Shallow to marginal marine ichnoassemblages from the Upper Pliocene Slama Formation (Lower Chelif Basin, NW Algeria)

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Abstract: The Slama Formation (Upper Pliocene, Lower Chelif Basin, Algeria) displays siliciclastic deposits distributed in five determined stratigraphic members: Lower Sandstone Member, Lower Marls Member, Middle Sandstone Member, Upper Marls Member, and Upper Sandstone Member. It is characterised by low to moderate ichnofossil diversity consisting of 16 ichnotaxa: *Arenicolites* isp., *Conichnus conicus*, *Gyrolithes polonicus*, *G. variabilis*, *Gyrolithes* isp., *Macanopsis* isp., *Macaronichnus segregatis*, *Ophiomorpha* cf. *annulata*, *O. irregulaire*, *O. nodosa*, *Palaeophycus* isp., *Skolithos linearis*, *Skolithos* isp., *Thalassinoides horizontalis*, *T. paradoxicus*, and *T. suevicus*. Trace fossils are grouped into four ichnoassemblages. The *Thalassinoides* ichnoassemblage (Lower Sandstone Member and Lower Marls Member) represents a mixed *Cruziana/Skolithos* ichnofacies. The *Skolithos* ichnoassemblage (Middle Sandstone Member) represents the archetypical *Skolithos* ichnofacies and corresponds to middle shoreface settings. The *Macaronichnus–Gyrolithes* ichnoassemblage (Upper Marls Member) indicates shoreface/foreshore contact. The *Ophiomorpha* ichnoassemblage (Lower Sandstone Member) can be interpreted as the proximal *Skolithos* ichnofacies, which possibly corresponds to foreshore settings. The suggested dominant, regressive phase corresponds to the second half of the Upper Pliocene eustatic cycle in the northern Tell Atlas foreland domain.

Keywords: shallow marine, trace fossils, Pliocene, Slama Formation, Lower Chelif Basin.

Introduction

Numerous, yet discontinuous and isolated marginal Pliocene basins exist along the Alboran and Western Mediterranean coasts. The most significant ones, starting from north to south, are as follows: Roussillon (France; Clauzon et al. 1987; Martinell 1995); Alt Empordà, Baix Llobregat and Baix Ebre (Catalonia, Spain; Martinell 1988; Martinell et al. 1989; Fleta et al. 1991); Bajo Segura (Valencian Community, Spain; Caracuel et al. 2019); Mazarrón, Cabo Cope and Águilas-Terreros (Region of Murcia, Spain); Vera, Almería-Níjar-Carboneras, Málaga, and Estepona (Andalousia, Spain; Sendra et al. 2020); Boudinar and the internal Rif rias (Morocco; El Kadiri et al. 2011; Cornée et al. 2014; Merzeraud et al. 2019); and Lower Chelif (Algeria). The geological and palaeontological features of these basins are generally well-known. The marine Pliocene sediments that infill them are essentially marls and sands with a rich, fossil content (body and trace fossils), deposited in shallow environments within a transgressive–regressive sequence. They are predominantly Early Pliocene in age. Although extensive literature on invertebrate and vertebrate body fossils in these sediments exists, their ichnological record has received sporadic attention. This is especially true,

since bioturbation traces are widespread among them; however, they have only been studied in-depth in the Northern Baix Ebre (Gibert & Martinell 1996), Vera (Sendra et al. 2020) and Bajo Segura (Soria et al. 1996) basins.

The Lower Chelif Basin displays an exceptionally continuous and complete Neogene series ranging from the Burdigalian to the Pliocene. In fact, it had already been the subject of interest even before the end of the 19th century (Bleicher 1875; Pomel 1892; Repelin 1895; Brives 1897), resulting in the first stratigraphic and palaeontological data. Further research addressed its geodynamic and palaeogeographic evolution (Anderson 1936; Dalloni 1952; Perrodon 1957; Gourinard 1958; Mazzola 1971; Delteil 1974; Fenet 1975; Guardia 1975; Rouchy 1982; Thomas 1985; Neurdin-Trescartes 1995). Neogene stratigraphy was later established on foraminifers (e.g., Belkebir et al. 2008; Atif et al. 2008) and palynomorphs (e.g., Tchouar 2013) around the beginning of the 21th century. Nevertheless, the Pliocene of the Lower Chelif Basin is still poorly-known without lithological subdivision, since its macrofauna has only been briefly reported (Perrodon 1957; Satour et al. 2014), while its sedimentological and ichnological features have never been studied. This paper presents for the first time the lithostratigraphic, sedimentological and ichnological
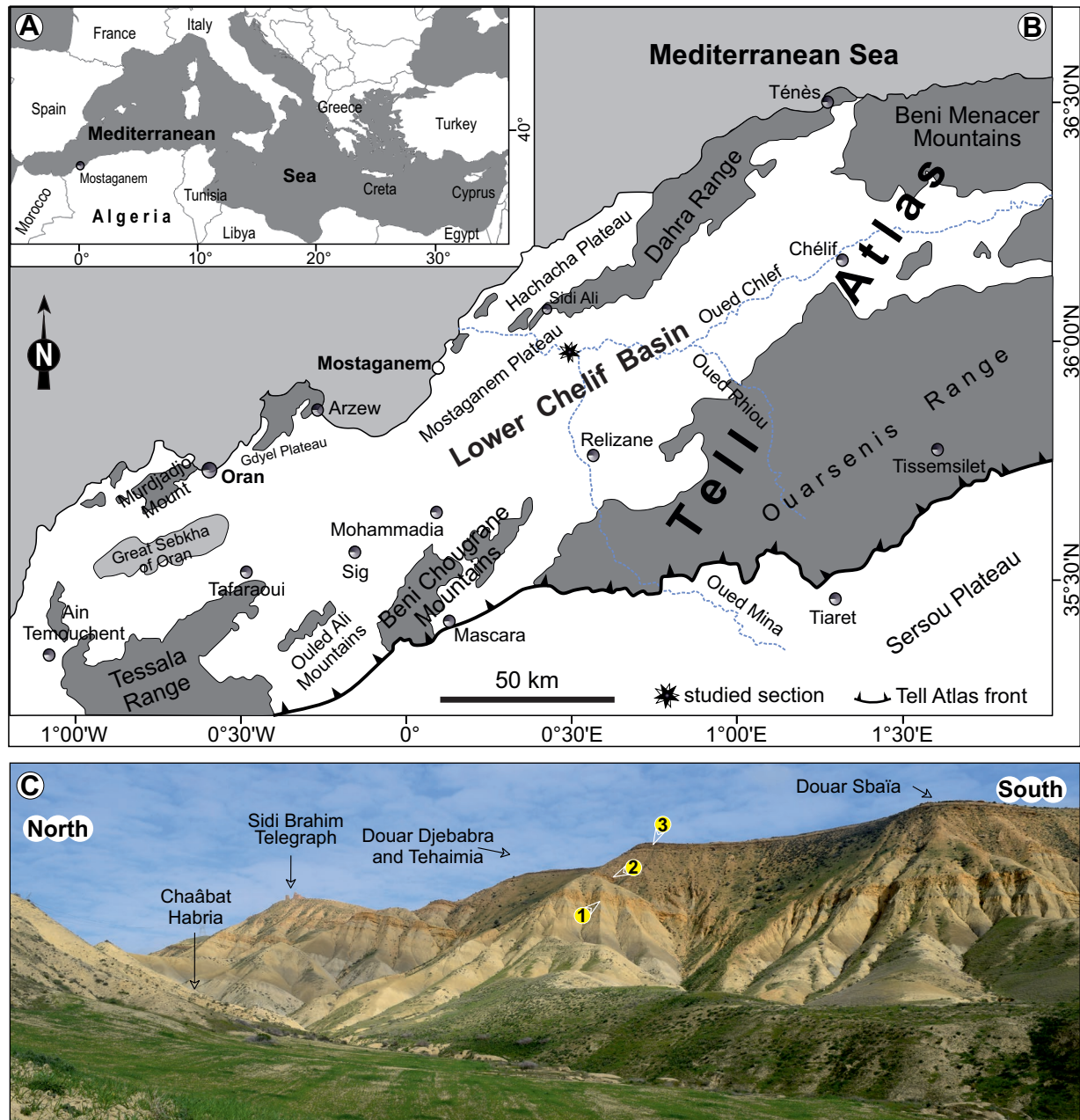
Fig. 1. Location of the studied area. **A** — Location of the studied section within the Mediterranean Basin; **B** — Position of the studied section within northwestern Algeria; **C** — Panoramic view of the studied succession (1 – Lower Sandstone Member; 2 – Middle Sandstone Member; 3 – Upper Sandstone Member).

characterisation of the Piacenzian Slama Formation in the Lower Chelif Basin. The identified ichnoassemblages are also compared with those described in other Pliocene Western Mediterranean basins.

Geological framework

The study area covers a part of the eastern edge of the Lower Chelif Basin, which is considered one of the sublittoral Neogene basins in northwestern Algeria and belongs to the Tell

Atlas (Fig. 1A,B). This latter is formed by mountain ranges over 1,500 km in length along Northern Algeria. The Lower Chelif Basin is an elongated furrow running parallel to the Mediterranean coast and is 300 km-long and 60 to 80 km-wide. It is bounded by the Oranian coastal massifs that stretch from Mount Murdjadjo to the Beni Menacer Mountains in the north, as well as by the Tessala Range, Ouled Ali Mountains, Beni Chougrane Mountains, and the Ouarsenis Range in the south (Fig. 1B).

The Lower Chelif Basin is a compressional basin formed in the last stages of the Alpine Orogeny with several stages of

neo-tectonic activity (Perrodon 1957). A tensional phase triggered the opening of the basin from the late Serravallian to the early Tortonian, and so horst-and-graben structures were formed. These structures had been filled with a thick series of late Tortonian and Messinian marls that included diatomaceous earths in some places, following the Late Tortonian transgression. In the Early Pliocene, an important compressive phase initiated the formation of folds (N110 direction of axis). It culminated after the Early Pliocene deposition phase, resulting in the enhancement of late Tortonian and Messinian fold structures. The Late Pliocene N–S compression deformed the coeval continental deposits into folds with E–W-trending axes. The second important compressive phase, with NNW–SSE/NW–SE shortening, both folded and deformed the Quaternary strata (Perrodon 1957).

Sedimentary fill of the Neogene Lower Chelif Basin is usually subdivided into Miocene and Pliocene sedimentary cycles (Perrodon 1957). The first one is subdivided into two phases: (1) the transgressive Early Miocene (Burdigalian) overlies Cretaceous sediments in a non-conforming manner. It consists of conglomerates, sandstones and marls, which are commonly called "marnes bleues" (blue marls); (2) the Late Miocene (Vindobonian) phase marked by a new transgression. Like in other Mediterranean basins, thick packages of evaporites (gypsum and halite) were deposited in the Lower Chelif Basin during the Messinian Salinity Crisis (MSC; 5.97–5.33 Ma; Rouchy 1982). The Pliocene cycle began with a large-scale marine transgression over the Upper Miocene strata and terminated with the Astian regression (Perrodon 1957). In the basin center (Sidi Brahim area; Fig. 1C), sediments younger than Messinian gypsum are characterised by reworked gypsum deposits at their base (conglomerates and also possibly breccias of gypsum blocks). The deposition continues with yellow, sandy marls, as well as grey and eventually white marls (Atif et al. 2008). White marls can be compared to the 'Trubi' facies (Zanclean) as described by the Italian authors Grasso et al. (1987) and Atif et al. (2008), or the Tahria Formation described by Anderson (1936).

The Piacenzian is subdivided into marine and continental facies groups. Marine Pliocene consists of sandstones ('grès astien' of Perrodon 1957) intercalated by sandy marls (The Slama Formation of Anderson 1936). They are well-represented in the Lower Chelif Basin. They are widely-exposed along the entire southeastern edge of the Dahra Massif, as well as the Mostaganem and Gdyel plateaus. In contrast, they appear only sporadically along the southern edge (Beni Chougrane Mountains) where they pass into continental formations (Perrodon 1957). Continental Pliocene is represented by clastic deposits of the Hamri Formation (Anderson 1936) exposed along the southwestern edge of the Dahra Range, and to a lesser extent, on the Mostaganem Plateau in the western part of the basin.

The Pliocene outcrop that we analyzed corresponds to the Slama Formation at the western edge of the Dahra Range (UMTS coordinates: 35°59'41.33"N, 0°28'52.87"E), some 40 km east of Mostaganem city. It is bordered by the village of

Sidi Ali in the north and the *wilaya* track CW 07 (and *wilaya* of Relizane) in the south (Fig. 1B), as well as by the *douar* agglomerations of Djebabra and Tehaimia in the east and the Chaâbat Habria in the west (Fig. 1C). It is marked by relics of an old Turkish telegraph facility, which is commonly called 'Télégraphe de Sidi Brahim' (Fig. 1C).

Material and methods

With all its members, the Slama Formation shows large and complete natural outcrops rich in trace fossils that are favourable for sedimentological and ichnological analyses: primary sedimentary structures, textures, strata geometries, and trace fossils contents. One hundred and forty-four specimens were documented, collected and examined in detail. Most of the trace fossils were well-preserved in fine- to medium-grained sandstones and subsequently collected from each member and studied accordingly.

Trace fossils were identified according to their standard characteristics and morphological criteria, such as branching, burrow infill and wall lining, with the intention of identifying them down to an ichnospecific level (cf. Bertling et al. 2006).

Slama Formation

The Slama Formation (Zanclean–Piacenzian) occurs in the western part of the Dahra Range (Anderson 1936). It is underlain by the Zanclean Tahria Formation (Early Pliocene), which is a thick series (≈250 m) of blueish to greyish marls with biodetrital beds rich in bivalves, gastropods, scaphopods, and cirripedes, continuing to yellowish sandy marls in its upper part. The overlying Hamri Formation (97 m, Upper Pliocene) consists of red clays and sandstones with continental fauna. In the Sidi Brahim Telegraph section, the Slama Formation (72 m) typically displays five overlaying lithological members (Figs. 1C, 2).

Lower Sandstone Member (10 m): Yellowish sandy marls with ostreid shells (*Ostrea edulis* Linnaeus, 1758) densely alternate with beds of fine- to medium-grained bioturbated sandstone (0.1–0.9 m) showing parallel lamination and cross bedding (Fig. 2). A discontinuous conglomerate bed with rounded pebbles and mollusc debris is present at the base. Bioturbation structures consists of numerous *Thalassinoides* in a horizontal network and scarce *Skolithos*. In some places, the marl facies are also intercalated with thin shell beds showing erosive bases, a fragmented and size-graded bivalve, as well as gastropod shells (Fig. 3A,C). Sandy marls intercalated within sandstones contain Zanclean dinoflagellate cysts and nannofossils (Tchouar 2013).

Lower Marls Member (22 m): Greyish biodetrital marls, which turn beige or even yellowish by the action of weathering, are intercalated with sandstone or sandy marl beds with benthonic fauna (0.1–0.3 m thick) at its top (Fig. 2). Marls contain shells of ostreids (*O. edulis* Linnaeus, 1758) and inner
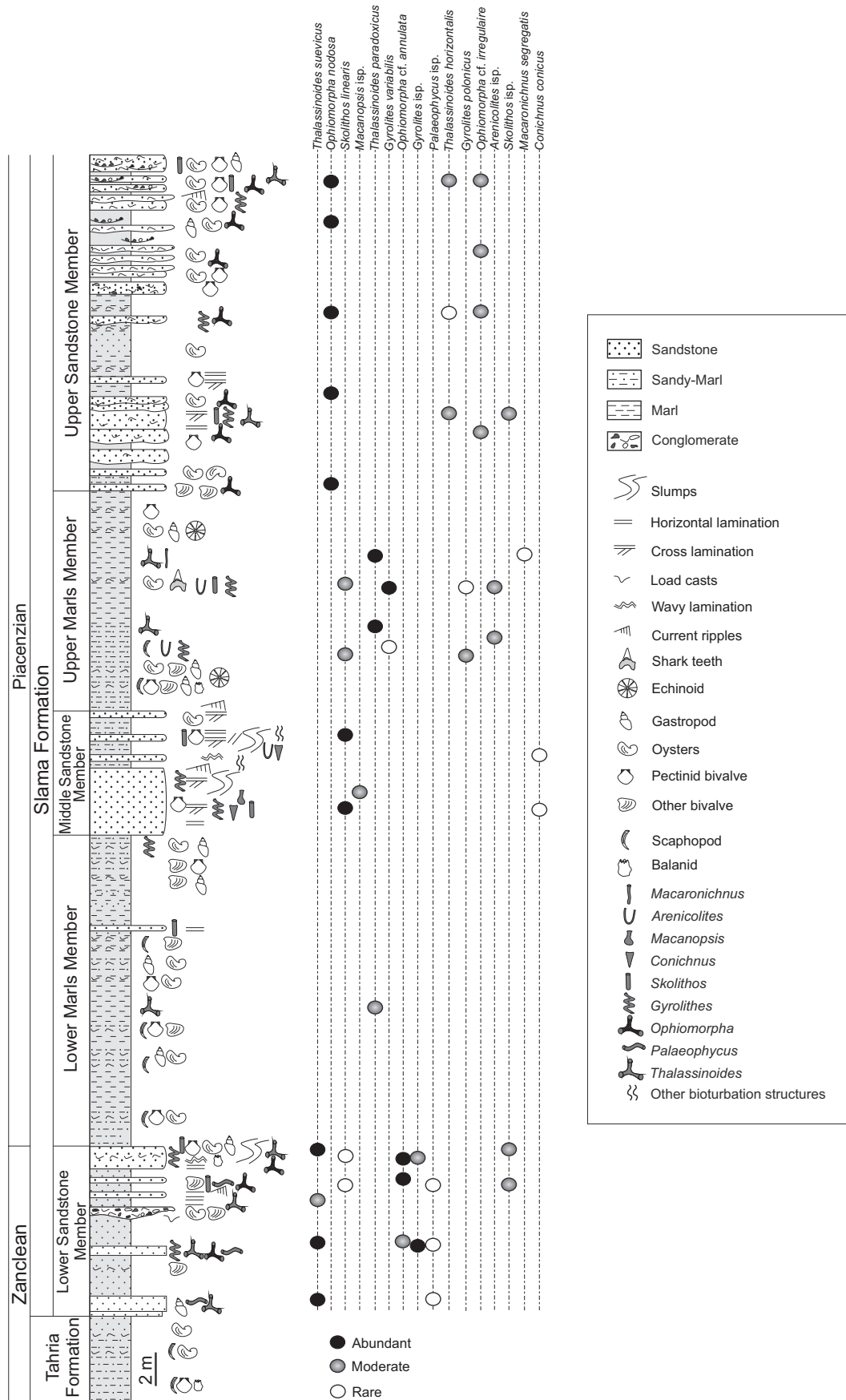
Fig. 2. Lithostratigraphic log of the Slama Formation showing the distribution of trace fossils.

moulds of venerids: *Pelecyora brocchii* (Deshayes, 1836) and *Pelecyora* sp., as well as pectinids (*Pecten* sp. and *Chlamys* sp.), gastropods (*Helminthia vermicularis*, *Neverita olla* and *Cochlis* sp.), and scaphopods (*Antalis* sp.). Ichnofossils are represented mostly by *Thalassinoides* and *Skolithos*. The basal part of these marls contains Piacenzan dinocysts and calcareous nannofossils (Tchouar 2013).

Middle Sandstone Member (7 m) consists of fine- to medium-grained sandstone characterised by a high frequency of channel structures, planar and parallel laminations, trough cross-bedding, slumps, fluid-escape structures, planar cross-bedding, and symmetrical wave ripples. It is particularly interesting that it can be locally rich in simple vertical and helical trace fossils. Sandstone beds are characterised by a channel structure, planar and parallel laminations, trough and planar cross-bedding, fluid-escape structures, and wave-ripple cross-laminations (Fig. 2). The tops of the beds are frequently shaped by asymmetrical wave ripples. The uppermost sandstone beds show syn-sedimentary structures of slump type (Fig. 3F).

The *Upper Marls Member* (13 m) is characterised by the intercalation of fine- to medium-grained sandstone beds showing parallel lamination, mud sheets, wave ripples, trough cross-bedding, mud drapes, and reactivation surfaces. The basal part of the member is marked by a thin (25 cm) sandstone bed with parallel lamination, reactivation surfaces, mud drapes (Fig. 3D), and mud sheets. Overlying biodetrital marls contain bivalve- and gastropod-rich shell beds. A greyish marly bed with channelised shell beds (0.2–0.4 m-thick), which is situated at the base, is rich in the gastropods *Bivetiella, Helminthia, Solatia, Tritia, Cochlis* sp., and *Subcancilla* sp., as well as the bivalves *Aequipecten* aff. *Spinovatus* (Sacco, 1897)*, Clausinella fasciata* (da Costa, 1778)*, Glycymeris* cf. *bimaculata* (Poli, 1795)*, Pelecyora brocchii* (Deshayes, 1836), and *Pecten* sp. with a higher degree of disarticulation. This shell bed is overlain by greyish marls with the trace fossils *Gyrolithes* and *Thalassinoides*, rare pectinid bivalves (*Pecten benedictus* sensu Fontannes, 1881*,* and *Pecten* sp.), oysters (*Ostrea edulis* Linnaeus, 1758), shark teeth (*Carcharodon carcharias* Linnaeus, 1758) and rare plates of clypeasterid echinids. The upper part of this unit is intercalated with lumachellic sandstone beds that are brown to reddish in colour with a nearly monospecific bivalve fauna: *Modiolus adriaticus* (Lamarck, 1819) bioturbated by *Skolithos* and *Gyrolithes* (Fig. 2).

The *Upper Sandstone Member* (20 m) consists of greyish to yellowish sandy marls, intercalated with beige, compact, channelised lumachellic sandstone beds (0.25–1 m-thick; Figs. 2, 3E) with calcareous cement, shells of ostreids (*O. edulis* Linnaeus, 1758), broken large-size pectinids (*Flabellipecten* sp., and *Pecten* sp.), and rare gastropods (*Cochlis* sp.). Lumachellic sandstones may pass locally into calcarenites. Thin, microconglomeratic beds, including rounded clasts, are intercalated in the upper part of the member. Bioturbation structures consist of *Ophiomorpha, Skolithos* and *Gyrolithe*s. The upper surfaces of the lumachellic sandstone beds display

asymmetric wave ripples. The topmost part of the section shows a sandstone level rich in shells (e.g., with *Oichnus, Entobia* and *Meandropolydora*) of *Ostrea lamellosa*.

Ichnology

The Slama Formation in the Lower Chelif Basin deposits reveal moderate ichnological diversity with 16 ichnospecies belonging to 9 ichnogenera. Trace fossils are presented alphabetically and described in detail, with their respective occurrence and associated trace fossils in individual stratigraphic members. The number of specimens, their assumed ethological categories and their respective occurrences in different stratigraphic members are presented in Table 1. In addition to the burrowing traces, frequent borings of variable states of preservation were found on macrofossil shells, which were not the subject of the study. Despite this, the abundance of bioerosion structures in both bivalve and gastropod shells indicates that the skeletal material had been exposed on the sea floor for some time before its eventual burial.

Ichnogenus *Arenicolites* Salter, 1857

Arenicolites isp. (Fig. 4A) is represented by vertical, slender, cylindrical, U-shaped burrows without any spreite, 2 to 5 mm in diameter perpendicular to bedding planes, and preserved as a full relief in cross-sectional views. The absence of spreite differs *Arenicolites* from *Diplocraterion* (Fürsich 1974b). Their base is regularly rounded as seen in vertical sections. The limbs are mostly parallel, diverging slightly only rarely. Depth ranges from 50 to 80 mm with the distance between limbs from 15 to 30 mm. Burrow widths and limb diameters are uniform throughout the height of the burrow. Other specimens show only fragments of cross-section, and the base of the trace was not found. *Arenicolites* is filled with red, fine-grained material, which is distinguishable from the surrounding grey sandy marl.

Arenicolites is commonly interpreted as a domichnion of suspension-feeding, worm-like organisms (Fürsich 1974b). However, Bromley (1996) noted that similar traces in modern environments are produced by deposit feeders, such as polychaetes, holothurians and enteropneusts. These are typically shallow marine trace fossils with several deep-water occurrences, although they may occur in non-marine environments where they are produced by annelids (Bromley & Asgaard 1979).

Ichnogenus *Conichnus* Männil, 1966

Conichnus conicus Männil, 1966 (Fig. 4B): A vertical to slightly-inclined conical burrow observable in cross-section. It displays steeply-inclined lateral margins and a distinctly-rounded basal termination. Its observable depths range from 15 to 30 cm and has diameters from 5 to 11 cm. The burrow is filled with sand that is identical to the host rock. *Conichnus* is
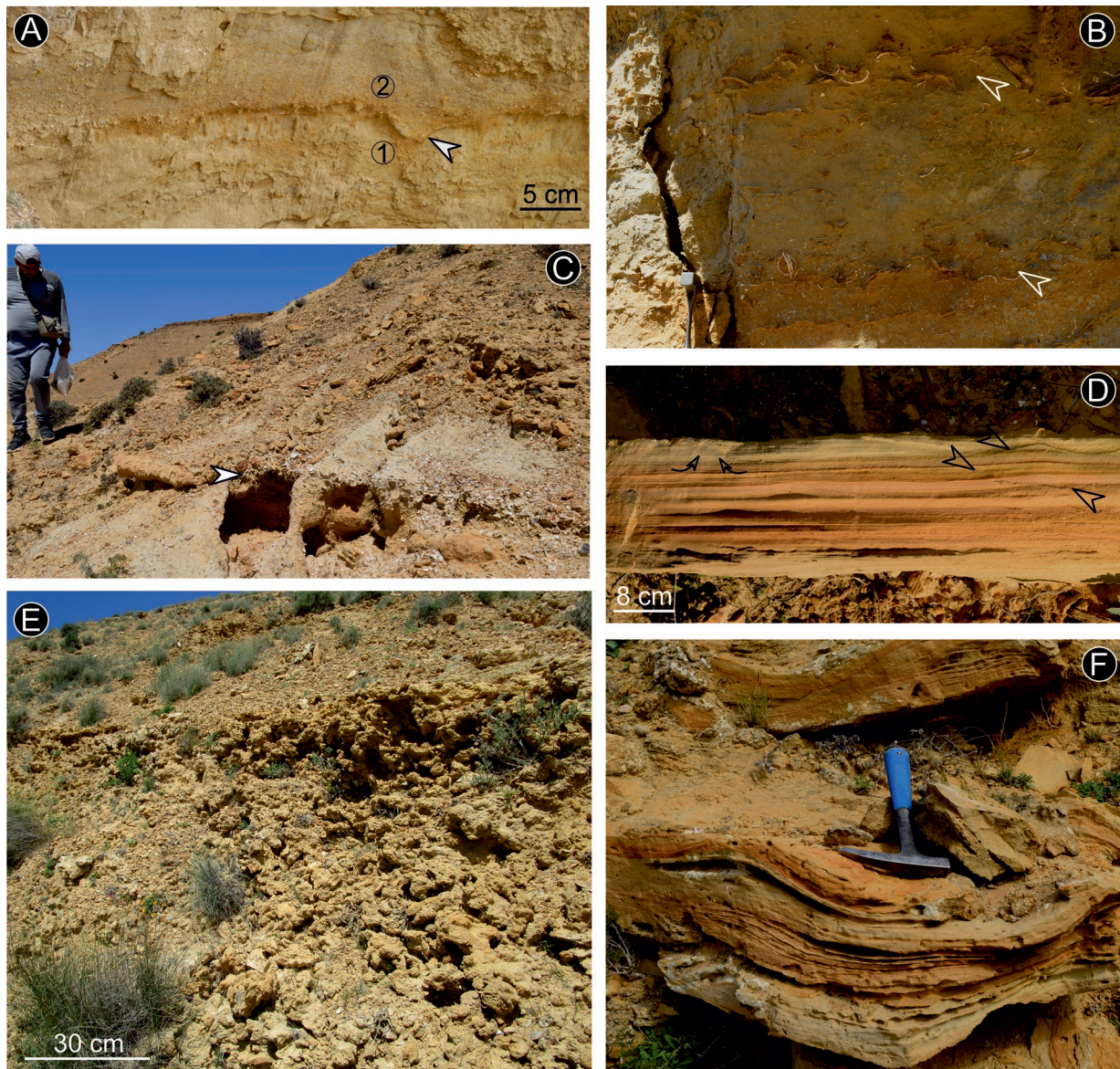
Fig. 3. Outcrops of the Slama Formation. **A, B** — Shell beds (2) interbedded with sandstones (1) (Lower Sandstone Member). Note the presence of erosion surface (A); **C** — Shell beds interbedded with sandy marls in the lowermost part of the Upper Marls Member; **D** — Parallel-laminated sandstone showing mud drape structures (arrows, Upper Marls Member); **E** — Strongly bioturbated, biodetrital sandstone bed (Upper Sandstone Member); **F** — Slumped sandstone bed (Upper Marls Member).

interpreted as a dwelling or resting burrow made by a polypoid animal (Pemberton et al. 1992; Savrda 2002; Curran 2007) and is largely attributed to sessile suspension-feeders like sea anemones (Knaust 2017). *Conichnus* is widely-reported from shoreface and lower foreshore deposits (MacEachern & Pemberton 1992; Pemberton et al. 1992; Savrda 2002; Vinn et al. 2015). *Conichnus* is usually associated with *Ophiomorpha* and *Skolithos* and is considered an important element of the *Skolithos* ichnofacies (MacEachern & Pemberton 1992; Buck & Goldring 2003). It is typically associated with marginal marine depositional environments that experience uniform or small episodic increments of sedimentation (MacEachern & Pemberton 1992).

Ichnogenus *Gyrolithes* Saporta, 1884

This ichnogenus is represented by helical, rarely-branched burrows. The helix is essentially vertical and consists of dextral, sinistral, or reversing coils, which are not in contact with one another (Uchman & Hanken 2013).

Gyrolithes **isp.** (Figs. 4C–5F) consists of branched tubes with circular to elliptical cross-sections and are perpendicular or oblique to bedding planes. Their diameters range from 0.4 to 1 cm; all the specimens of the Lower Sandstone Member only show their last coil. The external part of the burrow shows a diagenetic ferruginous lining. *Gyrolithes* likely represents a dwelling structure of decapod crustaceans

comparable with those constructed by *Ophiomorpha* and *Thalassinoides* (Uchman & Hanken 2013). Corkscrew-shaped structures are interpreted as the result of a soldier crab using its appendages on only one side of its body to dig, causing the body to rotate and produce a spiral-shaped burrow (Schmidt 1965). *Gyrolithes* occurs mostly in shallow and marginal marine sediments (Gernant 1972; Fillion & Pickerill 1990; Muñiz & Belaústegui 2019).

Gyrolithes polonicus Fedonkin, 1981 (Fig. 4D): Unbranched, smooth, spiral burrows are orientated perpendicularly to the bedding planes, and the sediment of the burrow is slightly different from the surrounding material. It consists of coils which are not in contact; in cross-section, the burrows are circular to sub-circular. The burrow diameter ranges from 0.5 to 1.3 cm and its depth from 8 to 15 cm. The maximum whorl number is 4 and

Table 1: A record of trace fossils from the Slama Formation with their respective ethology, stratigraphic units and the number of specimens.

Trace fossils	Ethological category	Stratigraphic units	Specimens number
Arenicolites isp.	Domichnia	Upper Marls Member	6
Conichnus conicus	Domichnia	Middle Sandstone Member	5
Gyrolithes isp.	Domichnia	Lower Sandstone Member	3
Gyrolithes polonicus	Domichnia	Upper Marls Member	5
Gyrolithes variabilis	Domichnia	Upper Marls Member	6
Macanopsis isp.	Domichnia	Middle Sandstone Member	3
Macaronichnus segregatis	Pascichnia/Fodinichnia	Upper Marls Member	≥40
Ophiomorpha nodosa	Domichnia	Upper Sandstone Member	17
Ophiomorpha cf. *annulata*	Domichnia	Lower Sandstone Member	2
Ophiomorpha cf. *irregulaire*	Domichnia	Upper Sandstone Member	5
Palaeophycus isp.	Domichnia	Lower Sandstone Member	2
Skolithos isp.	Domichnia	Lower–Upper Sandstone Member	4(Lower)–2(Upper)
Skolithos linearis	Domichnia	Middle Sandstone Member; Upper Marls Member	≥30; 4
Thalassinoides horizontalis	Fodinichnia/Domichnia	Upper Sandstone Member	1
Thalassinoides paradoxicus	Fodinichnia/Domichnia	Lower Marls Member	2
Thalassinoides suevicus	Fodinichnia/Domichnia	Lower Sandstone Member	9

the height between whorls ranges from 1.5 to 3 cm. Although recent papers have included such specimens in *Gyrolithes scintillus* (Herringshaw et al. 2017; Laing et al. 2018), this ichnospecies has a higher number of whorls and penetrates much deeper into the substrate than *G. polonicus* (Laing et al. 2018).

Gyrolithes variabilis Mayoral & Muñiz, 1995 (Fig. 4E, F) consists of vertical (perpendicular to the bedding) and dextrally or sinistrally helical burrows preserved as a full relief. In cross-section, the burrow is circular to ellipsoidal, filled with sediments similar to the host rock. The maximum diameter of the burrows is 0.8–2 cm, and the whorl radius is 1.3–3.5 cm; their observable height ranges from 8 to 14 cm. In general, the external part of the burrows is covered with diagenetic ferruginisation that results in a ferruginous lining. Some specimens of *G. variabilis* show a downwards decreasing width.

Ichnogenus *Macanopsis* Macsotay, 1967

Macanopsis isp. (Fig. 4G) is examplified by a vertical to slightly-inclined, cylindrical shaft structure, without any branching, up to 9 cm long. The diameter is constant along the vertical part of the burrow (2 cm), except for the basal chamber at its bottom. The burrow is preserved in full relief on a bedding plane and passively filled with sediments similar to the host rock. *Macanopsis* occurs in both marine and non-marine environments. It was recorded from fluvial (Pemberton et al. 2001), palaeosoil (Serrano-Brañas & Centeno-García 2014) and lacustrine settings (Buatois & Mángano 1995). It also occurs in confined, shallow-water marine environments protected by subtidal bars under low to moderate energy,

which is attributed to the *Cruziana* ichnofacies (Muñiz et al. 1998). It is interpreted as a domichnion trace fossil, which is produced by crustaceans, most likely brachyurans (MacSotay 1967; Muñiz & Mayoral 2001). Similar structures were described in the Oligocene point bar deposits of the nearshore fluvial Jebel Qatrani Formation in Egypt (Bown 1982). They were interpreted as a dwelling trace of insects or spiders (Bown & Kraus 1983). *Macanopsis*-like burrows in Holocene sediments are attributed to a variety of invertebrates, including insects, spiders, decapods and molluscs (Bown & Kraus 1983).

Ichnogenus *Macaronichnus* Clifton & Thompson, 1978

Macaronichnus segregatis Clifton & Thompson, 1978 (Fig. 4H) consists of simple, unbranched, variously inclined burrows, which are straight or slightly winding and 1–1.5 mm in diameter and 30–40 mm-long. The burrow is actively filled by light-coloured sand which contrasts with the yellow host rock. *Macaronichnus* is interpreted as a pascichnion (Savrda et al. 1998) or fodinichnion (Rindsberg 2012). The assumed producing organisms are deposit-feeding polychaetes, most likely opheliids, by analogy in modern environments: *Ophelia limacine* (Clifton & Thompson 1978; Seike et al. 2011) and *Euzonus mucronata* (Seike 2007; Dafoe et al. 2008a,b). *Macaronichnus* is a component of the *Skolithos* ichnofacies (Pemberton et al. 2001; Buatois & Mángano 2001; MacEachern et al. 2007) and in the *Cruziana* ichnofacies (Pemberton et al. 2001). This trace fossil has also been reported from the mixed *Skolithos–Cruziana* ichnofacies (Rossetti & Santos Jr. 2004). *Macaronichnus* is most common in well-oxygenated fore-shore and shoreface sand deposits (Clifton & Thompson 1978; Pemberton et al. 2001).
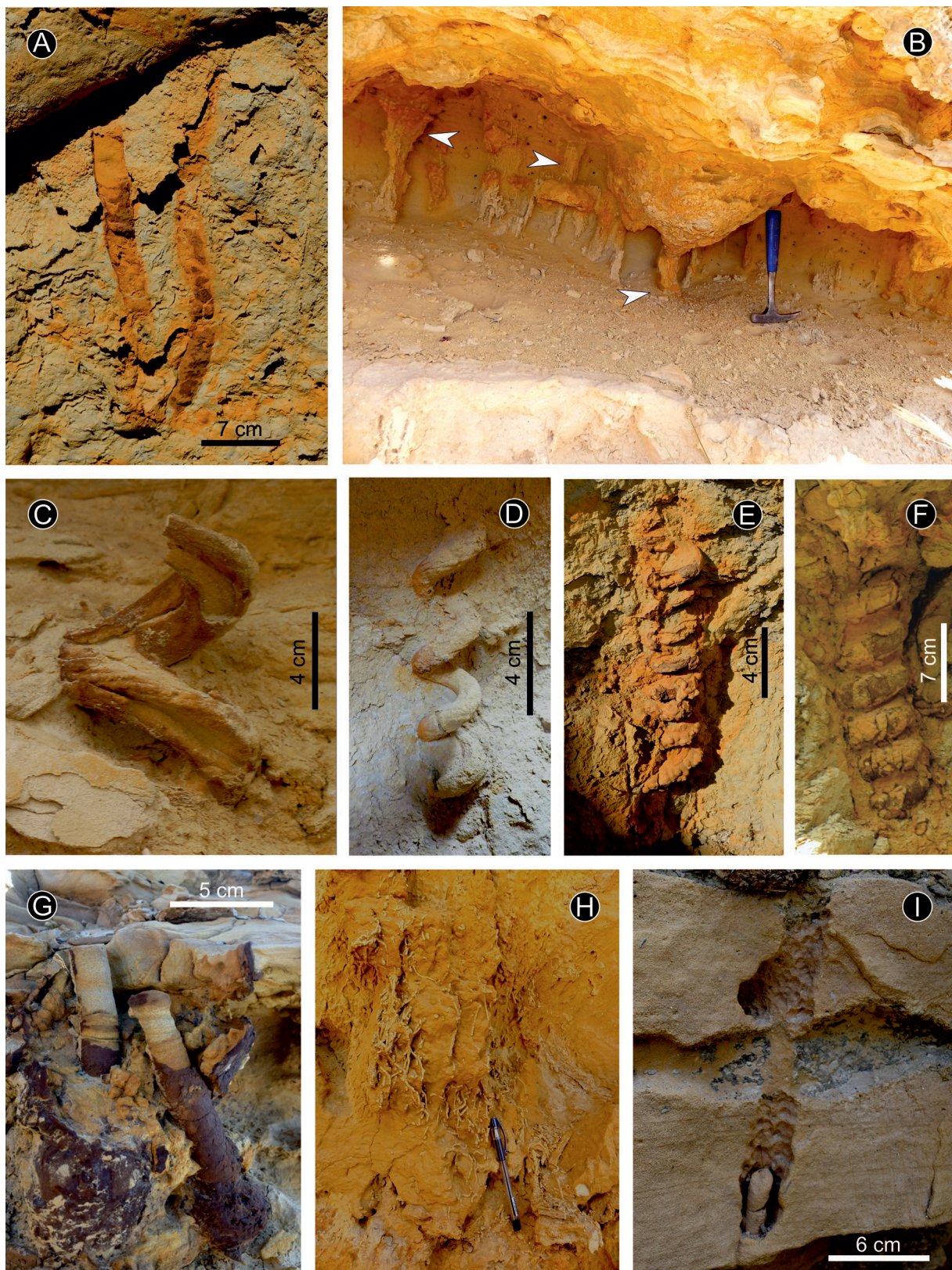
Fig. 4. Invertebrate trace fossils from the Slama Formation: **A** — *Arenicolites* isp.; **B** — *Conichnus conicus*; **C** — *Gyrolithes* isp. (recorded in the Lower Sandstone Member); **D** — *Gyrolithes polonicus*; **E, F** — *Gyrolithes variabilis*; **G** — *Macanopsis* isp. (Middle Sandstone Member); **H** — *Macaronichnus segregatis*; **I** — *Ophiomorpha nodosa* (Upper Sandstone Member). Note that A, D, E, F, and H are reported exclusively from the Upper Marls Member.
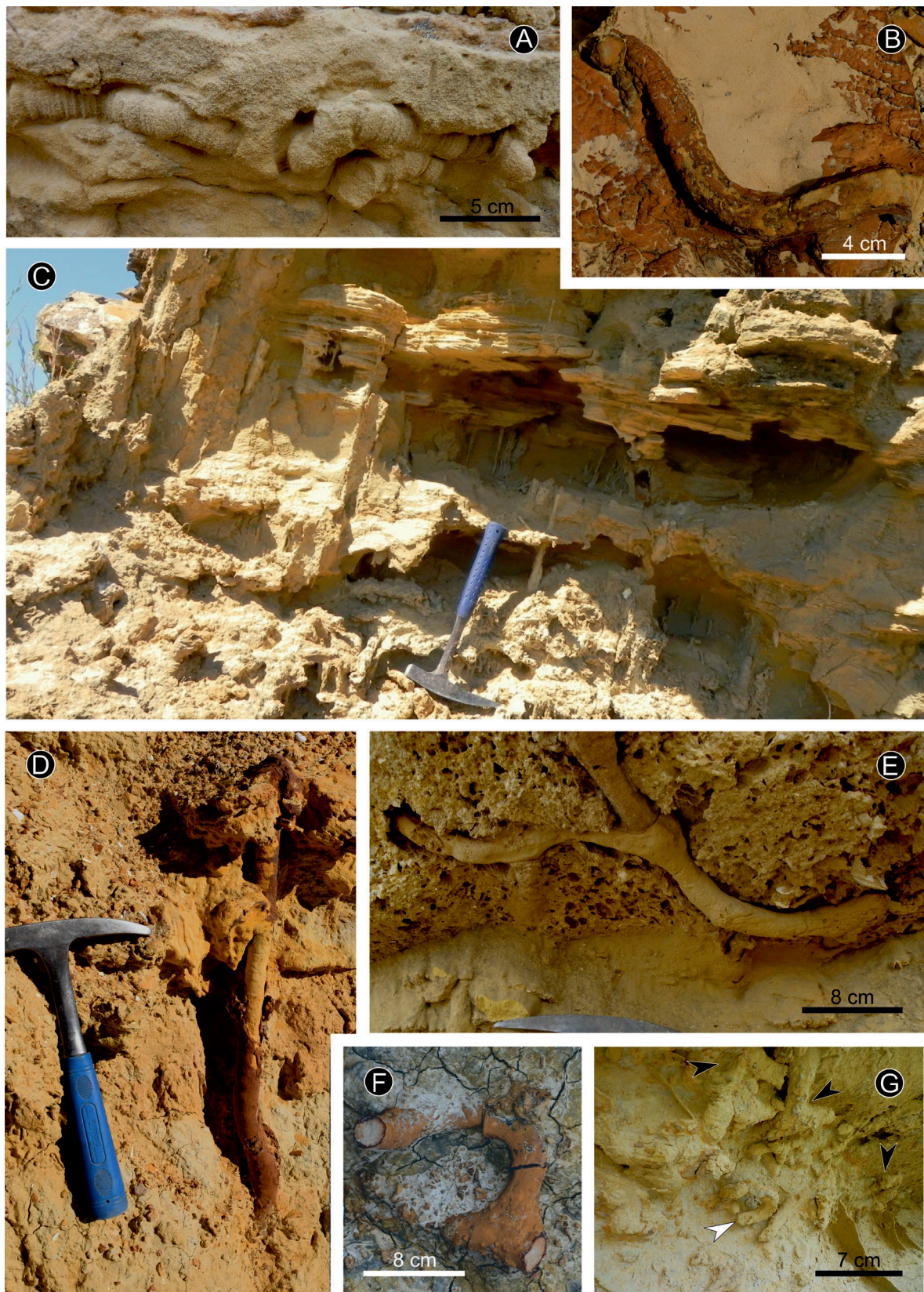
Fig. 5. Invertebrate trace fossils from the Slama Formation: **A** — *Ophiomorpha* cf. *annulata*; **B** — *Ophiomorpha* cf. *irregulaire*; **C** — *Skolithos linearis*; **D** — *Thalassinoides* shaft; **E** — *Thalassinoides horizontalis*; **F** — *Thalassinoides paradoxicus*; **G** — *Gyrolithes* isp. (white arrow) and *Thalassinoides suevicus* (black arrow). Note that A and E are reported from the Upper Sandstone Member, B and G from the Lower Sandstone Member, C from the Middle Sandstone Member, and F from the Lower Marls Member.

Ichnogenus *Ophiomorpha* Lundgren, 1891

Ophiomorpha Lundgren, 1891 (Figs. 4I, 5A,B) is a simple to branched complex burrow system (shafts and tunnels), distinctly lined with agglutinated pellets (Uchman 1998, 2009; Nagy et al. 2016). The pellets may vary within a single specimen (Frey et al. 1978); they are predominantly dense, regularly distributed, discoid, ovoid, or irregularly polygonal. They are usually interpreted as supporting the structure to prevent collapse of unconsolidated sediment (Bromley 1996).

Ophiomorpha nodosa Lundgren, 1891 (Fig. 4I) is represented by vertical or slightly inclined, burrows circular in cross section, 2–4 cm in diameter, 10–16 cm-long, with a roughly crenulated outline. The outer burrow surface displays a lining composed of robust, irregularly spaced, dispersed, ovoid pellets. Quite often, only a part of the pellets is preserved. In the Slama Formation, *O. nodosa* is a vertical, simple burrow, usually filled with fine skeletal remains.

Ophiomorpha cf. *annulata* (Książkiewicz, 1977) (Fig. 5A) is generally a horizontal, slightly winding, unbranched, cylindrical burrow in the form of an exichnial tunnel parallel to the bedding planes, up to 30 cm-long and 2 cm in diameter. The outer surface shows regular and equidistant rings about 1 cm from each other.

Ophiomorpha cf. *irregulaire* Frey et al. 1978 (Fig. 5B) is predominantly horizontal, generally branched, Y-shaped, sub-circular, showing thin, sinuous burrows preserved in full relief to the bedding plane. Their cross sections are circular, with diameters ranging from 1 to 2.5 cm; the observable length is about 7–10 cm. The outer surface of the burrow reveals a lining represented by sub-conical pellets. *Ophiomorpha* has been generally attributed to the activity of crustaceans, mostly (but not only) decapods (Frey et al. 1978; Monaco et al. 2007; Bouchemla et al. 2020); in modern environments, it is produced by the mud shrimp *Callichiurus* (Frey et al. 1978; Uchman & Gaździcki 2006; Dworschak et al. 2012). The ethology of this trace fossil maker is complex and may represent a variable combination of deposit- and suspension-feeding behaviours (Uchman & Gaździcki 2006; Leaman et al. 2015). An outline of the trophic strategies of modern callianassids is given by Bromley (1996) and includes deposit- and suspension-feeding, as well as bacterial gardening (Bromley 1996; Nagy et al. 2016). *Ophiomorpha* is considered a cross-facies trace fossil from shallow- to deep-water environments (Monaco et al. 2007). *O. nodosa* has been registered in shallow-water deposits that are characteristic of the *Skolithos* ichnofacies (Pemberton et al. 2001), but also occurs in deeper-shelf tempestites (e.g., Uchman & Gaździcki 2006). *O. irregulaire* (see Table 1) has also been recorded in shallow waters (Uchman & Gaździcki 2006). Horizontal *O. annulata* has been recorded in deep marine strata related to the distribution of organic material within the substrate (Uchman 1995). Uchman (2007) considered *O. annulata* one of the accessory ichnotaxa of the *O. rudis* ichnosubfacies, which is characteristic of deep-sea fans (channels and proximal lobes).

Ichnogenus *Palaeophycus* Hall, 1847

Palaeophycus is a very common trace fossil in the sedimentary record, even though it has a confusing, taxonomic, nomenclatural history. Pemberton and Frey (1982) considered the burrow sculpting and wall lining to be the basic criteria for recognising the trace. Morphologically, this ichnogenus refers to sub-horizontal, straight or slightly-curved, but essentially cylindrical burrows with a lining and passive fill (Knaust 2017).

Palaeophycus isp. is a simple, straight, distinctly-lined horizontal to sub-horizontal, unbranched, unornamented, cylindrical burrow, which is 0.9 to 1.8 cm in diameter; it is filled with the same sediment as the host rock. In the Sidi Brahim section, *Palaeophycus* isp. occurs as endichnion in the Lower Sandstone Member. *Palaeophycus* is a eurybathic trace interpreted as dwelling burrows of polychaete worms (Tchoumatchenco & Uchman 2001) or predatory worms (Pemberton & Frey 1982).

Ichnogenus *Skolithos* Haldeman, 1840

Skolithos isp. is an unbranched, vertical to steeply inclined, straight to slightly curved, cylindrical to sub-cylindrical, row of lined or unlined burrows, with or without funnel-shaped tops, with 1.8–9 mm in diameter, preserved as an endichnion. *Skolithos* differs from *Monocraterion* in the absence of funnel-shaped uppermost top and full-relief tubes. Five ichnospecies of *Skolithos* were recognised by Alpert (1974), namely *S. linearis*, *S. verticalis*, *S. annulatus*, *S. ingens*, and *S. magnus*. In the study area, only *S. linearis* was identified; furthermore, a number of indeterminable specimens found in *Skolithos* isp. occur. Concentric, vertical coloured cylinders, which developed around a vertical burrow of *Skolithos*, are not regarded as a wall lining. They are interpreted as tubular tidalites (Gingras & Zonneveld 2015). Some of these burrow openings are visible on top of the sandstone beds and display circular outlines.

Skolithos linearis Haldeman, 1840 (Fig. 5C) is a straight to slightly curved, predominantly vertical to subvertical, cylindrical row of burrows, orientated perpendicularly or obliquely to bedding planes. It shows more or less uniform diameters of 3–30 mm and lengths between 70 and 450 mm, but frequently about 100 mm, filled with sediment similar to the host rock, and preserved as endichnial full relief with distinct or indistinct walls.

Skolithos has been widely recognised in shallow marine environments (Alpert 1974; Fillion & Pickerill 1990), especially in intertidal deposits (Seilacher 1967). It is interpreted as a domichnion made by annelids or phoronids (Alpert 1974) and suspension-feeding or passive-predator polychaetes (Patel & Desai 2009) that colonise sediments which had been rapidly deposited during storms or in areas with actively migrating bed forms (Pemberton & Frey 1984; Fillion & Pickerill 1990). To date, *Skolithos* has been seldom reported from non-marine environments (Bromley & Asgaard 1979; Gregory et al. 2006).

These shafts are attributed to insects or spiders as dwellings or shelters (Ratcliffe & Fagerstrom 1980). Rocks containing abundant *Skolithos* are commonly referred to as pipe-rock ichnofabric (Desjardins et al. 2010), which is characteristic of the *Skolithos* ichnofacies. It is indicative of relatively high-energy environments and shallow-water conditions in nearshore to marginal marine settings (Buatois & Mángano 2011).

Ichnogenus *Thalassinoides* Ehrenberg, 1944

Thalassinoides **isp.** (Fig. 5D–F) displays horizontal, smooth-walled, unlined, unornamented burrows, showing frequent Y-shaped branchings. Constrictions or swellings at both junctions and inter-junction segments are lacking.

Thalassinoides horizontalis Myrow, 1995 (Fig. 5E): Horizontal, hypichnial, branching, unlined, unornamented burrows, having Y-shaped branches, with no vertical offshoots. It is 1–2 cm in diameter and 25–30 cm-long. Constrictions or swellings are absent. The burrow is preserved in full relief in the Upper Sandstone Member as a full relief.

Thalassinoides paradoxicus (Woodward, 1830) (Fig. 5F): Horizontal to slightly oblique, three-dimensional irregular burrow system, extending along bedding planes and crossing them mostly by oblique shafts; the bifurcations are commonly T-shaped. Its diameter varies between 2 and 3 cm and their visible lengths exceed 10 cm; the filling is passive and identical with the host rock, but locally, it may contain skeletal debris. The external part of the burrow is generally ferruginous.

Thalassinoides suevicus (Rieth, 1932) (Fig. 5G): Hypichnial, horizontal, smooth, unlined, three-dimensional cylindrical burrows, showing Y-shaped bifurcations, 10–20 cm-long and 1–3 cm in diameter. The filling is identical to the host rock.

Thalassinoides are feeding and dwelling burrows produced by crustaceans or some other type of arthropods (Frey et al. 1984; Bromley 1996) in oxygenated and soft, but cohesive deposits (Bromley 1990; Bouchemla et al. 2021).Though mostly characteristic of shallow marine environments, *thalassinoides* are considered a facies-crossing form (Myrow 1995; Bouchemla et al. 2020; Vinn et al. 2020) ranging from tidal flats (Curran 2007), shorelines (Kamola 1984), outer shelf facies (Bendella et al. 2011; Bouchemla et al. 2021) to deep-sea marine settings (Bendella & Ouali Mehadji 2014; Srivastava et al. 2017).

Ichnoassemblages and palaeoenvironments

The trace fossils shown in Table 1, as well as those mentioned above, were grouped into four ichnoassemblages (Fig. 6). Their names do not follow the names of the most frequent trace fossils, but rather follow the ichnotaxa with presumed high palaeoecological and palaeoenvironmental significance.

Thalassinoides ichnoassemblage

It is dominated by *Skolithos* isp., *Thalassinoides suevicus*, *Gyrolithes* isp., *Ophiomorpha* cf. *annulata*, and *Palaeophycus* isp. The ichnoassemblage is an example of an ethologically diverse group of trace fossils (vertical and horizontal burrows), suggesting that biogenic structures are dependent on taphonomic restrictions rather than water depth (Seilacher 1967; MacEachern et al. 2007). Among the vertical burrows, *Skolithos* isp. is worth mentioning, since it generally characterises shallow-water environments (Seilacher 1967; Alpert 1974; Fillion & Pickerill 1990). Tracemakers of *Skolithos* colonise sediments, which are rapidly deposited during storm events (Pemberton & Frey 1984; Fillion & Pickerill 1990). *Gyrolithes* isp. in the Lower Sandstone Member may branch and interconnect with other burrows (often *Thalassinoides* networks). According to Gernant (1972) and Bromley (1996), *Gyrolithes* is restricted to brackish or marginal marine palaeo-environments. *Skolithos* and *Gyrolithes* are typical elements of the *Skolithos* ichnofacies.

Horizontal structures, especially *Thalassinoides suevicus*, are the most abundant trace fossils and are generally interpreted as domichnial burrows. The ichnogenus *Thalassinoides* is facies-crossing and produced by crustaceans (Frey et al. 1984; Knaust 2017), ranging from shallow to deep water environments (Ehrenberg 1938; Uchman 1995; Myrow 1995; Kim et al. 2002; Bouchemla et al. 2021). *Palaeophycus* is interpreted as eurybathic dwelling burrows produced by polychaete worms (Tchoumatchenco & Uchman 2001) or predatory worms (Pemberton & Frey 1982). *Ophiomorpha* cf. *annulata* is poorly represented within the Lower Sandstone Member. As observed by Uchman (1995), this ichnotaxon is mainly developed as a horizontal tunnel network, and its precise position is likely related to the distribution of organic material within the substrate.

Lower Sandstone Member

Bioturbation structures are distributed into two intervals of lower shoreface setting: (1) the lower interval, which is relatively strongly bioturbated, is dominated by horizontal structures of deposit feeders formed during low-energy periods (cf. MacEachern & Pemberton 1992; Buatois & Mángano 2011), and (2) the upper interval, which is dominated by vertical structures of suspension feeders produced by opportunistic organisms; it reflects brief colonisations during relatively high-energy conditions (cf. Buatois & Mángano 2011).

Trace fossils of the first ichnoassemblage document the presence of organisms with the capability of moving in a vertical direction in response to changes in the water/sediment interface corresponding to high sedimentation rates and/or erosion events (Bromley 1996). This mixed trace fossils assemblage of different ethologies is characteristic of the lower shoreface setting, where the proximal *Cruziana* ichnofacies typically occurs (e.g., Pemberton et al. 2001).
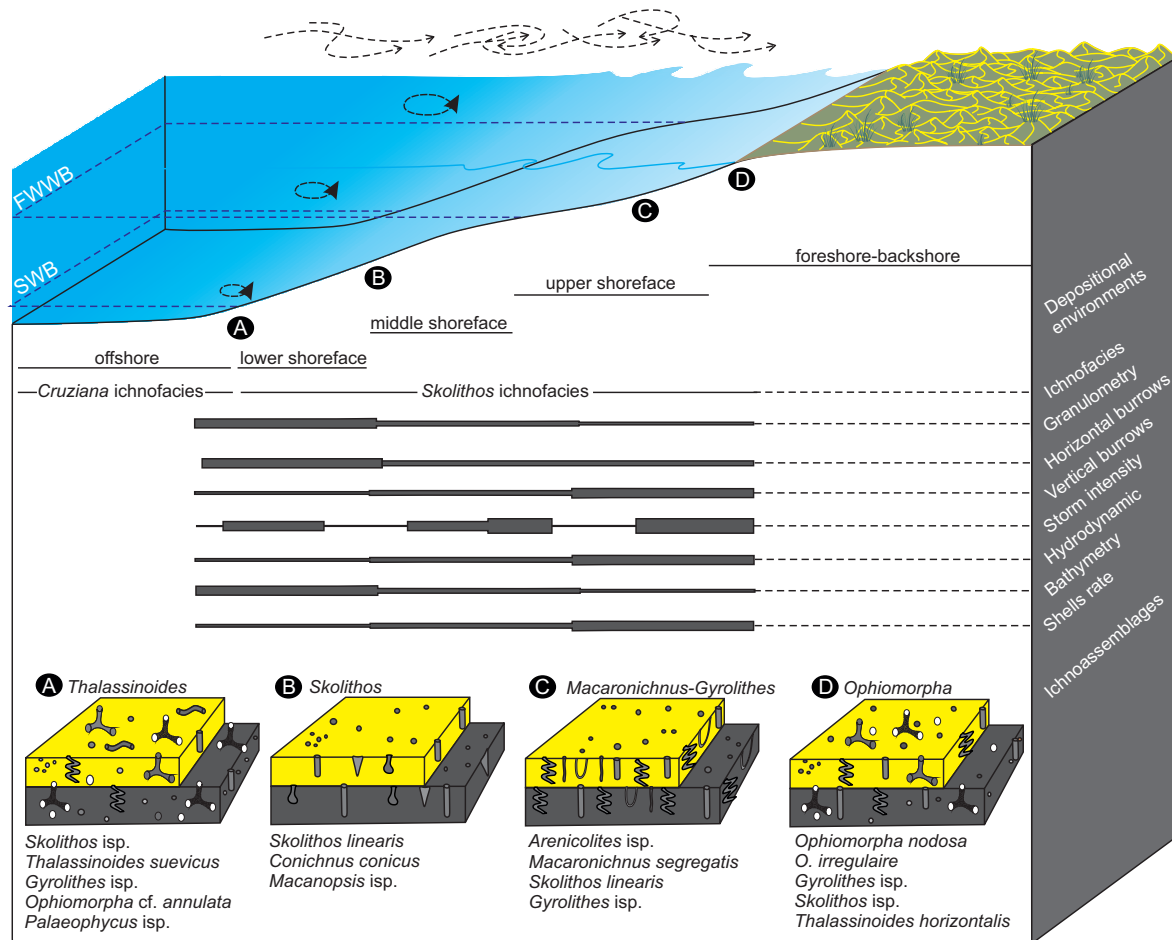
Fig. 6. Graphical representation of the depositional environments of the Slama Formation according to the ichnoassemblage distributions, ecological features and hydrodynamic data. FWWB=Fair-Weather Wave Base; SWB=Storm Wave Base.

Vertical structures of the upper interval are related to the opportunistic colonisation of storm beds (post-event assemblage). Storm bed currents can transport their tracemakers into deeper environments (Frey et al. 1990). Horizontal trace fossils are likely related to fair-weather conditions. They represent the 'local community'. The co-existence of vertical and horizontal structures suggests fluctuating energy conditions and a stressful environment (Fürsich 1974a; Pemberton et al. 2004; Buatois et al. 2005; Fürsich et al. 2018). Here, the assemblage most likely represents a lower shoreface zone, which is typical of the mixed proximal *Cruziana*/*Skolithos* ichnofacies. The *Cruziana* ichnofacies with the dominance of deposit feeders occurs where current action is less intense and food particles settle on the bottom. The *Skolithos* ichnofacies generally grades seawards into the *Cruziana* ichnofacies, as presented in numerous idealised shoreface models for ichnofacies (e.g., Frey et al. 1990; Pemberton & MacEachern 1995).

Lower Marls Member

The fauna is represented by a parautochthonous shell assemblage under conditions of a decreasing siliciclastic accumulation rate. As expected, shells were concentrated due to storm deposition (Brenchley et al. 1993; Bouchemla et al. 2020), which was reflected by the planar lamination and unsorted sediment constituents.

Ichnological data reveal the presence of *Skolithos linearis* and *Thalassinoides paradoxicus*. These ichnotaxa occur in several sea-influenced, soft ground ichnofacies (Monaco et al. 2007), as well as in diverse environments, such as salt marshes, tidal flats and channels, estuaries, delta fronts, prodeltas, and inner and outer shelves, including pelagic facies, yet in uneven frequency (*Thalassinoides*, like several other significant ichnotaxa, has a conspicuous palaeoenvironmental trend, Bottjer et al. 1988). *Thalassinoides* is reported from shallow-water, more commonly from *Cruziana* and *Skolithos* ichnofacies, among which diverse crustaceans thrived (Pemberton & MacEachern 1995). The presence of deep *Thalassinoides* isp. indicates relatively high-energy environments with a high content of organic matter in bottom sediments. Here, trace fossils are relatively rare and *Thalassinoides* occurs along with an opportunistic monospecific assemblage of *Skolithos linearis*. The external part of these burrows is often covered by a mixture of ferruginous minerals, which is a common

diagenetic feature of many ichnoassemblages (e.g., Bendella et al. 2011; Bouchemla et al. 2020). This ichnoassemblage also shows a relatively high abundance of large *Thalassinoides*, which is recognised as an important indicator of oxic marine conditions (Savrda & Bottjer 1989; Gingras et al. 2001; Savrda 2007). *Callichiurus* is one of the recent trace-makers of *Ophiomorpha* and *Thalassinoides*; it burrows in estuaries and tolerates salinities from 12 to 30 ‰, even as low as 10 ‰ (Frey et al. 1978). Certain tracemakers of *Ophiomorpha* and *Palaeophycus* are strongly associated with high sedimentation rates (Gingras et al. 2011). We also assume that the lower biodetrital marl represents a lower shoreface setting.

Skolithos ichnoassemblage

Sedimentary structures of the Middle Sandstone Member support the idea that sediments were mainly transported by storms in a shoreface setting (cf. Brenchley et al. 1993; Dumas & Arnott 2006). Here, the occurrence of slumps and fluid-escape structures are interpreted as soft sediment deformation structures (SSDS) induced by various natural processes, such as earthquakes (Owen 1996) and storm waves (Moretti & Sabato 2007). However, the presence of bioerosion structures and encrustation indicates that the skeletal material had been exposed for some time on the sea floor before their eventual burial, which allows us to conclude a low sedimentation rate (McKinney 1996; El-Hedeny 2005, 2007).

The bioturbation is dominated by traces of suspension fee-ders, i.e., opportunistic invertebrates that inhabited sandy sub-strates. It mainly includes vertical, simple *Skolithos linearis* and *Conichnus conicus*, as well as the basal chamber burrow *Macanopsis.*

Skolithos predominantly occurs in various shallow marine environments (Buatois & Mángano 2011) and is generally regarded as a dwelling–feeding burrow of annelids or phoro-nids (e.g., Alpert 1974). Occasionally, it has been reported from non-marine environments (Bromley & Asgaard 1979), where it may have originated from the burrowing activities of insects or spiders, and can be interpreted as dwelling struc-tures or shelters (Ratcliffe & Fagerstrom 1980). *Skolithos* is an extreme facies-crossing trace fossil resulting from the sim-ple nature of these structures. The sole occurrence of *Skolithos* does not indicate any particular environment. In the Slama Formation, *Skolithos* occurs along with *Conichnus conicus*, which is characteristic of a high-energy, shallow-water envi-ronment (Gibert & Ekdale 2010). *Conichnus* is attributed to sea anemones, and it is reported from sediments deposited in high-energy environments, such as a tidal setting (Savrda 2002) and wave/tide influenced environments (Curran & White 1997). *Conichnus* is an important element of the *Skolithos* ichnofacies (MacEachern et al. 2007; Curran 2007). According to Gernant (1972) and Bromley (1996), *Gyrolithes* is common in brackish settings; however, Mikuláš (2000) reported typical *Gyrolithes* from the Cambrian *Cruziana* ichnofacies of the Barrandian area (Czech Republic). Also,

the ichnospecies *Gyrolithes cycloides* (Mikuláš & Pek 1994) occurs in calcareous sandstone deposited below the daily wave base at the type locality. Uchman & Hanken (2013) reported thirteen ichnospecies of *Gyrolithes* with a new trace fossil *G. lorcaensis* from Miocene of SE Spain and presented a critical review of the *Gyrolithes* ichnospecies. *Skolithos* and *Gyrolithes* are typical elements of the *Skolithos* ichnofacies.

Macanopsis has been described from marine settings (Bown & Kraus 1983), but was later recorded in fluvial floodplain deposits as well (Hasiotis et al. 1993). It is interpreted as a dwelling trace of insects or spiders (Bown & Kraus 1983).

The *Skolithos* ichnoassemblage indicates an environment of relatively high wave energy with low depositional rates. Thanks to an abundance of oxygen and food supplies, a moderate degree of bioturbation and medium diversity of ichnofossils in the Middle Sandstone Member showed that wave-dominated environments were more favoured by orga-nisms than in the Lower Sandstone Member environments (cf. Frey et al. 1990). Large burrow diameters imply larger animals, which is another reliable indicator of a favourable environment. The trace fossil assemblage is interpreted as the *Skolithos* ichnofacies. Ichnotaxa present within this assem-blage exhibit a strong similarity with the archetypal *Skolithos* ichnofacies (MacEachern et al. 2007). Likewise, the deposi-tional environment of the deposits with the *Skolithos* assem-blage likely represent the middle shoreface as the most commonly interpreted depositional setting for such *Skolithos* ichnofacies (Pemberton et al. 1982; MacEachern et al. 2007). Moderate ichnofossil abundance and medium diversity of this association are also identical with the characteristics of the *Skolithos* ichnofacies (Pemberton et al. 1992; MacEachern et al. 2007). Frequent water movements supplied sufficient food as well as optimised the environments for suspension-feeding animals to thrive (Bromley 1996).

Macaronichnus–Gyrolithes ichnoassemblage

Sedimentary structures in the basal part of the Upper Marls Member indicate a tidal-influenced environment. The lami-nated fill of *Skolithos linearis* is represented by couplets, each one comprising light and dark laminae (tubular tidalites *sensu* Gingras & Zonneveld 2015), which are typical of tidal currents (Wetzel et al. 2014; Gingras & Zonneveld 2015). The remaining part of this unit is characterised by bioerosion structures and taphonomic features of sedimentological con-centrations according to Kidwell et al. (1986), which are com-monly interpreted as storm deposits (tempestites). There is a general agreement that *Gyrolithes* is a deep-dwelling bur-row common in shallow and marginal-marine settings (Muñiz & Belaústegui 2019), and that its vertical helical morphology represents a specialised burrowing architecture for seeking refuge from extreme salinity fluctuations in brackish-water environments (Buatois et al. 2005). Infaunalisation is a com-mon survival strategy in harsh environments characterised by extreme salinity fluctuations. The deep infaunal habitat is

a refuge from stressful environmental conditions, especially on the sediment surface (Rhoads 1975). Since fine-grained sediment slows down the exchange of pore water, the impact of salinity fluctuations is reduced (Sanders et al. 1965).

Arenicolites has been recognised in diverse environments. It commonly occurs in a shallow-water form (Pickerill et al. 1984) and is rarely found in deep water (Edwards 1985), although it has been reported from non-marine environments as well (Bromley & Asgaard 1979; Kamola 1984). Bromley & Asgaard (1991) proposed that the *Arenicolites* ichnofacies represents the work of opportunistic organisms that produce *Arenicolites* and *Skolithos*. Its modern analogues may occur at depths up to 200 m or more (Jansa 1974). It is generally considered an indication of a high-energy environment with shifting substrates (Bromley & Asgaard 1991). The distinct burrow outline, absence of lining, and passive burrow fill suggests a dwelling burrow of a suspension-feeding organism within partially compacted sediment. The tracemaker of *Arenicolites* was able to inhabit high-energy environments that lacked fine-grained material, which is attractive to deposit-feeding animals; therefore, it is interpreted as the dwelling place of a suspension-feeding tracemaker.

Macaronichnus segregatis is attributed to polychaetes (Clifton & Thompson 1978; Pemberton et al. 2001; Gingras et al. 2002). *M. segregatis* has often been associated with very shallow waters (Seike et al. 2011), though some larger forms have been recorded in deeper environments (Seike et al. 2011). *Ophelia*, which is a modern *Macaronichnus* tracemaker, has a tendency to tolerate lower salinities (Clifton & Thompson 1978).

Quiroz et al. (2010) suggested that *Macaronichnus* is typically associated with upwelling conditions in tropical settings that cause strong seasonality of cold waters and replenish surface waters with nutrients. Furthermore, based on the distribution of the modern *Euzonus* worm (a possible producer of *Macaronichnus*), two aspects have been then addressed: (a) the variation of burrowing behaviour in response to the magnitude of beach topographical changes due to wave conditions (Seike 2008), and (b) the relationship between the vertical thickness of *Macaronichnus segregatis*-bearing beds and ancient beach morphodynamics; a greater bed thickness being associated with a decreasing beach-face gradient (Seike 2009).

Macaronichnus represents the activity of deposit-feeding worms in well-oxygenated sediments, at a depth usually below 20 cm from the water-sediment interface, thereby allowing a deep-tier position (Pemberton et al. 2001; Bromley et al. 2009).

Sediment structures suggest a high-energy, agitated, shallow marine environment affected by tidal flows (Terwindt 1988; Shanmugam 2003) that are typical of the *Skolithos* ichnofacies (MacEachern et al. 2007). However, the taphonomic character of shells (high frequency of disarticulated and fragmented valves; rare complete valves of *Modiolus adriaticus* are oriented convex-upward) typically indicates storm events (Brenchley et al. 1993; El-Sabbagh 2008). Consequently,

the upper part of the Upper Marls Member corresponds to a storm- and tide-influenced sedimentary environment. The ichnoassemblage of *Gyrolithes, Arenicolites*, *Macaronichnus* and *Skolithos linearis* reflects the upper shoreface–foreshore contact corresponding to the *Skolithos* ichnofacies.

Ophiomorpha ichnoassemblage

Trace fossils are generally poorly preserved and scarce in the Upper Sandstone Member: *O. nodosa*, *O. irregulaire*, *Gyrolithes* isp., *Skolithos* isp. and *Thalassinoides horizontalis*. *Ophiomorpha nodosa* is the most abundant trace fossil in this member. *O. nodosa* is a substrate-controlled ichnotaxon recorded mainly from fine- to medium-grained sand deposits (Gibert et al. 2006). In modern analogues, *Ophiomorpha* is produced by the shrimp-like crustacean *Callichiurus*, which lives in a burrow habitat in high-energy coastal marine sand settings. *O. nodosa* is a prominent and striking vertical structure that commonly forms a low-abundance and low-ichnodiversity community, preserved in thick-bedded sandstones and/or shell sandstones.

The common occurrence of *O. nodosa* in nearshore settings is considered a palaeobathymetric indicator (Frey et al. 1978; Curran & White 1991; Pemberton et al. 2001) that is most abundant in foreshore to upper shoreface settings (Pemberton et al. 2001). The monospecific dominance of *Ophiomorpha* assemblages suggests opportunistic colonisation behaviour under restricted environmental conditions. This ichnogenus is typical for *Skolithos* ichnofacies and reflects short-time energy fluctuations. In shallow, storm-dominated environments, prevailing hydrodynamic conditions and availability of nutrients are often the most important factors controlling the distribution of trace fossils (Fürsich et al. 2006, 2018).

The presence of vertical *O. nodosa* indicates the abundance of suspended organic particles in water (Buatois & Mángano 2011).

The Upper Sandstone Member is characterised by fluctuating periods of deposition and erosion in the littoral–sublittoral zone, resulting in the absence of shallow tiers (Bromley 1990; Bromley & Asgaard 1991).

Discussion and conclusions

The Pliocene basins, where bioturbation has been studied the most in-depth in the Western Mediterranean, are those located to the NE of the Iberian Peninsula (Martinell 1988; Gibert & Martinell 1995, 1999) and SE of France (Gibert et al. 2007). In all cases, the general stratigraphic sequence of the marine strata is characterised by a unit of blue clays, a unit formed by an alternation of sandy levels with other more clayey ones, and finally a conglomerate unit. These units grade both vertically and laterally, indicating a transition from open marine facies to more littoral ones. The trace fossils are better preserved in the sandy levels. The depositional environments vary from bays or gulfs (Baix Ebre, Alt Empordà) to

estuaries (Baix Llobregat) or deltas (Roussillon). Such variety of littoral environments involves very specific ichnoassemblages. Moreover, these basins are Zanclean in age and therefore, not coeval with the Slama Formation in the Lower Chelif Basin. Despite both conditions, it could be relevant to establish some ichnotaxonomic and palaeoenvironmental comparisons among some of the basins.

The ichnodiversity of the Slama Formation, with 16 described ichnotaxa, is the highest among the considered basins.

The Roussillon and Alt Empordà basins display a poor trace fossils content with regards to both ichnodiversity (2 and 5 recorded ichnotaxa, respectively) and abundance. *Ophiomorpha nodosa* and *Thalassinoides* isp. are common with the Slama Formation in the Rousillon basin. Gibert & Martinell (1998) describe the *Planolites–Teichichnus–Thalassinoides* ichnofabrics from the ichnoassemblage in Roussillon, which has no equivalence in the Slama Formation. In the Alt Empordà, coincidences concern *Skolithos linearis* and *Thalassinoides* isp., whereas Gibert & Martinell (1998) described shell-filled *Thalassinoides* ichnofabrics that are typical of shallow bay environments of low or moderate energy. Again, it should be noted that no similarities were found with the ichnoassemblages in the Slama Formation.

The Baix Llobregat and Baix Ebre basins hold a high level of ichnodiversity, although lower than that of the Slama Formation (14 and 12 ichnotaxa, respectively; Gibert & Martinell 1996, 1999). Ichnotaxonomic coincidences were limited to 4 domichnion-fodichnion ichnotaxa (*Ophiomorpha nodosa*, *Skolithos linearis, Thalassinoides suevicus* and *Palaeophycus* isp.) recorded at Baix Llobregat, and 3 (*S. linearis, Thalassinoides* isp. and *Palaeophycus* isp.) at Baix Ebre.

As in the Slama Formation, four ichnoassemblages related to the depositional environment (proximal to distal) were defined in the Baix Llobregat Basin, where the *Ophiomorpha* assemblage represents the most proximal association (Gibert & Martinell 1999). In the Slama Formation, the four ichnoassemblages reflect shallow environments from a lower shoreface to foreshore settings. In the Baix Llobregat Basin, the ichnoassemblage distribution shows transitions from proximal environments (*Ophiomorpha* assemblage) to more distal ones (*Scalarituba–Scolicia* assemblage).

The Vera Basin on the Southern Iberian peninsula, upper Pliocene strata contain trace fossils. Coarse sands display a low level of ichnodiversity, since only 4 ichnotaxa have been described there. *Ophiomorpha nodosa* and *Skolithos* (domichnia) are the common ichnotaxa with the Slama Formation. Two ichnotaxa of domichnia/equilibrichnia and domichnia/fodichnia (*Diplocraterion* and *Teichichnus*) are the only remaining ones. The assemblage could represent the *Skolithos* ichnofacies, typical of very shallow marine environments.

The Upper Pliocene Slama Fomation exposed in the Sidi Brahim Telegraph area (Lower Chelif Basin, Algeria) contain marine trace fossils changes in benthonic ecologic conditions. The distribution of trace fossils is conditioned by the oxygen content in the sediment; the abundance of nutrients was likely generated by upwelling and the sedimentation rate rather than by bathymetry. Ichnofossil diversity and size parameters (burrow diameters, vertical penetration depths) generally increase, resulting in the production of distinct ichnoassemblages which reflect shallow marine environments, indicating a shallowing trend from the lower shoreface to the foreshore settings:

- The *Thalassinoides* ichnoassemblage (Lower Sandstone Member and Lower Marls Member) represents the mixed *Cruziana/Skolithos* ichnofacies, which reflects lower shoreface conditions.
- The *Skolithos* ichnoassemblage (Middle Sandstone Member) represents the archetypical *Skolithos* ichnofacies and corresponds to the middle shoreface setting.
- The *Macaronichnus–Gyrolithes* ichnoassemblage (Upper Marls Member) indicates a shoreface–foreshore contact.
- The *Ophiomorpha* ichnoassemblage (Upper Sandstone Member) can be interpreted as the proximal *Skolithos* ichnofacies, which most likely corresponds to foreshore settings.

A comparison with other Western Mediterranean Pliocene basins denotes a wide range of ichnoassemblages with very particular features – all of them indicating shallow or very shallow environments (shoreface-foreshore).

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