Although the cohabitation of different *Macaronichnus* ichnosubespecies in modern settings has not yet been reported, the modern mixed-energy storm-wave to tidal shallow water settings (offshore transition) could represent an instance of favourable environmental conditions for such a co-occurrence.

4. Conclusions

Late Miocene deposits in the Betic Cordillera show an abundant record of large *Macaronichnus segregatis degiberti* in a mixed carbonate-siliciclastic unit, associated to a storm-wave dominated, tide-influenced shoreface/subtidal to offshore transition setting occurring during a regressive to transgressive cycle. Occurrence of *M. s. degiberti* is the result of the interaction of tides and waves, in storm-influenced environment, determining high-energy conditions, and associated palaeoenvironmental parameters such as shifting substrates, organic matter availability, and oxygenated pore and bottom-waters. Locally, associated to *M. s. degiberti* appear small, sinuous traces infilled by light material that were previously assigned to *Macaronichnus segregatis maeandriformis*, and very rare *Macaronichnus segregatis spiriformis*. However, the absence of the typical rim of *Macaronichnus* avoid a conclusive assignment. The co-existence, if confirmed, of both small ?*M. s. maeandriformis* and large *M. s. degiberti* is identified in the deposits underlying the mudstone layers, revealing the importance of mud deposition during tidal slack water intervals or linked to fluid mud events favouring the co-ocurrence of the trace makers of both *Macaronichnus* ichnosubespecies. These conditions occurred during a transgressive stage of a regressive-transgressive cycle. This observation may have significant palaeobiological and palaeoecological implications as it is the first coetaneous record of both ichnosubspecies. The latter were hitherto interpreted as an instance of ecological segregation of the trace makers in different habitats.

Data availability

No data was used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Associate-Editor, Emmanuel Fara, and the reviewer, Alfred Uchman, for their detailed and useful comments that significantly contributed to improve the manuscript. This research was funded by Grants PID2019-104625RB-100 funded by MCIN/AEI/10.13039/501100011033, and Grants BRNM-072-UGR18, A-RNM-368-UGR20 and P18-RT-4074 funded by Consejería de Universidad, Investigación e Innovación and by “ERDF A way of making Europe”. Research Group RNM178 (Junta de Andalucía), as well as the “Ichnology and Paleoenvironmental Research Group” (UGR). Funding for open access charge: Universidad de Granada / CBUA.

References

Ainsworth, R.B., Bosscher, H., Newall, M.J., 2000. Forward stratigraphic modelling of forced regressions: evidence for the genesis of attached and detached lowstand systems. In: Hunt, D., Gawthorpe, R.L. (Eds.), Sedimentary response to forced regressions. Geological Society of London, Special Publication 172, pp. 163–176.

Amorosi, A., 1995. Glaucony and sequence stratigraphy: a conceptual framework of distribution in siliciclastic sequences. Journal of Sedimentary Research 65, 419–425.

Bromley, R.G., 1990. Trace fossils: biology and taphonomy. Unwin Hyman, London.

Bromley, R.G., Uchman, A., Milàn, J., Hansen, K., 2009. Rheotactic *Macaronichnus*, and human and cattle trackways in Holocene beachrock, Greece: reconstruction of paleoshoreline orientation. Ichnos 16, 103–117.

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

Cheel, R.J., Leckie, D.A., 1992. Coarse-grained storm beds for the Upper Cretaceous Chungo Member (Wapiabi Formation), southern Alberta, Canada. Journal of Sedimentary Petrology 62, 933–945.

Chiarella, D., Longhitano, S.G., 2012. Distinguishing depositional environments in shallow-water mixed bio-siliciclastic deposits on the basis of the degree of heterolithic segregation (Gelasian, Southern Italy). Journal of Sedimentary Research 82, 969–990.

Chiarella, D., Longhitano, S.G., Sabato, L., Tropeano, M., 2012. Sedimentology and hydrodynamics of mixed (siliciclastic-bioclastic) shallow-marine deposits of Acerenza (Pliocene, Southern Apennines, Italy). Italian Journal of Geosciences 131, 136–151.

Clifton, H.E., Thompson, J.K., 1978. *Macaronichnus segregatis*: a feeding structure of shallow marine polychaetes. Journal of Sedimentary Petrology 48, 1293–1302.

Dafoe, L.T., Gingras, M.K., Pemberton, S.G., 2008a. Determinating *Euzonus mucronata* burrowing rates with application to ancient *Macaronichnus segregatis* tracemakers. Ichnos 15, 78–90.

Dafoe, L.T., Gingras, M.K., Pemberton, S.G., 2008b. Analysis of mineral segregation in *Euzonus mucronata* burrow structures: one possible method in the construction of ancient *Macaronichnus segregates*. Ichnos 15, 91–102.

Dalrymple, R.W., Choi, K., 2007. Morphologic and facies trends through the fluvial marine transition in tide-dominated depositional systems: a schematic framework for environmental and sequence-stratigraphic interpretation. Earth-Science Reviews 81, 135–174.

Dalrymple, R.W., Baker, E.K., Harris, P.T., Hughes, M.G., 2003. Sedimentology and stratigraphy of a tide-dominated, foreland-basin delta (Fly River, Papua New Guinea). In: Hasan Sidi, F., Nummedal, D., Imbert, P., Darman, H., Posamentier, H.W. (Eds.), Tropical Deltas of Southeast Asia—Sedimentology, Stratigraphy, and Petroleum Geology. SEPM, Special Publication 76, pp. 147–173.

Dorador, J., Rodríguez-Tovar, F.J., Miguez-Salas, O., 2021. Trace fossils affecting rock porosity: The complex case of *Macaronichnus*. Scientific Reports 11, 1975.

Dott, R.H., Bourgois, J., 1982. Hummocky stratification: significance of its variable bedding sequences. Geological Society of America Bulletin 93, 663–668.

Duke, W.L., 1985. Hummocky cross-stratification, tropical hurricanes, and intense winter storms. Sedimentology 32, 167–194.

Duke, W.L., Arnott, R.W.C., Cheel, R.J., 1991. Shelf sandstones and hummocky cross-stratification: new insights on a stormy debate. Geology 19, 625–628.

Dumas, S., Arnott, R.W.C., Southard, J.B., 2005. Experiments on oscillatory-flow and combined-flow bed forms: implications for interpreting parts of the shallow-marine sedimentary record. Journal of Sedimentary Research 75, 501–513.

Fitzsimmons, R., Johnson, S., 2000. Forced regressions: recognition, architecture and genesis in the Campanian of the Bighorn Basin, Wyoming. In: Hunt, D., Gawthorpe, R.L. (Eds.), Sedimentary Response to Forced Regressions. Geological Society of London, Special Publication 172, pp. 113–140.

Giannetti, A., Baeza-Carratalá, J.F., Soria-Mingorance, J.M., Dulai, A., Tent-Manclús, J. E., Peral-Lozano, J., 2018. New paleobiogeographical and paleoenvironmental insight through the Tortonian brachiopod and ichnofauna assemblages from the Mediterranean-Atlantic seaway (Guadix Basin, SE Spain). Facies 64, 24.

Gingras, M.K., MacMillan, B., Balcom, B.J., Saunders, T., Pemberton, S.G., 2002. Using magnetic resonance imaging and petrographic techniques to understand the textural attributes and porosity distribution in *Macaronichnus*-burrowed sandstone. Journal of Sedimentary Research 72, 552–558.

Gordon, J., Pemberton, G., Gingras, M., Konhauser, K.O., 2010. Biogenically enhanced permeability: a petrographic analysis of *Macaronichnus segregatus* in the Lower Cretaceous Bluesky formation, Alberta, Canada. AAPG Bulletin 49, 1779–1795.

Hale, R.P., Ogston, A.S., 2015. In situ observations of wave-supported fluid-mud generation and deposition on an active continental margin. Journal of Geophysical Research Earth Surface 120, 2357–2373.

Hobbs, T.W., 2003. Integrated ichnological, sedimentological and sequence stratigraphic analysis of along-strike variations in the Albian Upper Falher and basal Notikewin members, NW Alberta and NE British Columbia, Canada. M.Sc. Thesis, Simon Fraser University, Burnaby, British Columbia, 423 p. (Unpubl.).

Ichaso, A.A., Dalrymple, R.W., 2009. Tide- and wave-generated fluid mud deposits in the Tilje Formation (Jurassic), offshore Norway. Geology 37, 539–542.

Kineke, G.C., Sternberg, R.W., Trowbridge, J.H., Geyer, W.R., 1996. Fluid-mud processes on the Amazon continental shelf. Continental Shelf Research 16, 667–696.

Knaust, D., 2017. Atlas of Trace Fossils in Well Core. Springer, Berlin.

Kotake, N., 2007. *Macaronichnus* isp. associated with *Piscichnus waitemata* in the Miocene of Yonaguni-jima Island, Southwest Japan. In: Miller, W., III (Ed.), Trace Fossils: Concepts, Problems, Prospects. Elsevier, Amsterdam, pp. 492–501.

Longhitano, S.G., Mellere, D., Steel, R.J., Ainsworth, R.B., 2012. Tidal depositional systems in the rock record: A review and new insights. Sedimentary Geology 279, 2–22.

MacEachern, J.A., Bann, K.L., 2008. The role of ichnology in refining shallow marine facies models. In: Hampson, G.J., Steel, R.J., Burgess, P.B., Dalrymple, R.W. (Eds.), Recent Advances in Models of Siliciclastic Shallow-Marine Stratigraphy. SEPM Special Publication, pp. 73–116.

Masuda, F., Yokokawa, M., 1988. Pleistocene beach deposits in Tsukuba Upland. Tsukuba Environmerntal Studies 11, 113–122 [In Japanese with English abstract.].

Mehta, A.J., 1991. Understanding fluid mud in a dynamic environment. Geo-Marine Letters 11, 113–118.

Miguez-Salas, O., Rodríguez-Tovar, F.J., De Weger, W., 2020. *Macaronichnus* and contourite depositional settings: bottom currents and nutrients as coupling factors. Palaeogeography, Palaeoclimatology, Palaeoecology 545, 109639.

Miguez-Salas, O., Rodríguez-Tovar, F.J., De Weger, W., 2021. The Late Miocene Rifian corridor as a natural laboratory to explore a case of ichnofacies distribution in ancient gateways. Scientific Reports 11, 4198.

Mulder, T., Alexander, J., 2001. The physical character of subaqueous sedimentary density flows and their deposits. Sedimentology 48, 269–299.

Nara, M., 1998. Depositional environments and sequence stratigraphic analysis of the middle Pleistocene Kongochi Formation. Journal of Geography 107, 77–91 [In Japanese with English Abstract.].

Nara, M., 2014. The *Bichordites* ichnofabric in the Pleistocene ocean current-generated sand ridge complex. Spanish Journal of Palaeontolology 29, 191–202.

Nara, M., Fujibayashi, S., Oonaka, T., 2007. Ichnology of tidal flat systems distributed in the Miocene Shirahama Formation, Japan. In: Abstracts with Programs of the 2007 Annual Meeting 524. The Paleontological Society of Japan, p. 37.

Nara, M., Seike, K., 2004. *Macaronichnus* segregatis-like traces found in the modern foreshore sediments of the Kujukurihama Coast, Japan. Journal of Geological Society of Japan 110, 545–551 [In Japanese with English abstract.].

Nara, M., Seike, K., 2019. Palaeoecology of *Macaronichnus segregatis degiberti*: reconstructing the infaunal lives of the travisiid polychaetes. Palaeogeography, Palaeoclimatology, Palaeoecology 516, 284–294.

Nara, M., Kusuhashi, N., Okamoto, T., Imai, S., 2017. The Kuma and Misaki groups: Geological and palaeoenvironmental records, preserved in the Miocene forearc deposits during the opening of the Sea of Japan. Journal of Geological Society of Japan 123, 471–489 [In Japanese with English abstract.].

Olariu, M.I., Olariu, C., Steel, R.J., Dalrymple, R.W., Martinius, A.W., 2012. Anatomy of a laterally migrating tidal bar in front of a delta system: Esdolomada Member, Roda Formation, Tremp-Graus Basin, Spain. Sedimentology 59, 356–378.

Pearson, N.J., Mángano, M.G., Buatois, L.A., Casadío, S., Raising, M.R., 2013. Environmental variability of *Macaronichnus* ichnofabrics in Eocene tidal-embayment deposits of southern Patagonia. Lethaia 46, 341–354.

Pemberton, S.G., Spila,M., Pulham, A.J., Saunders, T., MacEachern, J.A., Robbins, J., Sinclair, I. K., 2001. Ichnology and sedimentology of shallow marginal marine systems. Geological Association of Canada, Short Course Notes, 15. St John's.

Pemberton, G., MacEachern, J., Dashtgard, S., Bann, K., Gingras, M., Zonneveld, J.-P., 2012. Shorefaces. In: Knaust, D., Bromley, R. (Eds.), Trace Fossils as Indicators of Sedimentary Environments. Development in Sedimentolology, vol. 64. Elsevier, Amsterdam, pp. 563–603.

Pérez-Asensio, J.N., Aguirre, J., Rodríguez-Tovar, F.J., 2017. The effect of bioturbation by polychaete (Opheliidae) on benthic foraminiferal assemblages and test preservation. Palaeontology 60, 807–827.

Plint, A.G., 1988. Sharp-based shoreface sequences and 'offshore bars' in the Cardium Formation of Alberta: Their relationship to relative changes in sea level. In: Wilgus, Ch.K., Hastings, B.S., Posamentier, H., Van Wagoner, J., Ross, Ch. A., Kendall, Ch.G.St.C. (Eds.), Sea-level changes: An integrated approach. SEPM Special Publication 42, pp. 357–370.

Pomar, L., Bassant, P., Brandano, M., Ruchonnet, C., Janson, X., 2012. Impact of carbonate producing biota on platform architecture: Insights from Miocene examples of the Mediterranean region. Earth-Science Reviews 113, 186–211.

Posamentier, H.W., Morris, W.R., 2000. Aspects of the stratal architecture of forced regressive deposits. In: Hunt, D., Gawthorpe, R.L. (Eds.), Sedimentary Responses to Forced Regressions. Geological Society of London, Special Publication 172, pp. 19–46.

Puig, P., Palanques, A., Guillen, J., 2001. Near-bottom suspended sediment variability caused by storms and near-inertial internal waves on the Ebro mid continental shelf (NW Mediterranean). Marine Geology 178, 81–93.

Quiroz, L.I., Buatois, L.A., Mángano, M.G., Jaramillo, C.A., Santiago, N., 2010. Is the trace fossil Macaronichnus segregatis an indicator of temperate to cold waters? Exploring the paradox of its occurrence in tropical coasts. Geology 38, 651–654.

Quiroz, L.I., Buatois, L.A., Seike, K., Mángano, M.G., Jaramillo, C.A., Sellers, A.J., 2019. The search for an elusive worm in the tropics, the past as a key to the present, and reverse uniformitarianism. Scientific Reports 9, 18402.

Rodríguez-Tovar, F.J., Aguirre, J., 2014. Is *Macaronichnus* an exclusively small, horizontal and unbranched structure? *Macaronichnus segregatis degiberti* isubsp. nov. Spanish Journal of Palaeontology 29, 131–142.

Seike, K., 2009. Influence of beach morphodynamics on the distributions of the opheliid polychaete *Euzonus* sp. and its feeding burrows on a sandy beach: paleoecological and paleoenvironmental implications for the trace fossil *Macaronichnus segregatis*. PALAIOS 24, 799–808.

Seike, K., Yanagishima, S.I., Nara, M., Sasaki, T., 2011. Large *Macaronichnus* in modern shoreface sediments: identification of the producer, the mode of formation, and paleoenvironmental implications. Palaeogeography, Palaeoclimatology, Palaeoecology 311, 224–229.

Soria, J.M., Fernández, J., García, F., Viseras, C., 2003. Correlative lowstand deltaic and shelf systems in the Guadix Basin (Late Miocene, Betic Cordillera, Spain): The stratigraphic record of forced and normal regressions. Journal of Sedimentary Research 73, 912–925.

Tamura, T., Masuda, F., 2005. Bed thickness characteristics of inner-shelf storm deposits associated with a transgressive to regressive Holocene wave-dominated shelf, Sendai coastal plain, Japan. Sedimentology 52, 1375–1395.

Traykovski, P., Geyer, W.R., Irish, J.D., Lynch, J.F., 2000. The role of wave induced density-driven fluid mud flows for cross-shelf transport on the Eel River continental shelf. Continental Shelf Research 20, 2113–2140.

Uchman, A., Krenmayr, H.G., 2004. Trace fossils, ichnofabrics and sedimentary facies in the shallow marine Lower Miocene Molasse of upper Austria. Jahrbuch der GeoloGischen bundesanstalt 144, 233–251.

Uchman, A., Johnson, M.E., Rebelo, A.C., Melo, C., Cordeiro, R., Ramalho, R., Ávila, S.P., 2016. Vertically-oriented trace fossil Macaronichnus segregatis from Neogene of Santa Maria Island (Azores; NE Atlantic) records a specific palaeohydrological regime on a small oceanic island. Geobios 49, 229–241.

Yu, Q., Wang, Y., Shi, B., Ping Wang, Y., Gao, S., 2017. Physical and sedimentary processes on the tidal flat of central Jiangsu Coast, China: Headland induced tidal eddies and benthic fluid mud layers. Continental Shelf Research 133, 26–36.