



Ichnofabrics of the Capdevila Formation (early Eocene) in the Los Palacios Basin (western Cuba): Paleoenvironmental and paleoecological implications



Jorge Villegas-Martín ^{a,*}, Renata Guimarães Netto ^a, Ernesto Luis Correa Lavina ^a,
Reinaldo Rojas-Consuegra ^b

^a Graduate Program in Geology, Universidade do Vale do Rio dos Sinos-UNISINOS, Av. Unisinos, 950, 93022-000 São Leopoldo, RS, Brazil

^b Museo Nacional de Historia Natural de Cuba. Obispo 61, Habana Vieja, Ciudad de la Habana, Cuba

ARTICLE INFO

Article history:

Received 30 April 2014

Accepted 7 September 2014

Available online 18 September 2014

Keywords:

Ichnology

Turbidites

Eocene

Capdevila Formation

Cuba

ABSTRACT

The ichnofabrics present in the early Eocene siliciclastic deposits of the Capdevila Formation exposed in the Pinar del Rio area (Los Palacios Basin, western Cuba) are analyzed in this paper and their paleoecological and paleoenvironmental significance are discussed. Nine ichnofabrics were recognized in the dominantly sandy sedimentary succession: *Ophiomorpha*, *Asterosoma*, *Thalassinoides*, *Palaeophycus*, *Scolicia*, *Bichordites-Thalassinoides*, *Rhizocorallium*, *Scolicia-Thalassinoides* and rhizobioturbation. Diversity of ichnofauna is low and burrows made by detritus-feeding organisms in well oxygenated and stenohaline waters predominate. Suites of the Cruziana and Skolithos Ichnofacies lacking their archetypal characteristics were recognized, being impoverished in diversity and presenting dominance of echinoderm and decapods crustacean burrows as a response to the environmental stress caused by the high frequency of deposition. The ichnofabric distribution in the studied succession, its recurrence in the sandstone beds and the presence of a Glossifungites Ichnofacies suite with rhizobioturbation associated reflect a shoaling-upward event with subaerial exposure of the substrate. The integrated analysis of the ichnology and the sedimentary facies suggests deposition in a shallow slope frequently impacted by gravitational flows and high-energy events. The evidence of substrate exposure indicates the occurrence of a forced regression and suggests the existence of a sequence boundary at the top of the Capdevila Formation.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

Trace fossils are known for their importance to help to evaluate different aspects such as substrate consistency, salinity, oxygenation, and hydrodynamic energy on the paleoecologic and paleoenvironmental reconstructions (e.g. Buatois and Lopez-Angriman, 1992; Buatois and Mángano, 2011; Buatois et al., 2010; Netto and Rossetti, 2003; Netto et al., 2009; Uchman, 1991, 1992), as well as to infer relevant shifts of facies and key-stratigraphic surfaces (e.g. Pemberton et al., 2001; Buatois and Mángano, 2011). In Cuba, the

use of the ichnofossils for these interpretations is scarce, being only mentioned in literature under mistaken or obsolete terms such as: “bioglyphes”, “hieroglyphic”, “traces”, “channels”, “bioturbation”, or “bioerosion” (Albear and Iturralde-Vinent, 1985; Jakus, 1983; Pszczólkowski, 1987; Rojas-Consuegra, 1999). Only in some recent studies these structures are being identified and have received more attention (Menéndez-Peñate et al., 2011; Pszczólkowski, 2002; Pszczólkowski and Myczyński, 2009; Villegas-Martín and Rojas-Consuegra, 2011; Villegas-Martín et al., 2012).

In the Capdevila Formation the ichnological record is restricted to *Chondrites* in outcrops of the La Havana region (Brönnimann and Rigassi, 1963) and the occurrence of abundant trace fossils in the Los Palacios Basin (Brust et al., 2011). Nevertheless, materials present in the paleontological collection of the National Museum of Natural History of Cuba revealed the existence of a particular ichnofauna in Eocene deposits of the Capdevila Formation, which is subject of study in this work.

* Corresponding author.

E-mail addresses: jvillegasmartin@gmail.com (J. Villegas-Martín), nettorg@unisinos.br (R.G. Netto), lavina@unisinos.br (E.L.C. Lavina), Cuba.rojas@mnhnc.inf.cu (R. Rojas-Consuegra).

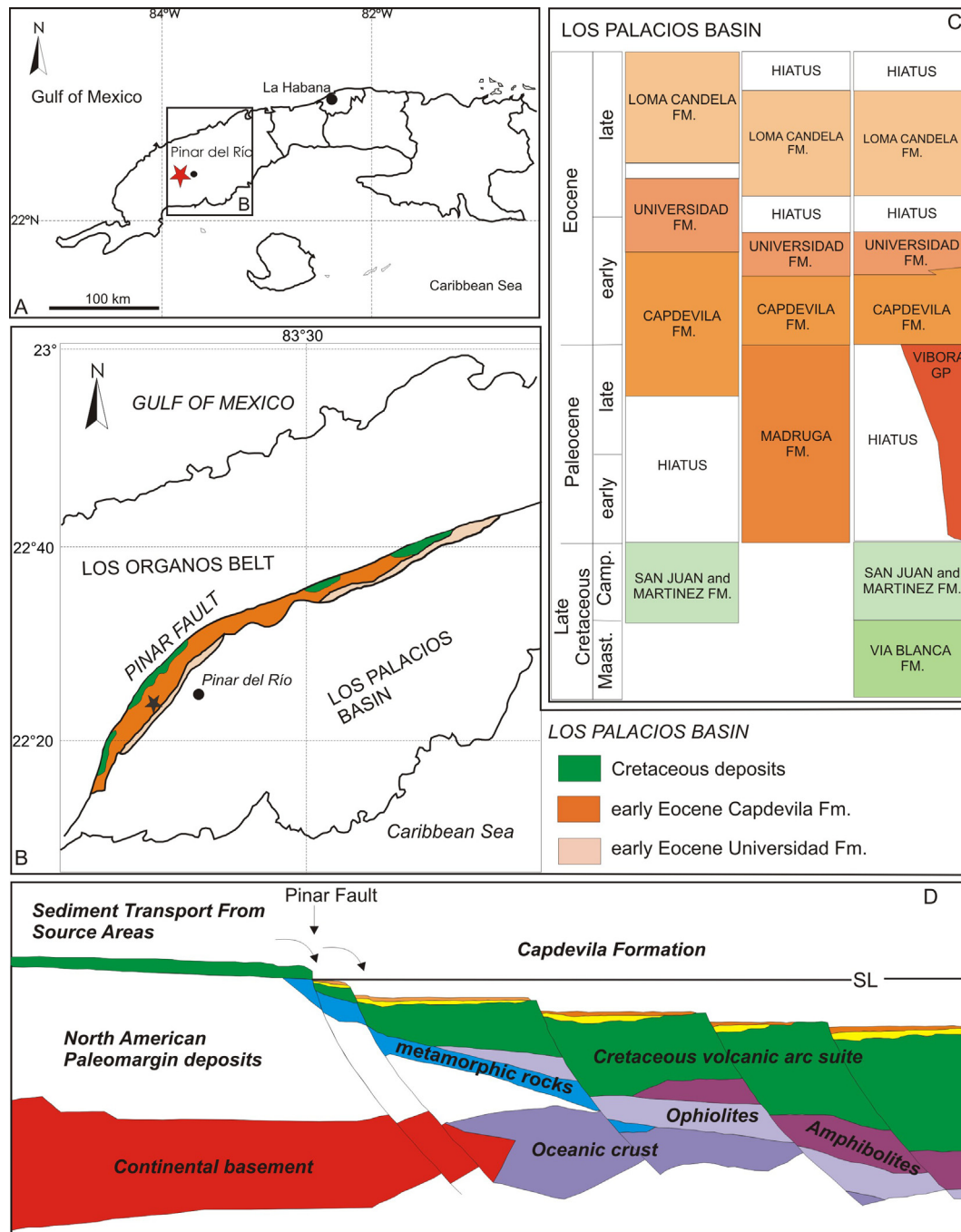


Fig. 1. A–B. Geographic location (A) of the study area (star) and its geological situation, near the Pinar fault (B), which demarcates the limit between the Los Palacios Basin and the Sierra de los Órganos, in western Cuba (modified from Albear and Iturralde-Vinent, 1985). C. Stratigraphy of the Los Palacios Basin showing the stratigraphic position of the Capdevila Formation (modified from Brust et al., 2011). D. Architecture of the Los Palacios Basin during the Eocene, as estimated by Brust et al. (2011), showing the deposition of the Capdevila Formation and the potential sediment source areas.

Thus, the objectives of this contribution are three-fold: (i) to identify and to describe the ichnofossils of the studied section, (ii) to recognize the facies associations and the trace fossil assemblages present in the succession and (iii) to analyze in an integrated way the facies and the ichnofauna of the Capdevila Formation to improve paleoenvironmental and paleoecological interpretations.

2. Materials and methods

The trace fossil assemblage of the Capdevila Formation is preserved mainly as ichnofabrics, which were described through direct

observations in the field in almost all beds of the exposed sedimentary succession in the study area. Some well-preserved specimens from samples previously collected in equivalent sedimentary successions of the Capdevila Formation were also analyzed and allowed the recognition of some ichnotaxa at ichnospecies level. These specimens (around 12) are housed in the paleontological collection of the National Museum of Natural History of Cuba under the numbers MNHNCu-96.003567, MNHNCu-96.001291, MNHNCu-96.002933, MNHNCu-96.001297, MNHNCu-96.001292, MNHNCu-96.001294, MNHNCu-96.001296, MNHNCu-96.003689, MNHNCu-96.001295, MNHNCu-1272.

The ichnofabric description considered the main general ichnotaxobases (general morphology, burrow walls, burrow infill, branching, *sensu* Bromley, 1996) and followed the guidelines for ichnotaxonomy and the stratigraphic classification as stated by Bertling et al. (2006) and Seilacher (1964), respectively. The bioturbation index (BI) was measured based on the scale proposed by Reineck (1967). The sedimentary facies are described taking into account basic lithology, physical sedimentary structures, contact between two beds and ichnofabrics. The model of Mutti (1992) for turbiditic facies was adopted herein for facies interpretation.

3. Geographic and geological context

3.1. Los Palacios basin

The Los Palacios Basin is a strike-slip and piggy-back basin (Iturralde-Vinent, 1995, 1996; Sommer, 2009) presenting a half-graben geometry placed at the south of the Pinar fault in western Cuba (Fig. 1) which formed syn to post-orogenic (Maastriichtian–Eocene) sediment traps derived from emerged land sections (Brust et al., 2011). Its deposits are mainly Paleogene and Neogene in age, although it goes from the Upper Cretaceous (Maastriichtian) to the Quaternary (Bralower and Iturralde-Vinent, 1997).

According to stratigraphic studies (Piotrowski, 1987; Bralower and Iturralde-Vinent, 1997), the basin infill starts with a predominance of fossiliferous (rudists) limestones, sandstones and conglomerates (in minor scale) deposited in a shallow marine environment, barely affected by tectonic activity (Martínez and San Juan formations). The Vibora Group (late Paleocene) unconformably overlies the basal deposits and consists of limestones, fine-grained sandstones and conglomerates. The Capdevila Formation is represented by the overlain deposits which are separated from the Vibora Group by a depositional hiatus. It is characterized by coarse-grained siliciclastic sandstones, conglomerates and calcareous sandstones deposited under predominant marine conditions during the early–early Eocene.

During the Eocene the basin was strongly affected by tectonic activity which caused its shoaling upward and local emergence of some portions. Deposition generated at this time characterizes the sedimentary succession of the Capdevila Formation. The basin stabilization after these events originated the deposition of hemipelagic marly chalks which characterizes the Universidad Formation (late–early Eocene) (Piotrowski, 1987). A depositional hiatus occurs between the latter and the Loma Candela Formation (middle Eocene) which is characterized by the sedimentation of conglomerates, limestones, sandy carbonates and sandstones (Piotrowski, 1987). Two hypotheses were suggested for this tectonic activity during the Eocene, one attributed to orogenic movements in the Guaniguanico mountains at the end of the collision that took place in western Cuba (Piotrowski, 1987) between the late Paleocene and the early Eocene (Bralower and Iturralde-Vinent, 1997) and another related to block movements all along the Pinar fault during the early Eocene (Gordon et al., 1997). It is suggested that the source of the sediments could have been elevated areas situated at the NE of the basin (Brust et al., 2011).

3.2. Capdevila Formation

The Capdevila Formation was originally described by Palmer (1934). It is composed of an up to 400 m-thick well-exposed sedimentary succession in the provinces of La Havana, Artemisa and Pinar del Río (western Cuba), forming part of the infill of the Anticlinal Havana–Matanzas and of the Los Palacios and Bahía Honda basins (Albear and Iturralde-Vinent, 1985; Bralower and

Iturralde-Vinent, 1997; Brönnimann and Rigassi, 1963; García-Delgado and Torres-Silva, 1997; Gordon et al., 1997). The unit is attributed to the early Eocene due to foraminiferal assemblages (Brönnimann and Rigassi, 1963; Brönnimann and Stradner, 1960) and nanofossil biozones (NP 11 and NP 12 biozones of ODP Site 865, according to Bralower and Iturralde-Vinent, 1997).

Brönnimann and Rigassi (1963) made a detailed description of the Capdevila Formation, recognizing four mixed siliciclastic-carbonate units in the city of La Havana. In the Los Palacios Basin the lower part of the Capdevila Formation is formed by muddy and sandy sediments intercalated with carbonates while sandstones, conglomerates and few mudstones predominate in the upper part (Brust et al., 2011). The fossil assemblage reported for this unit is formed by a variety of microfossils (foraminifera, ostracods and nanofossils), corals (*Amphiroa*, *Lithophyllum*), red algae (*Solenopora*), echinoderm fragments, bivalves, brachiopods, and small fragments of macroscopic plants (Brönnimann and Rigassi, 1963; Brönnimann and Stradner, 1960; Brust et al., 2011; Cushman and Bermudez, 1949; Piotrowski, 1987).

The deposits of the Capdevila Formation have been assumed as a bathyal marine sequence formed during an active tectogenesis period in which massive amounts of terrigenous materials were carried into the basin by turbiditic currents, forming a typical flysh-type deposition (Albear and Iturralde-Vinent, 1985). Recent studies carried out by Brust et al. (2011) in the deposits of the Capdevila Formation in Pinar del Río region placed its accumulation in a slope associated with a narrow platform.

3.3. Geology of the study area

The studied section (Fig. 2) is composed of siliciclastic deposits and corresponds to the Capdevila Formation from the Los Palacios Basin (Fig. 1). It is located approximately 20 km northeast from the Pinar del Río city (22°23'16.8" N and 83°47'10.4" W), in the province of Pinar del Río, close to the Pinar fault (tectonic limit between the Guaniguanico mountains and the Los Palacios Basin) (Fig. 1A–B). It is mainly formed by tabular sandstone beds of different grain sizes (fine to very coarse) with predominance of massive and parallel-laminated beds (Figs. 2 and 3).

Six sedimentary facies could be recognized in the study area: (i) massive sandstone; (ii) fluidized sandstone; (iii) sandstone with parallel lamination; (iv) sandstone with ripples; (v) siltstone; (vi) paraconglomerate (Figs. 3 and 4). Amalgamated beds up to 70 cm thick that sometimes show a normal gradation compose the massive sandstone facies (Fig. 4F). Clasts of assorted grain size (up to boulders) can be present in the base of the coarse-grained sandstones locally forming orthoconglomerates. Wood fragments are abundant in the beds of medium granulometry (Fig. 4G) and the ichnofabrics of *Ophiomorpha*, *Thalassinoides*, *Bichordites-Thalassinoides* and *Scolicia-Thalassinoides* have been recognized. The fluidized sandstone facies contains fluidized amalgamated beds up to 50 cm thick sometimes showing normal gradation (Fig. 4E, H). Wood fragments are abundant in medium-grained sandstone beds. The sandstone with parallel lamination facies is composed dominantly of parallel-laminated sandstone beds with normal gradation forming thinning-upward cycles (Fig. 4A, B, D). This cycles locally grade to the sandstone with ripples facies deposits. Boulders of volcanic rocks can be observed in the base of some beds. Wood fragments can be found in the medium to fine-grained sandstones, and the ichnofabrics of *Thalassinoides*, *Palaeophycus*, *Scolicia*, *Bichordites-Thalassinoides*, *Rhizocorallium* and rhizobioturbation are present in most of beds. The sandstone with ripple facies (Fig. 4A, C) is characterized by fine- to medium-grained sandstones with unidirectional ripples mainly preserved at the top of the beds. Massive siltstones homogenized by intense bioturbation characterize the



Fig. 2. Exposed siliciclastic deposits of the Capdevila Formation in Pinar del Río area, showing a general view of the lower portion (A) and the medium to upper portion (B) of the sedimentary succession described in this paper. Scales: 23 cm in A, 170 cm in B.

siltstone facies (Fig. 4D), in which the ichnofabric of *Asterosoma* has been recognized, while polymitic conglomerates supported by matrix, composed by fine to coarse gravels and forming lenticular beds characterize the paraconglomerate facies (Fig. 4E, I). The

matrix is composed of medium to very coarse-grained sandstones and normal and inverse gradation can be observed in the beds. Angular, subrounded and rounded clasts are present, with a predominance of the first ones. Clasts can touch each other locally.

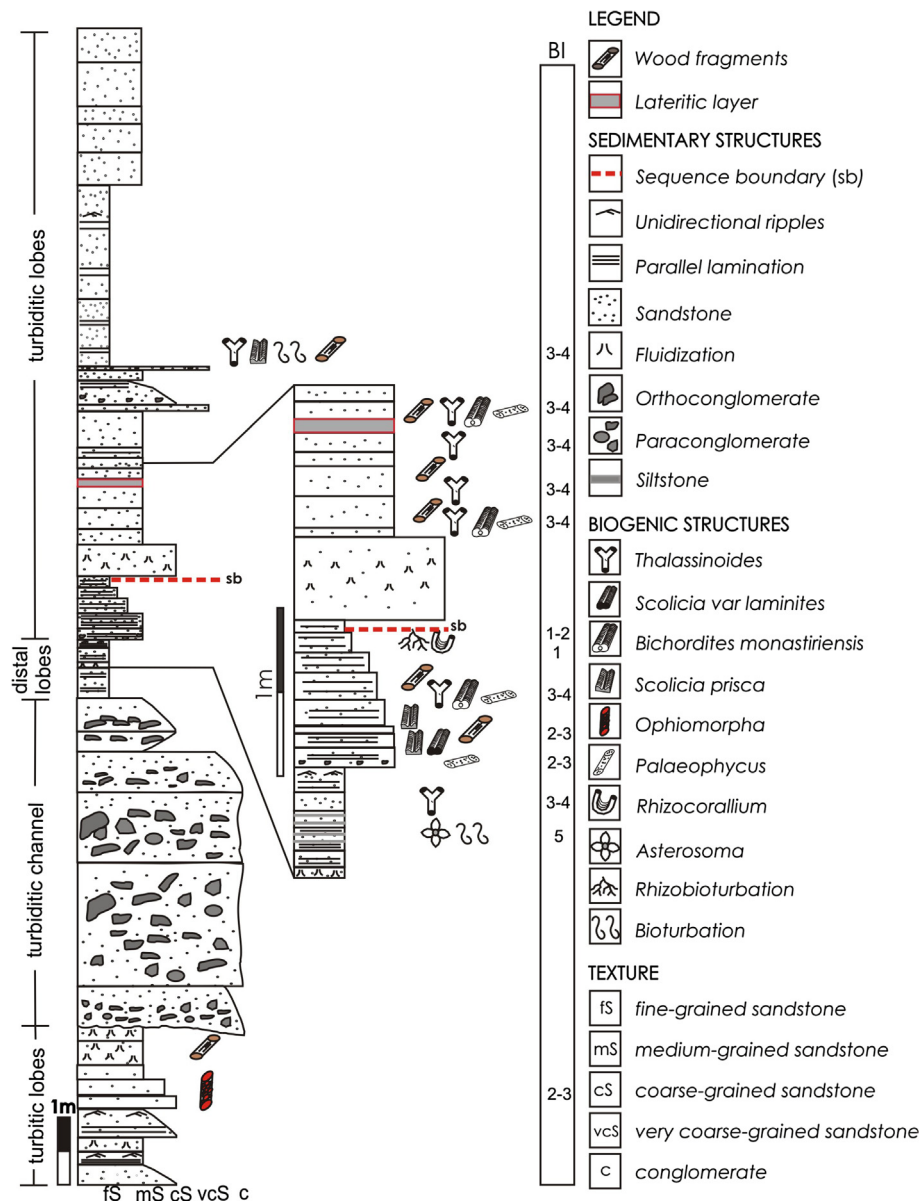


Fig. 3. Schematic profile of the Capdevila Formation sedimentary succession in the study area signaling the trace fossil distribution and the bioturbation index (BI) per bed.



Fig. 4. Sedimentary facies of the Capdevila Formation exposed in the study area. A. Massive sandstones capped by sandstones with parallel lamination and sandstones with ripples. B. Tabular beds of sandstones with parallel lamination. C. Sandstones with ripples. D. Tabular beds formed by interbedded siltstones and sandstones with parallel lamination. E. Fluidized sandstones and paraconglomerates. F. Massive sandstones. G. Wood fragment pavements in the sandstone beds. H. Fluidized sandstones. I. Paraconglomerates. Scales: 11 cm (A), 13 cm (B, F), 3.7 cm (C), 5 cm (D, H), 11 cm (E, I), 2 cm (G).

In overall, most of the sedimentary facies result from gravitational flows. The sandstone beds correspond to the F5, F8, and F9 of Mutti (1992) while the paraconglomerates represent the non tractive deposits of the F2 and the siltstones are assumed as deposited by low intensity flows and decantation, corresponding to the F9. The sandy facies predominate and are genetically related among them, possibly characterizing deposition in turbiditic lobes. The sandstones with ripples settle over the sandstones with parallel lamination forming thinning-upward cycles. The massive sandstone facies could form the base of these cycles but, in general they appear isolated in the succession, suggesting frequent erosion. The massive and the fluidized sandstone facies suggest the action of high-concentration turbiditic flow (Walker, 1965), the latter reflecting rapid deposition (Stow et al., 1996). The parallel-laminated sandstones where deposited during the dominance of upper flow regime while the sandstones with ripples reflect deposition in a lower flow regime and a turbiditic slowdown flow

(Stow et al., 1996; Walker, 1965). The siltstone facies correspond to the settlement of the sediment carried mainly in suspension (Stow et al., 1996) while the paraconglomerate facies characterize cohesive-matrix detritic flows that represent channel infill. Muddy deposits are mostly absent, suggesting dominance of highly erosive processes or of high depositional frequency.

The deposits described in the study area are equivalent to those described by Brust et al. (2011) for the upper portion of the Capdevila Formation in the Los Palacios Basin. These authors attributed the deposition of the paraconglomerates as a product of the tectonic activity in that period all along the Pinar Fault zone.

4. Ichnofabrics of the capdevila formation

Nine ichnofabrics could be recognized in the Capdevila Formation in the study area. Except for *Bichordites monastiriensis*, *Scolicia prisca* and *Scolicia* var *laminites*, all the biogenic structures present

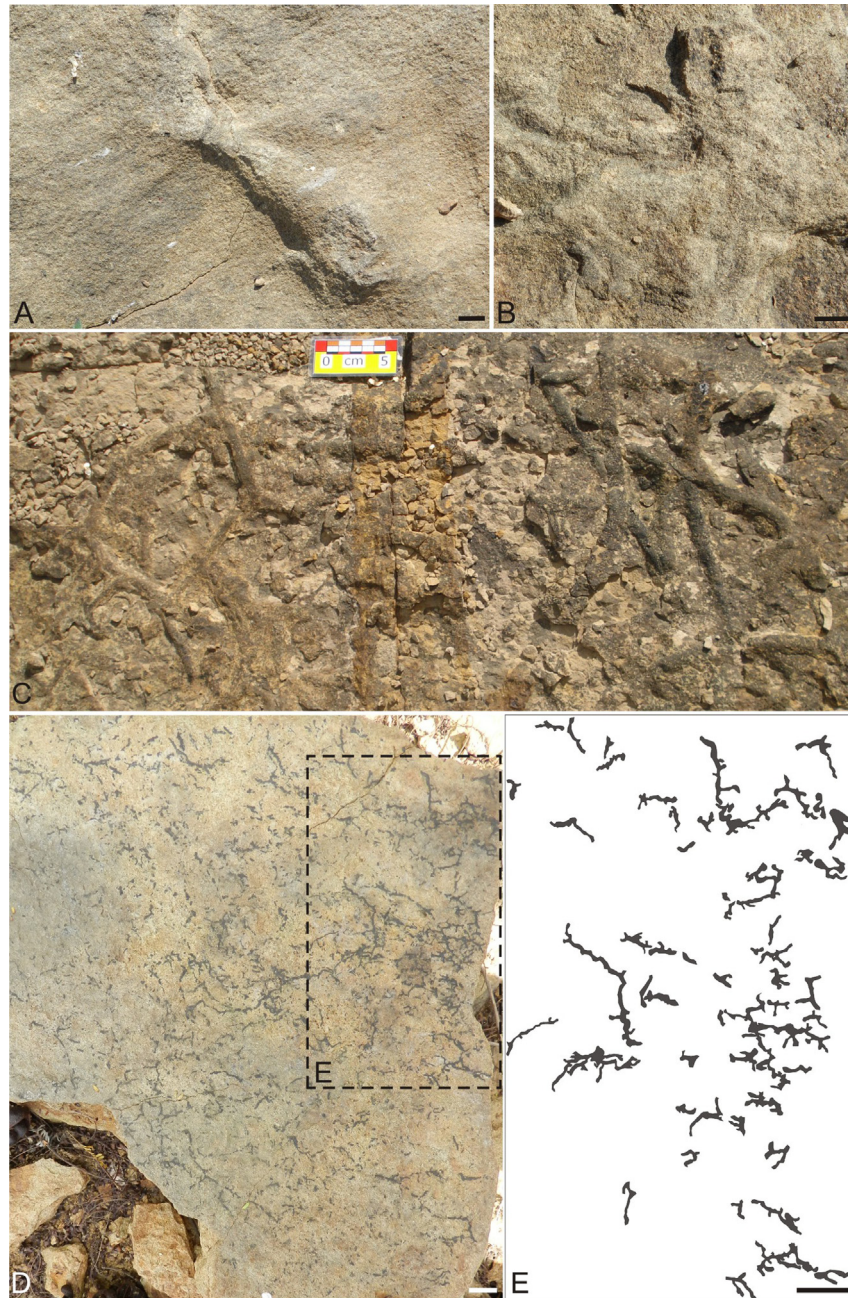


Fig. 5. Ichnofabrics of the Capdevila Formation in the study area. A–B, *Asterosoma* ichnofabric. C, *Thalassinoides* ichnofabric. D–E, Rhizobioturbation. Scales: 2 cm, except for C, which measures 5 cm.

in the ichnofabrics were identified only at ichnogenus level as they do not present morphologies that allow the observation of the ichnospecific characteristics. Except for the *Asterosoma* ichnofabric, cross-cutting relationships were not observed.

4.1. The *Asterosoma* ichnofabric

It is formed by *Asterosoma* (Fig. 5A–B) and dense undetermined bioturbation, showing a BI 5, locally 6. The structures attributed to *Asterosoma* show a star-like shape, constituted by a central sub-circular or circular tube, from which four elongated bulbous-like, sub-rounded ending tunnels with smooth edges emerge. *Asterosoma* is preserved in negative and positive epirelief at the top of the siltstone facies beds (Fig. 3) and cross-cut the previous ichnofabric, which in some less bioturbated areas show faint branched

burrows that resembles *Thalassinoides* and also horizontal burrows that could be attributed to *Palaeophycus*. The best preservation of *Asterosoma* in this ichnofabric suggests colonization of the medium layer of the substrate (see Bromley and Ekdale, 1986) and denotes paleoecological and sedimentological aspects that will be discussed later.

4.2. The *Thalassinoides* ichnofabric

Composed exclusively of *Thalassinoides* (Fig. 5C), with BI 3–4, which occurs as a dychotomic-branched burrow system with horizontal and vertical components, predominating the horizontal ones and presenting a straight to lightly inclined trajectory. In many cases the burrows were observed as independent Y-shaped short fragments. The burrow walls are smooth and circular or subcircular

in cross section. The infill is equal to the host rock. The burrows are preserved at the top of the beds of the sandstones with parallel lamination facies and at the top of the beds of the massive sandstones facies with medium granulometry (Fig. 3).

4.3. The *Rhizocorallium* ichnofabric

It is only formed by *Rhizocorallium* (Fig. 6A–B), with BI 1–2. It is characterized by U-shaped burrows disposed parallel or slightly inclined to the bedding plane which are subcylindrical in cross section. The characteristic spreiten is poorly preserved (virtually absent) and scratch marks are common in the burrow wall. Branches are lacking. *Rhizocorallium* is preserved in positive epirelief, in the fine to medium-grained beds of the sandstones with parallel lamination facies (Fig. 3). Abundant organic material was found at the level containing this ichnofabric.

4.4. The *Scolicia* ichnofabric

It is composed exclusively of *Scolicia* (Fig. 6 C–F), presenting a BI 2–3 and preserved in positive and negative epirelief at the top of the sandstones with parallel lamination facies (Fig. 3). The structures preserved in negative epirelief are assigned to *Scolicia prisca* (sensu Uchman, 1995, Fig. 6 C–E) and show a straight to lightly meandering trajectory in certain portions. They are preserved as grooves formed by a floor and two lateral walls. The upper margins of the lateral walls are lightly elevated just over the surface of the bed; the walls go from inclined to lightly curved and can be covered

by asymmetric size-varied laminae. The floor is convex, being either smooth or presenting a laminated infill. Two sediment strings are disposed at each side of the floor, close to the lateral walls. In cross section they have subcircular or U-shaped form. Branches are not observed. The structures preserved in positive epirelief are assigned to *Scolicia* var *laminites* (sensu Uchman, 1995, Fig. 6F). In longitudinal section it characterizes a bilobated burrow with a median groove. The burrow infill is formed by barely visible menisci. The burrows show a lightly meandering trajectory. In some samples, features of *S. prisca* morphology can also be distinguished. Small wood fragments were found in *Scolicia* ichnofabric-bearing beds.

4.5. The *Palaeophycus* ichnofabric

It is formed exclusively by *Palaeophycus* (Fig. 7D) and shows a BI 2–3. Horizontal, non-branched burrows with a mainly inclined trajectory and infill of the same matrix as the host rock predominate in this ichnofabric. A discrete lining is observed in the burrow wall which is irregular in some portions. The burrows are preserved as positive epirelief in the fine to medium-grained beds of the sandstones with parallel lamination facies (Fig. 3).

4.6. The *Bichordites*-*Thalassinoides* ichnofabric

It is composed of *Bichordites*, *Thalassinoides* and *Palaeophycus* (Fig. 7A–C, E) with BI 3–4, being *Bichordites* and *Thalassinoides* the most common ichnogenera. *Bichordites* is represented by the

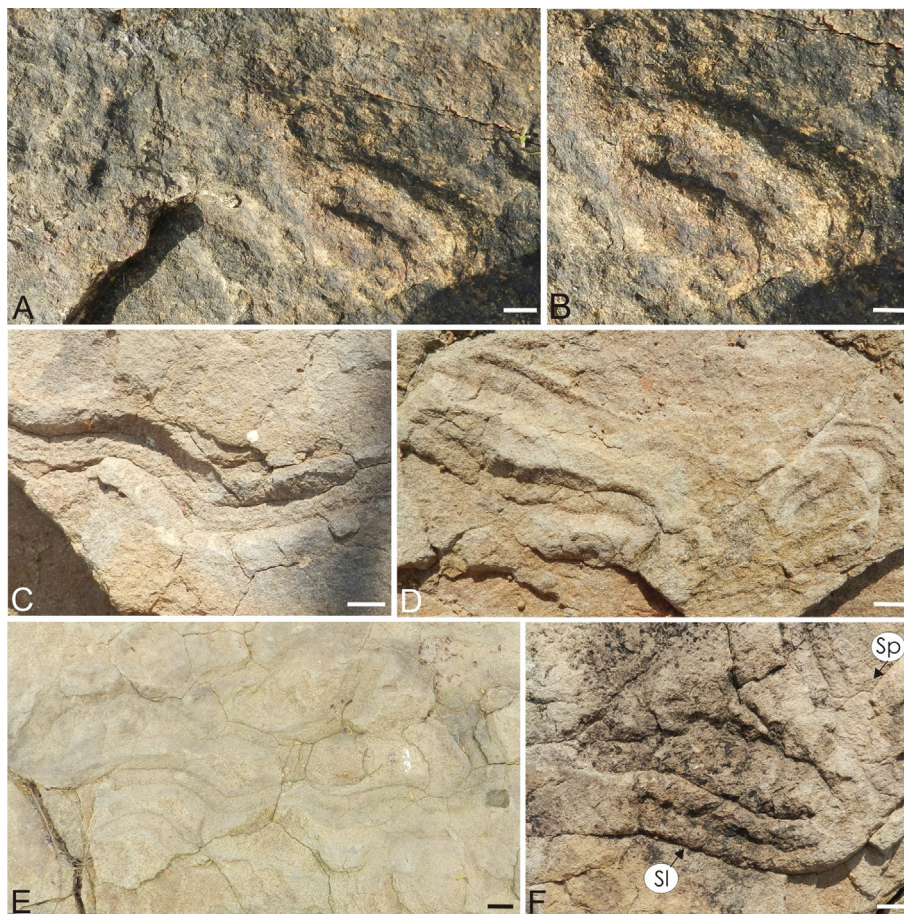


Fig. 6. Ichnofabrics of the Capdevila Formation in the study area. A–B. *Rhizocorallium* ichnofabric, showing the sharp walls with scratch marks. C–F. *Scolicia* ichnofabric, mainly represented by *Scolicia prisca* (C–E), *Scolicia* var *laminites* (Sl) and *Scolicia prisca* (Sp) (F). Scales: 2 cm.

ichnospecies *B. monastiriensis* (sensu Uchman, 1995) (Fig. 7A, C, E). It is formed by non-branching subhorizontal and horizontal burrows with an inclined to straight trajectory, circular to subcircular in cross section, crossed by a central string that can either have a circular or hearty form. A concentric lamination infill can be observed in some specimens (Fig. 7A, C). A discrete groove can be present in the upper part of the central string and a ridge can appear over the central string, in some specimens. The samples of *Thalassinoides* (Fig. 7B–C, E) and *Palaeophycus* (Fig. 7C, E) in this suite present the same morphological characteristics as the homonymous ichnofabrics described in 4.2 and 4.5. The burrows are preserved in semirelief and in epirelief in beds rich in wood fragments of the fine to medium-grained sandstones with parallel lamination facies, as well as of the medium-grained massive sandstones facies (Fig. 3).

4.7. *Scolicia*-*Thalassinoides* ichnofabric

It is formed by *Scolicia*, *Thalassinoides*, rare *Palaeophycus* and undetermined bioturbation with BI 3–4. The burrows are preferentially horizontal to the bedding plane. The best preserved samples of *Scolicia* can be attributed to *S. prisca* and are preserved in negative epirelief, with a lightly meandering to straight trajectory. The morphology is equivalent to that described in the *Scolicia* ichnofabric (see Fig. 6C–F). The morphology of *Thalassinoides* and

Palaeophycus is also equivalent to that previously described in the homonymous ichnofabrics (see Figs. 5C, 7B–D). It is preserved in the fine-grained beds of the massive sandstone facies (Fig. 3).

4.8. The *Ophiomorpha* ichnofabric

It is formed exclusively by *Ophiomorpha* (Fig. 7F), presenting BI 2–3. The burrows are mainly vertical in relation to the bedding plane, circular in cross section, with a peletted lining. Pellets are irregularly distributed through the burrow wall and isolated pellets can occur locally. Branches are rarely observed. The burrow infill is the same of the host rock. The burrows are preserved in full relief in beds of the massive sandstones facies (Fig. 3).

4.9. The rhizobioturbation ichnofabric

It is composed of branched, irregular, horizontal, tiny (1–2 mm in diameter) tubules infilled with organic-rich sediment, showing BI 1–2 (Fig. 5D, E). The tubules are characterized by an irregular longer central stem from which shorter secondary ramifications are originated. The tubules diameter is highly variable all along each tubule and terminations are acute or subrounded. The diameter variation in a same tubule, the acute terminations and the absence of a regular dichotomic-branching pattern allow to infer rhizobioturbation and to distinguish it from *Chondrites*. Similar

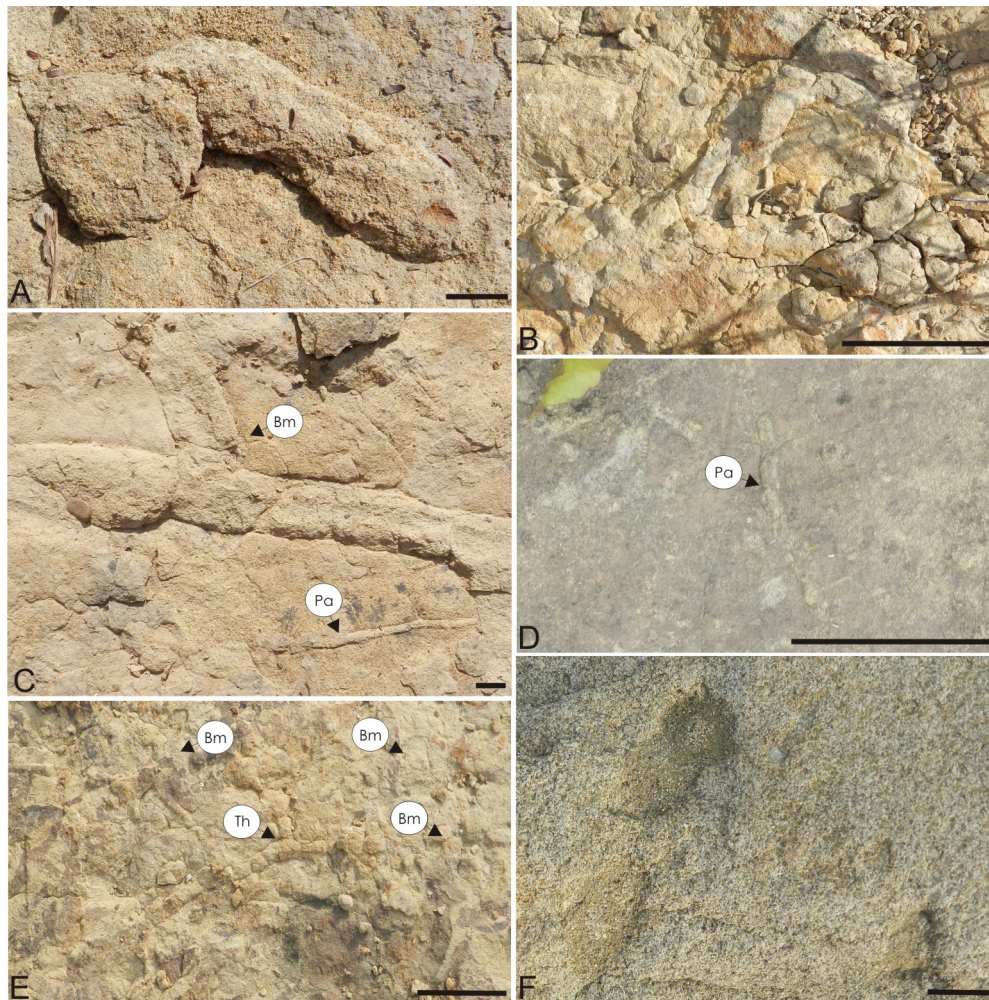


Fig. 7. Ichnofabrics of the Capdevila Formation in the study area. A–C, E. *Bichordites*-*Thalassinoides* ichnofabric showing *Thalassinoides* isp. (Th), *Palaeophycus* isp. (Pa) and *Bichordites monastiriensis* (Bm), the latter shown in close-up view in A. D. *Palaeophycus* ichnofabric. F. *Ophiomorpha* ichnofabric. Scales: 2 cm, except for B, that measures 9 cm.

structures were also described by Bromley and Uchman (2003) as rhizobioturbation. This ichnofabric occurs in fine to medium-grained beds of the sandstones with parallel lamination facies (Fig. 3).

The base of the Capdevila Formation in the study area is formed by the recurrence of the sandstone facies. The *Ophiomorpha* ichnofabric occurs in the massive sandstones preserved at the top of the basal beds (Fig. 3), which are capped by fluidized sandstones rich in wood fragments (Figs. 3 and 4G). Thick beds of paraconglomerates settle over the basal sandstones and represent high-energy channelled flows. The siltstones facies overlies the paraconglomerates and indicates the establishment of low hydrodynamic energy conditions. The high degree of bioturbation and the presence of the *Asterosoma* ichnofabric suggest deposition under fully marine condition in stable substrates from offshore settings. The occurrence of offshore deposits placed over channelled flows suggests shoaling up at the offshore-slope zones and configures the unique evidence of stable conditions in the Capdevila Formation sedimentary sequence in the study area.

Toward the top, the sandstone beds are ubiquitous, indicating that the high-energy processes were dominant throughout the deposition. The sandstones form thinning-upward cycles in the middle part of the succession and are rich in marine ichnofabrics (Fig. 3). The ichnofabric arrange of these cycles suggests a new shoaling upward event that culminates with the exposition of the substrate demarcated by the occurrence of rhizobioturbation and the *Rhizocorallium* ichnofabric. The presence of these ichnofabrics at the top of these cycles allows inferring a forced regression event and places a sequence boundary at the top of the middle portion of the Capdevila Formation succession in the study area (Fig. 3).

The upper portion is characterized by the reestablishment of the sandstone thinning-upward cycles comprising marine ichnofabrics which are frequently interrupted by the entry of massive sandstones, suggesting the return of the high depositional frequency conditions.

5. Paleocological analysis

The ichnofauna of the Capdevila Formation is mostly composed of truly marine ichnotaxa which reflect well-oxygenated substrates. *Thalassinoides*, *Scolicia* and *Bichordites* are the most common ichnogenera and are good indicators of the oxic conditions (Bromley et al., 1995). The burrows preserved in the Capdevila Formation deposits reflect temporary or permanent domicile of polychaetes and decapod crustaceans, as well as epifaunal or infaunal displacement of irregular echinoids, and suggest the prevalence of detritus-feeding organisms in the endobenthic community (Bromley, 1996; Buatois and Mángano, 2011). The ichnodiversity, in general, is low and the amount of bioturbation is moderate, locally high.

Four paleoichnocoenoses could be differentiated in the studied section, according to the composition and distribution of the ichnofabrics and the nature and consistency of the substrate: (i) distal Cruziana, represented by a suite of soft substrates of low energy that suggests pre-event colonization (*sensu* Howard, 1978); (ii) impoverished Cruziana, represented by a suite of soft substrates of moderate to high energy that suggest post-event colonization; (iii) Skolithos, represented by a suite of soft substrates of high energy that also suggests post-event colonization; and (iv) Glossifungites, represented by a suite of firm substrates that suggests an omission suite (*sensu* Bromley, 1975).

The suite of soft substrates of low energy (SL) occurs exclusively in the siltstones facies (Fig. 3) and is composed of the *Asterosoma* ichnofabric. *Asterosoma* has been mainly reported in shelf environments, being more frequent in lower energy zones and in

offshore settings (e.g. Bromley and Uchman, 2003; Vossler and Pemberton, 1989). Although less common, *Asterosoma* has also been reported in turbiditic-influenced zones (Powichrowski, 1989; Rindsberg, 1982). The high amount of bioturbation in SL suite and its occurrence in siltstones indicate the predominance of low energy and more stable conditions, which allowed the accumulation of organic detritus in the substrate and favored the intense activity of detritivorous organisms. In the substrate tiering, *Asterosoma* generally occupies the medium to deep tiers, being a common element in the historical layer. This layer is less affected by the superficial erosion (Bromley, 1996) and, for this reason, shows intense bioturbation. Thus, the dominance of *Asterosoma* in SL suite suggests colonization of the lower part of the transitional layer, in a stable substrate at quiet, fully marine settings.

The suite of firm substrates (SF) is characterized by the *Rhizocorallium* and rhizobioturbation ichnofabrics. It presents low ichnodiversity and punctual occurrence of the bioturbation. The virtual absence of spreiten and the presence of irregular walls with scratch marks in *Rhizocorallium* indicate excavation in stiffgrounds (Gingras et al., 2000) and shoaling-upward deposits. The occurrence of rhizobioturbation suggests the subaerial exposure of the substrates. The preferential horizontal distribution and the apparently simple structure of the rhizobioturbation (small diameter and little development of the rootlets) suggest a relatively short period of subaerial exposure and the establishment of pioneer vegetation, capable of rapidly colonizing a denuded sandy substrate. Saha et al. (2010) has reported a similar situation in coastal marine regions where *Rhizocorallium* occurs together with rhizobioturbation. Occurrences of *Rhizocorallium* specimens with poorly preserved or no spreiten were also registered by Chrzastek (2013) in stiffgrounds and firmgrounds.

The suite of soft substrates of moderate to high energy (SM) is characterized by the *Thalassinoides*, *Scolicia*, *Palaeophycus*, *Scolicia-Thalassinoides* and *Bichordites-Thalassinoides* ichnofabrics. The exclusive presence of *Thalassinoides* ichnofabric in several beds of the studied succession suggests substrates affected by high energy events. These events might either inhibiting the colonization by other detritus-feeding organisms whose traces are common in outer shelf settings or destroying the burrows made in the upper tiers (e.g. Gibert and Martinell, 1998). The *Thalassinoides* tracemakers (callianassid crustaceans) are capable of excavating in depths near to 2 m low in the sediment (e.g. Dworschak and Rodrigues, 1997) and survive to erosive events caused by the action of currents. Frequent moderate to high energy processes can generate sandy substrates in deeper areas, favoring the establishment of stable populations of deep-gallery burrowers in detriment of those made by shallower ones, as well as those made from organisms living in low energy settings. In this way, *r*-selected organisms such as some decapod crustaceans have more chance to survive to the stress established in these environments by the high energy or the high frequency of the processes (e.g. Pemberton et al., 2001). Nevertheless, the abundance of *Thalassinoides* in the studied deposits and its presence in the composition of several ichnofabrics that characterize the SM suite suggest the existence of optimal conditions for the *Thalassinoides* tracemakers, not representing here an opportunistic behavior.

Scolicia and *Palaeophycus* ichnofabrics occur in the fine to medium-grained sandstones with parallel lamination facies, being *Scolicia* the dominating one, while the *Scolicia-Thalassinoides* ichnofabric occurs in the fine-grained massive sandstones facies (Fig. 3). The variation of the ichnodiversity and the amount of bioturbation among the ichnofabrics in SM suite are apparently related to the energy of the processes that conditioned the sandstones deposition. Therefore, the *Scolicia* and *Palaeophycus* ichnofabrics represent substrates affected by more frequent deposition,

while the *Scolicia-Thalassinoides* ichnofabric represents substrates affected by less frequent deposition. Wood fragments can be found in the beds bearing the SM suite, being less frequent in those beds where the *Scolicia-Thalassinoides* occurs. That backs up the idea that those beds have been deposited under more energetic conditions or in areas which are closer to the vegetation source.

Trace fossil assemblages including *Thalassinoides*, *Palaeophycus* and *Scolicia* ichnogenera are reported in marine environments from shoreface to slope (e.g. Crimes et al., 1981; Buatois et al., 2003; Uchman, 1995), being the record of *Scolicia* abundant in deep marine deposits influenced by turbiditic currents since the Mesozoic (Wetzel and Uchman, 1998, 2001; Uchman, 1995, 1998). According to Uchman (1995), the *S. prisca* morphologies found in deep-marine turbiditic facies correspond to the basal portion of spatangoid burrows made in the mud–sand interface (post-event colonization), whose top was eroded by the turbiditic currents. The absence of the lateral walls or their small height in many specimens of *S. prisca* preserved in the study area demonstrates the dominance of erosion processes. *S. prisca* is mostly reported in turbiditic deposits of deep marine waters (Rodríguez-Tovar et al., 2010; Uchman, 1995; Wetzel and Uchman, 1998, 2001). Modern *Scolicia* tracemakers (*Spatangus* group, Smith and Crimes, 1983) live in benthic settings from shelf to deep slope, preferring sandy substrates (Kanazawa, 1992; Kroh and Hansson, 2013). The abundance of *Scolicia* in the SM suite could be a response to the preference of their tracemakers for sandy substrates, being these more tolerant than the other organisms to the increase in the sedimentation rates (sensu Vermeij, 1978).

According to Aguirre et al. (2010), frequent sedimentation pulses with little or none erosion favor the establishment of echinoderm populations in the substrate. Having this in mind, the dominance of the *Scolicia* ichnofabric in some beds can reflect not only the action of high energy processes but also the existence of frequent deposition.

The *Bichordites-Thalassinoides* ichnofabric occurs in the massive sandstone and the sandstone with parallel lamination sedimentary facies and the main components of this ichnofabric are commonly recorded in shelf environments, having *Bichordites* been registered mainly in shallow water settings (Aguirre et al., 2010; Bernardi et al., 2010; Nara, 2004; Plaziat and Mahmoudi, 1988; Pickerril et al., 1993). *Bichordites* is the product of the displacement of spatangoid echinoderms, mainly *Echinocardium*, *Eupatagus* and *Martelia* (Bromley and Asgaard, 1975; Gibert and Goldring, 2008; Bernardi et al., 2010). These organisms are distributed up to 150 m depth in modern seas (Kanazawa, 1992; Mortensen, 1951), being *Echinocardium* (*Echinocardium cordatum*) restricted to the first 40 m (Ernst et al., 1973; Howard et al., 1974; Kanazawa, 1992). Under 30–40 m depth, the individuals of the genus *Echinocardium* lose their reproductive capacity (Buchanan, 1966), which restrict them to the shallowest settings. Their presence in lower depths (50–150 m) is related to storm events (Radwanski and Wysocka, 2001) that exhume the individuals of the shallow substrates and carry them to deeper areas. The abundance of wood fragments associated to the *Bichordites-Thalassinoides* ichnofabric might indicate proximity of the continental settings or an increase in the fluvial discharges.

The *Bichordites-Thalassinoides* and *Scolicia-Thalassinoides* ichnofabrics in the SM suite show a relatively bigger ichnodiversity if compared with the other ichnofabrics which suggest more stable conditions in the substrate, with a decrease of the deposition frequency.

The soft substrate of high energy suite (SH) is composed exclusively of the *Ophiomorpha* ichnofabric that occurs in the fine to medium-grained beds of the massive sandstones facies disposed in the lower portion of the sedimentary succession (Fig. 3). The

predominance of vertical burrows in subaqueous sandy substrates, in general, reflects high energy conditions, being mainly related to shallow settings where the action of waves or tides predominate (Buatois and Mángano, 2011). The substantial presence of *Ophiomorpha* in shoreface substrates since the Mesozoic reflects the efficiency of the callianassid decapods in creating extensive galleries in these settings (Frey et al., 1978), being assumed as beachline biomarkers (Pollard et al., 1993). However, the fining-upward arrangement of the beds containing the *Ophiomorpha* ichnofabric, the absence of sedimentary structures generated by wave or tide action, and the occurrence of paraconglomerates overlying these deposits suggest deposition linked to turbiditic regimes in deeper settings, below storm wave base. *Ophiomorpha* has also been reported in offshore deposits (Manley and Lewis, 1998) and in deep marine waters influenced by turbiditic currents (Uchman, 1995, 1998), in which it represents pioneer colonizing (sensu Föllmi and Grimm, 1990), characterizing opportunistic behavior (Crimes et al., 1977).

The paleoichnocoenoses of the Capdevila Formation and the recurrence of the trace fossil suites throughout the studied succession suggest that burrowing vagile organisms such as echinoderms, crustaceans and polychaetes were favored by the colonization windows generated in each event of significant sediment input in deeper zones, being these organisms able to (i) surviving to the erosion of the shallow substrates and tolerate the transportation by dense currents to deeper settings and (ii) settling in the new substrates after each event (e.g. Savrda et al., 1998).

6. Paleoenvironment interpretation

The recognized paleoichnocoenoses in the deposits of the Capdevila Formation are representative of the Cruziana, Skolithos and Glossifungites Ichnofacies. Except for the Glossifungites Ichnofacies, the other two represent, in the studied deposits, impoverished expressions of their archetypal equivalents. The clear dominance of turbiditic deposits in the studied section suggests deposition in a slope context. The massive occurrence of trace fossil suites that are commonly present in shelf environments and the lacking of suites representative of the Nereites Ichnofacies suggest a shallower context in the slope realm (Wetzel and Uchman, 1998). This interpretation coincides with that stated by Brust et al. (2011) for the Capdevila Formation in the Los Palacios Basin. Similar trace fossil suites have also been recognized in sandy facies of slope deposits in different basins (e.g. Crimes et al., 1977, 1981; Cummings and Hodgson, 2011; Shultz and Hubbard, 2005). Except for *Bichordites*, all the other ichnogenera present in the ichnofauna of the Capdevila Formation can be found in slope deposits (Hubbard et al., 2012).

The low ichnodiversity and the predominance of only one trophic strategy (detritus feeding) of mainly truly marine organisms in the studied deposits do not reflect the typical conditions of the Cruziana Ichnofacies in marine settings, as stated by Bromley (1996), Buatois et al. (2005), Pemberton et al. (2001) and Buatois and Mángano (2011). These features, together with the predominance of the monospecific ichnofabrics suggest conditions of environmental stress (Buatois and Lopez-Angrián, 1992; Uchman, 1992; Buatois et al., 2010). The establishment of the impoverished suites of Cruziana Ichnofacies in marine settings in the studied deposits is mainly attributed to the dominance of high frequency deposition. The abundance of wood fragments in several sandstone beds with SM suite indicates the input of continental debris due to fluvial discharges, which could originate salinity fluctuations in the slope area. This hypothesis is coherent with the existence of a narrow shelf affected by a fluvio-deltaic system during early Eocene in the Los Palacios Basin, which resulted in the deposition of the Capdevila Formation (Brust et al., 2011). However, the abundance of

Scolicia and *Bichordites* in the studied section indicates that, if these discharges existed, they were sporadic and not so intense as to inhibit the stenohaline fauna. Both ichnotaxa represent bioturbation of spatangoids, which are truly marine organisms. The record of spatangoid burrows in stressed substrates of distal delta front and prodelta is scarce (e.g., McIlroy, 2007) and possibly represent pre-event colonization.

SM and SH suites represent the post-event colonization in the studied succession, being SM suite recurrent all along the

succession. They are restricted to certain sandstone beds, while others have no apparent bioturbation. The non-bioturbated intervals might represent deposits generated under higher energy conditions, which are expected in turbidites. In this case, high depositional frequency processes tend to inhibit the colonization (Carmona et al., 2009). The preferential preservation of the bioturbation at the top of the beds and the general lacking of cross-cutting might suggest rapid colonization of the new ecospace as the energy or the frequency of the sedimentation pulses decrease.

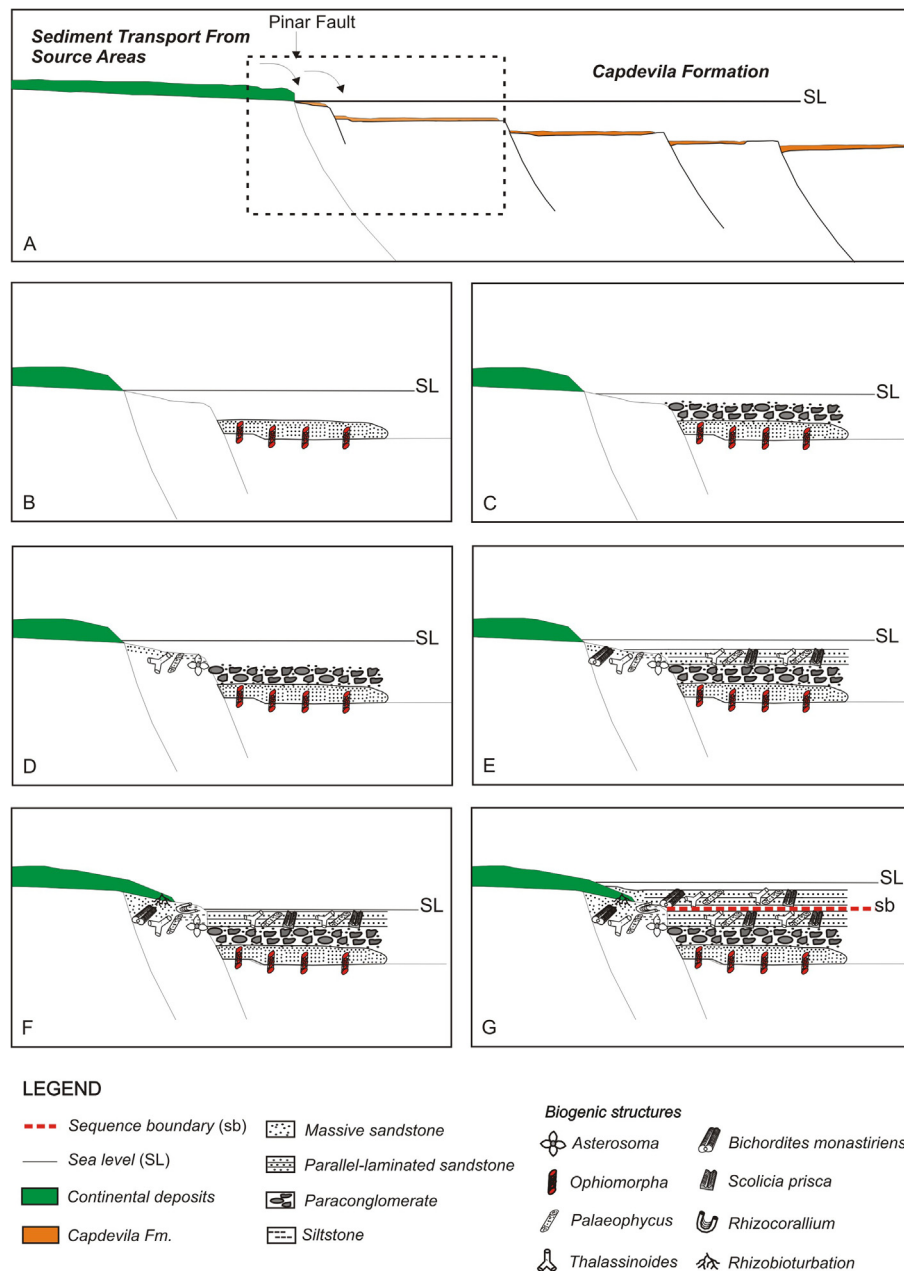


Fig. 8. Schematic draw with reconstruction of the inferred sea level oscillation during the early Eocene in Los Palacios Basin, based on the trace fossil distribution in Capdevila Formation. A. Geomorphology of the Los Palacios Basin during the early Eocene (according to Sommer, 2009; Brust et al., 2011). The dashed square limits the estimated settings where the rocks exposed in the studied section were deposited. B. Turbiditic massive sandstone deposition in slope area with opportunistic (post-event) colonization represented by the *Ophiomorpha* ichnofabric. C. Sea level fall and debris flow deposition, represented by the paraconglomerate facies. D. Pre-event colonization in siltstones and sandstones deposited in the shelf–slope transition, represented by the *Astrosoma* ichnofabric. E. Post-event colonization in turbiditic parallel-laminated sandstones in shallow slope, represented mainly by the *Thalassinoides*, *Palaeophycus* and *Scolicia-Thalassinoides* ichnofabrics, and in shelf–slope transition deposits, represented by the *Bichordites-Thalassinoides* ichnofabric. F. Significant sea level fall (forced regression) and exposure of the shelf–slope transition zone, demarcated by the establishment of the *Glossifungites* Ichnofacies, represented by the *Rhizocorallium* suite and by rhizobioturbation. G. Sea level rising and the re-establishment of the turbiditic deposition with recurrence of post-event colonization in shallow slope settings, represented by the dominance of suites composed by the *Scolicia-Thalassinoides* and *Bichordites-Thalassinoides* ichnofabrics.

Similar situations have been reported in literature and attributed to high sedimentation rates and frequent turbulence (Gibert and Martinell, 1998, 1999). According to Mellere et al. (2002), the predominance of sandstones and the general scarcity of trace fossils indicate a high sedimentation rate. In environments subject to high sedimentation rates, a short period of deposition ceasing can be enough to allow biological activity (Buatois et al., 1997). The absence of ichnofabrics in the sandstone with ripples facies suggests that the bioturbated beds would be the relicts of deposits that were eroded by the action of high energy flows.

The Cruziana Ichnofacies suites are mostly distributed in shelf deposits, from upper shoreface to lower offshore (Pemberton et al., 1992; MacEachern et al., 2007; Buatois and Mangano, 2011), so their presence in slope deposits could be assumed as atypical. However, suites of Cruziana Ichnofacies have been reported in slope deposits as a consequence of the well-oxygenation of the substrate (e.g. Buck and Bottjer, 1985; Savrda et al., 2001; Shultz and Hubbard, 2005; Wetzel, 2008). Thus, the occurrence of suites representative of the distal Cruziana Ichnofacies in the Capdevila Formation (the SL suite) is assumed as the result of the substrate colonization in the offshore-slope transition previous to the arrival of the gravitational flows (pre-event colonization).

The SF suite evidences the temporary exposition of the substrate in which it is preserved and characterizes the Glossifungites Ichnofacies (e.g. Pemberton and Frey, 1985). The presence of a suite representative of the Glossifungites Ichnofacies at the top of the beds containing suites of the Cruziana Ichnofacies deposited in offshore-slope transition (SL suite) and in slope settings (SM suite) reveals the subaerial exposure of these substrates and suggests a significant base level fall. This signature reveals that a forced regression event took place in the Los Palacios Basin during the early Eocene and allows inferring the existence of a sequence boundary at the top of the middle portion of the Capdevila Formation succession (Figs. 3 and 8). The Glossifungites Ichnofacies has been reported in exhumed substrates of the submarine canyon edges in slope settings and in areas influenced for high-energy recurrent currents, being assumed as a sequence boundary biomarker (e.g. Savrda et al., 2001; Pemberton and MacEachern, 2005; Dasgupta and Buatois, 2012).

The SH suite represented by the *Ophiomorpha* ichnofabric represents an impoverished expression of the Skolithos Ichnofacies in the Capdevila Formation deposits. Its occurrence exclusively in the massive sandstones facies overlaid by the paraconglomerate deposits in the lower portion of the sedimentary succession, suggests opportunistic occupation of the sandy substrate accumulated in the slope by decapods transported from the shelf by the turbiditic currents. The amount of burrows in the *Ophiomorpha* ichnofabric diminishes as the sandstone grain size decreases suggesting that capacity of exhumation of the active currents in shallower settings might be reduced. The occurrence of Skolithos Ichnofacies in deep marine turbiditic deposits is common, overall in the surroundings of the submarine canyons and the upper slope zones (Crimes et al., 1977, 1981; Heard and Pickering, 2008).

Thus, the ichnological analysis of the studied deposits reveals that the substrate occupation by the burrowing benthic fauna mainly took place in a shallow slope (Fig. 8) after the depositional events and was conditioned by either high energy flows or high depositional frequency. The presence of an impoverished Skolithos Ichnofacies suite in the massive sandstones of the lower portion of the succession, whose deposition was interrupted by the thick paraconglomerate deposits, indicates the action of more energetic processes in the slope area, possibly related to the presence of channels. The establishment of distal Cruziana Ichnofacies suites in a thin bed of the siltstone facies over the paraconglomerate deposits indicates the substrate occupation by a resident benthic

fauna (pre-event colonization) and reflects the returning of the low energy, stable marine conditions which are normally characteristic of the offshore-slope transition area. That condition indicates a reduction of the impact of the progradational flows in the basin. The progradational flows are then reactivated, establishing the deposition of turbiditic lobes, which dominate the up going succession. The impoverished Cruziana Ichnofacies turns to be the dominant ichnological context and a shoaling-upward tendency is observed up to the subaerial exposure of the substrate. This tendency is marked by the replacement of the *Thalassinoides*, *Scolicia* and *Palaeophycus* ichnofabrics for that of *Bichordites-Thalassinoides* and then by the Glossifungites Ichnofacies suite. The latter represents an omission suite and delimits a coplanar surface, formed by a forced regression surface and a later flooding surface which led to infer a sequence boundary (Figs. 3 and 8). The dominance of the turbiditic sandy facies with the recurrence of the impoverished Cruziana Ichnofacies suites indicates the returning of the progradational flows and the reestablishment of the high frequency deposition promoted by these flows.

7. Conclusions

The integrated ichnological and sedimentological analyses of the Capdevila Formation sedimentary succession in the Los Palacios Basin revealed deposition in shallow slope settings impacted either by frequent, high-energy gravitational flows and high depositional frequency. This flow regime has conditioned the distribution and composition of the burrowing benthic fauna which is characterized by the dominance of burrows of stenohaline detritus-feeding organisms that inhabited well-oxygenated substrates, but showing low ichnodiversity. Cruziana and Skolithos Ichnofacies show atypical composition if compared to their archetypal equivalents, possibly as result of the stress caused by the prevalence of high-energy conditions and/or of high-frequency deposition during the infill of the Los Palacios Basin in the early Eocene.

The ichnological record of the Capdevila Formation also revealed the shoaling-upward of the shallow slope deposits in the studied section which culminated with the subaerial exposure of the substrate, signaling a forced regression event in the Los Palacios Basin and a sequence boundary at the top of the middle portion of the Capdevila Formation in Pinar del Río region. The reestablishment of the turbiditic deposition in the upper portion of the succession marks the subsequent base level rise and the maintenance of the high-energy conditions and/or the high-frequency deposition in the basin.

Acknowledgments

The authors thank to the Museo Nacional de Historia Natural de La Habana by the access to samples studied in this work; to Paulo Paim, Ubiratan Faccini and Elvio Bosetti for the critical comments that helped to improve this manuscript; and to Myriam Rozengurt for the English version; to The Brazilian Research and Technological Development Council (CNPq) for the PEC-PG grant number 190620/2011-0 to JVM, grants number 305208/2010-1 and 451731/2013-1 to RGN, and grant number 306699/2013-3 to ELCL; to the Instituto de Ecología y Sistemática (IES) de La Habana for the support to JVM.

References

- Aguirre, J., Gibert, J.M., Puga-Bernabéu, A., 2010. Proximal–distal ichnofabric changes in a siliciclastic shelf, early Pliocene, Guadalquivir Basin, southwest Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 291, 328–337.
- Albear, J.F., Iturralde-Vinent, M.A., 1985. Estratigrafía de las provincias de La Habana. In: Arroyo, A. (Ed.), *Contribución a la geología de las provincias de La Habana y Ciudad de La Habana*. Editorial Científico-Técnica, pp. 12–54.

- Bernardi, M., Boschele, S., Ferretti, P., Avanzini, M., 2010. Echinoid burrow *Bichordites monastiriensis* from the Oligocene of NE Italy. *Acta Palaeontol. Pol.* 55, 479–486.
- Bralower, T.J., Iturralde-Vinent, M.A., 1997. Micropaleontological dating of the collision between the North American and Caribbean plates in western Cuba. *Palaios* 12, 133–150.
- Bromley, R.G., 1975. Trace fossils at omission surfaces. In: Frey, R.W. (Ed.), *The Study of Trace Fossils*. Springer, New York, pp. 399–428.
- Bromley, R.G., 1996. *Trace Fossils. Biology, Taphonomy and Applications*, second ed. Chapman and Hall, London, p. 361.
- Bromley, R.G., Asgaard, U., 1975. Sediment structures produced by a spatangoid echinoid: a problem of preservation. *Bull. Geol. Soc. Den.* 24, 261–281.
- Bromley, R.G., Ekdale, A.A., 1986. Composite ichnofabrics and tiering of burrows. *Geol. Mag.* 123, 59–65.
- Bromley, R.G., Jensen, M., Asgaard, U., 1995. Spatangoid echinoids: deep-tier trace fossils and chemosymbiosis. *Neues Jahrb. für Geol. Paläontologie Abh.* 195, 25–35.
- Bromley, R.G., Uchman, A., 2003. Trace fossils from the lower and middle Jurassic marginal marine deposits of the Sorhat Formation, Bornholm, Denmark. *Bull. Geol. Soc. Den.* 52, 185–208.
- Brönnimann, P., Rigassi, D., 1963. Contribution to the geology and palaeontology of the area of the city of La Habana, Cuba and its surroundings. *Eclogae Geol. Helv.* 56, 193–430.
- Brönnimann, P., Stradner, H., 1960. Die Foraminiferen und Discoasteridenzonen von Kuba und ihre interkontinentale Korrelation. *Erdoel-Z* 76, 364–369.
- Brust, J., Hüneke, H., Meschede, M., Sommer, M., 2011. Facies and provenance of basin-margin deposits in the Los Palacios Basin (Capdevila Formation, Cuba). *Facies* 57, 73–92.
- Buatois, L.A., Lopez-Angrián, A.O., 1992. Icnología de la Formación Wisky Bay (Cretácico, Isla James Ross, Antártida): Implicaciones paleoecológicas y paleoambientales. *Ameghiniana* 28, 75–88.
- Buatois, L.A., Mángano, M.G., 2011. *Icnology: Organism-substrate Interactions in Space and Time*. Cambridge University Press, p. 370.
- Buatois, L.A., Bromley, R.G., Mángano, M.G., Bellosi, E., Carmona, N., 2003. Icnology of shallow marine deposits in the Miocene Chénque Formation of Patagonia: complex ecologic structure and niche partitioning in Neogene ecosystem. *Publicación Espec. la Asoc. Paleontológica Argent.* 9, 85–95.
- Buatois, L.A., Gingras, M.K., MacEachern, J.A., Mángano, M.G., Zonneveld, J.P., Pemberton, S.G., Netto, R.G., Martin, A., 2005. Colonization of brackish-water systems through time: evidence from the trace-fossil record. *Palaios* 20, 321–347.
- Buatois, L.A., Mángano, M.G., Maples, C.G., Lanier, W.P., 1997. The paradox of non-marine ichnofaunas in tidal rhythmites: Integrating sedimentologic and ichnologic data from the Late Carboniferous of Eastern Kansas, USA. *Palaios* 12, 467–481.
- Buatois, L.A., Saccavino, L.L., Zavala, C., 2010. Ichnologic signatures of hyperpycnal-flow deposits in Cretaceous river-dominated deltas, Austral Basin, southern Argentina. In: Slatt, R.M., Zavala, C. (Eds.), *Sediment Transfer from Shelf to Deep Water – Revisiting the Delivery System*. AAPG Studies in Geology, vol. 61, pp. 1–18.
- Buchanan, J.B., 1966. The biology of *Echinocardium cordatum* (Echinodermata: Spatangoida) from different habitats. *J. Mar. Biol. Assoc. U. K.* 46, 97–114.
- Buck, S.P., Bottjer, D.J., 1985. Continental slope deposits from a Late Cretaceous, tectonically active margin, Southern California. *J. Sediment. Petrol.* 55, 843–855.
- Carmona, N.B., Buatois, L.A., Ponce, J.J., Mángano, M.G., 2009. Icnology and sedimentology of a tide-influenced delta, Lower Miocene Chénque Formation, Patagonia, Argentina: trace-fossil distribution and response to environmental stresses. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 273, 75–86.
- Chrzastek, A., 2013. Trace fossils from the Lower Muschelkalk of Raciborowice Górne (North Sudetic Synclinorium, SW Poland) and their palaeoenvironmental interpretation. *Acta Geol. Pol.* 63, 315–353.
- Crimes, T.P., Legg, I., Marcos, A., Arborely, M., 1977. Late precambrian-low lower Cambrian trace fossils from Spain. In: Crimes, T.P., Harper, J.C. (Eds.), *Trace Fossils 2, Geological Journal Special Issue*, vol. 9, pp. 91–138.
- Crimes, T.P., Goldring, R., Homewood, P., van Stuijvenberg, J., Winkler, W., 1981. Trace fossil assemblages of deep-sea fan deposits, Gurnigel and Schlieren flysch (Cretaceous–Eocene). *Eclogae Geol. Helvetiae* 74, 953–995.
- Cummings, J.P., Hodgson, D.M., 2011. Assessing controls on the distribution of ichnotaxa in submarine fan environments, the Basque Basin, northern Spain. *Sediment. Geol.* 239, 162–187.
- Cushman, J.A., Bermúdez, P.J., 1949. Some Cuban species of *Globorotalia*: cushman. *Foraminifera. Res. Contrib.* 25, 26–45.
- Dasgupta, S., Buatois, L.A., 2012. Unusual occurrence and stratigraphic significance of the *Glossifungites* ichnofacies in a submarine paleo-canyon — Example from a Pliocene shelf-edge delta, Southeast Trinidad. *Sediment. Geol.* 269–270, 69–77.
- Dworschak, P.C., Rodrigues, S., 1997. A modern analogue for the trace fossil *Gyroolithes*: burrows of the thalassinidean shrimp *Axiandassa australis*. *Lethaia* 30, 41–52.
- Ernst, G., Hahnel, W., Seibert, E., 1973. Aktuopahiontologie und Merkmalsvariabilität bei Mediterranen Echiniden und Riekschliisse auf die Ökologie und Artumgrenzung fossiler Formen. *Paläont. Z.* 47 (3/4), 188–216.
- Föllmi, K.B., Grimm, K.A., 1990. Doomed pioneers: gravity-flow deposition and bioturbation in marine oxygen-deficient environments. *Geology* 18, 1069–1072.
- Frey, R.W., Howard, J.D., Pryor, W.A., 1978. *Ophiomorpha*: Its morphologic, taxonomic and environmental significance. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 23, 199–229.
- García-Delgado, D.E., Torres-Silva, A., 1997. Sistema Paleógeno. In: Furrázola-Bermúdez, G.F., Núñez-Cambra, K. (Eds.), *Estudios sobre geología de Cuba. Centro Iberoamericano de Investigación y Desarrollo de la Comunicación Gráfica*, pp. 115–140.
- Gibert, J.M. de, Goldring, G., 2008. Spatangoid-produced ichnofabrics (Bateig Limestone, Miocene, Spain) and the preservation of spatangoid trace fossils. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 270, 299–310.
- Gibert, J.M., Martinell, J., 1998. Ichnofabric of the pliocene marginal basins of the northwestern Mediterranean. *Rev. Soc. Geológica España* 11, 43–56.
- Gibert, J.M., Martinell, J., 1999. Proximal-distal variations of trace fossil assemblages in a Pliocene ria, Baix Llobregat, Northeastern Spain. *Rev. Soc. Geológica España* 12 (2), 209–214.
- Gingras, M.K., Pemberton, S.G., Saunders, T.D.A., 2000. Firmness profiles associated with tidal creek deposits: the temporal significance of *Glossifungites* assemblages. *J. Sediment. Res.* 70, 1017–1025.
- Gordon, M.B., Mann, P., Cáceres, D., Flores, R., 1997. Cenozoic tectonic history of the North American–Caribbean plate boundary zone in western Cuba. *J. Geophys. Res.* 102, 10055–10082.
- Heard, T.G., Pickering, K.T., 2008. Trace fossils as diagnostic indicators of deep-marine environments, Middle Eocene Ainsa-Jaca Basin, Spanish Pyrenees. *Sedimentology* 55, 809–844.
- Howard, J.D., 1978. Sedimentology and trace fossils. In: Basan, P.B. (Ed.), *Trace Fossil Concepts. Society of Economic Paleontologist and Mineralogist, Short Course*, pp. 11–42.
- Howard, J.D., Reineck, H.E., Rietschel, S., 1974. Biogenic sedimentary structures formed by heart urchins. *Senckenberg. Maritima* 6 (2), 185–201.
- Hubbard, S.M., MacEachern, J.A., Bann, K.M., 2012. Slope. In: Knaust, D., Bromley, R.G. (Eds.), *Trace Fossils as Indicators of Sedimentary Environments, Developments in Sedimentology*, vol. 64. Elsevier, pp. 607–642.
- Iturralde-Vinent, M.A., 1995. Cuencas sedimentarias del Paleoceno-Eoceno de Cuba. *Boletín Soc. Venez. Geol.* 20, 75–80.
- Iturralde-Vinent, M.A., 1996. Introduction to Cuban geology and tectonics. In: Iturralde-Vinent, M.A. (Ed.), *Ofiolitas y arcos volcánicos de Cuba. Museo Nacional de Historia Natural, Havana*, pp. 3–35.
- Jakus, P., 1983. Formaciones vulcanogénico-sedimentarias y sedimentarias de Cuba. In: Melis, C.T. (Ed.), *Contribución a la geología de Cuba oriental. Editorial Científico-Técnica*, pp. 17–85.
- Kanazawa, K., 1992. Adaptation of test shape for burrowing and locomotion in spatangoid echinoids. *Palaeontology* 35, 733–750.
- Kroh, A., Hansson, H., 2013. *Spatangus purpureus* O.F. Müller, 1776. In: Kroh, A., Mooi, R. (Eds.), *World Echinoidea Database*. Accessed through: World Register of Marine Species at. <http://www.marinespecies.org>.
- MacEachern, J.A., Pemberton, S.G., Gingras, M.K., Bann, K.L., 2007. The ichnofacies concept: a fifty-year retrospective. In: Miller III, W. (Ed.), *Trace Fossils. Concepts, Problems, Prospects*. Elsevier, Amsterdam, pp. 50–75.
- Manley, R., Lewis, D.W., 1998. Ichnocoenoses of the mount messenger formation, a Miocene submarine fan system, Taranaki Basin, New Zealand. *N. Z. J. Geophys.* 41 (1), 15–33.
- McIlroy, D., 2007. Icnology of a macrotidal tide-dominated deltaic depositional system: Lajas Formation, Neuquén Province, Argentina. In: Bromley, R.G., Buatois, L.A., Mángano, M.G., Genise, J.F., Melchor, R.N. (Eds.), *Sediment–Organism Interactions; A Multifaceted Icnology*, vol. 88. SEPM Special Publication, pp. 195–211.
- Mellere, D., Plink-Bjorklund, P., Steel, R., 2002. Anatomy of shelf deltas at the edge of a prograding Eocene shelf margin, Spitsbergen. *Sedimentology* 49, 1181–1206.
- Menéndez-Penate, L., Rojas-Consuegra, R., Villegas-Martín, J., López-Marín, R., 2011. Taphonomy, chronostratigraphy and paleoceanographic implications at turbidite of early Paleogene (Vertientes Formation), Cuba. *Rev. Geológica América Cent.* 45, 87–94.
- Mortensen, T., 1951. A Monograph of the Echinoidea. V (2) Spatangoida II. C.A. Reitzel, Copenhagen.
- Mutti, E., 1992. Turbidite Sanstone. San Donato Milanese, p. 275.
- Nara, M., 2004. Trace fossil *Bichordites monastiriensis* in Pleistocene shallow marine deposits of the Boso Peninsula, central Japan, and its paleoenvironmental significance. *J. Geol. Soc. Jpn.* 110, 19–20.
- Netto, R.G., Rossetti, D.F., 2003. Icnology and salinity fluctuations: a case study from the Early Miocene (lower Barreiras Formation) of São Luís Basin, Maranhão, Brazil. *Rev. Bras. Paleontol.* 6, 5–18.
- Netto, R.G., Balistieri, P.R.M.N., Lavina, E.L.C., Silveira, D.M., 2009. Ichnological signatures of shallow freshwater lakes in the glacial Itararé group (Mafra formation, upper Carboniferous–Lower Permian of Paraná Basin, S Brazil). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 272, 240–255.
- Palmer, R.H., 1934. The geology of Habana, Cuba and vicinity. *J. Geol.* 42 (2), 123–145.
- Pemberton, S.G., Frey, R.W., 1985. The *Glossifungites* ichnofacies: Modern Examples From the Georgia Coast, U.S.A. pp. 237–259. Special Publication, 35.
- Pemberton, S.G., MacEachern, J.A., Frey, R.W., 1992. Trace fossil facies models: environmental and allostratigraphic significance. In: Walker, R.G., James, N.P. (Eds.), *Facies Models: Response to Sea-level Change, Geotext*, vol. 1. Geological Association of Canada, St. John's, pp. 47–72.
- Pemberton, S.G., MacEachern, J.A., 2005. Significance of ichnofossils in applied stratigraphy. In: Koutsoukos, E.A. (Ed.), *Applied Stratigraphy*. Springer, Dordrecht, pp. 281–302.

- Pemberton, S.G., Spilla, M., Pulham, A.J., Saunders, T., MacEachern, J.A., Robins, D., Sinclair, I.K., 2001. Ichnology and Sedimentary of Shallow to Marginal Marine System: Ben Nevis and Avalon Reservoirs, Jeanne d'Arc Basin. Short course. Geological Association of Canada, p. 343.
- Piotrowski, J., 1987. Nuevo datos sobre los sedimentos Cretácico Superior tardío y el Paleógeno en la zona estructural de San Diego los Baños. In: Arroyo, A. (Ed.), Contribución a la geología de la provincia de Pinar del Río. Edición Científico-Técnicas, pp. 185–196.
- Pickerill, R.K., Donovan, S.K., Dixon, H.L., Doyle, E.N., 1993. *Bichordites monastiriensis* from the Pleistocene of southeast Jamaica. *Ichnos* 2, 225–230.
- Plaziat, J.C., Mahmoudi, M., 1988. Trace fossils attributed to burrowing echinoids: a revision including new ichnogenus and ichnospecies. *Geobios* 21, 209–233.
- Pollard, J.D., Goldring, R., Buck, S.G., 1993. Ichnofabrics containing *Ophiomorpha*: significance in shallow-water facies interpretation. *J. Geol. Soc. Lond.* 150, 149–164.
- Powichrowski, L.K., 1989. Trace fossils from the Helminthoid Flysch (Upper Cretaceous–Paleocene) of the Ligurian Alps (Italy): development of deep marine ichnoassociations in fan and basin plain environments. *Eclogae Geol. Helv.* 82 (2), 385–411.
- Pszczołowski, A., 1987. Secuencias miogeosinclinales de la Cordillera de Guaniguanico. Litoestratigrafía, desarrollo de facies y paleogeografía. In: Arroyo, A. (Ed.), Contribución a la geología de la provincia de Pinar del Río. Editorial Científico-Técnica, pp. 5–84.
- Pszczołowski, A., 2002. Crustacean burrow upper Maastrichtian deposits of South-Central Cuba. *Bulletin of the Polish Academy of Sciences. Earth Sci.* 50 (2), 147–163.
- Pszczołowski, A., Myczyński, R., 2009. Tithonian Early Valanginian evolution of deposition along the Proto-Caribbean margin of North America recorded in Guaniguanico succession (western Cuba). *J. South Am. Earth Sci.* 29, 225–253.
- Radwanski, A., Wysocka, A., 2001. Mass aggregation of Middle Miocene spine-coated echinoids *Echinocardium* and their integrated eco-taphonomy. *Acta Geol. Pol.* 51, 295–316.
- Reineck, H.G., 1967. Parameter von Schichtung und bioturbation. *Geol. Rundsch.* 56, 420–438.
- Rindsberg, A.K., 1982. Bathyal ichnology of north San Clemente Basin (California borderland). In: IAS International 11th Congress, Hamilton, Ontario, p. 25.
- Rodríguez-Tovar, F., Uchman, A., Payros, A., Orue-Etxebarria, X., Apellaniz, E., Molina, E., 2010. Sea-level dynamics and palaeoecological factors affecting trace fossil distribution in Eocene turbiditic deposits (Gorrondatxe section, N Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 285, 50–65.
- Rojas-Consuegra, R., 1999. Productividad de carbonatos en la secuencias del Arco Volcánico Cretácico. Master thesis. Pinar del Río University, p. 91.
- Saha, O., Shukla, U.K., Rani, R., 2010. Trace fossils from the late cretaceous Lameta formation, Jabalpur area, Madhya Pradesh: paleoenvironmental implications. *J. Geol. Soc. India* 76, 607–620.
- Savrdra, C.E., Krawinkel, H., McCarthy, F.M.G., McHugh, C.M.G., Olson, H.C., Mountain, G., 2001. Ichnofabrics of a Pleistocene slope succession, New Jersey margin: relations to climate and sea-level dynamics. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 171, 41–61.
- Savrdra, C.E., Locklair, R.E., Hall, J.K., Sadler, M.T., Smith, M.W., Warren, J.D., 1998. Ichnofabric, ichnocoenoses, and ichnofacies implications of an upper cretaceous tidal-inlet sequence (Eutaw Formation, Central Alabama). *Ichnos* 6, 53–74.
- Seilacher, A., 1964. Biogenic sedimentary structures. In: Imbrie, J., Newell, N. (Eds.), *Approaches to Paleocology*. Wiley and Sons, New York, pp. 296–316.
- Shultz, M.R., Hubbard, S.M., 2005. Sedimentology, stratigraphic architecture, and ichnology of gravity-flow deposits partially ponded in a growth-fault bounded slope mini-basin, Tres Pasos Formation, southern Chile. *J. Sediment. Res.* 75, 440–453.
- Smith, A.B., Crimes, T.P., 1983. Trace fossils formed by heart urchins – an study of *Scolicia* and related traces. *Lethaia* 16, 79–92.
- Sommer, M., 2009. Late Cretaceous to Miocene Tectonic Reconstruction of the Northwestern Caribbean-regional Analysis of Cuban Geology. Ph.D. Thesis. Greifswald University.
- Stow, D.A.V., Reading, H.G., Collin, J.D., 1996. Deep sea. In: Reading, H.G. (Ed.), *Sedimentary Environments*, third ed. Blackwell Science, pp. 395–453.
- Uchman, A., 1991. Trace fossils from stress environments in Cretaceous–Paleogene flysch of the Polish Outer Carpathians. *Ann. Soc. Geol. Pol.* 61, 207–220.
- Uchman, A., 1992. An opportunistic trace fossil assemblage from the flysch of the Inoceraman beds (Campanian–Palaeocene), Bystrica Zone of the Magura Nappe, Carpathians, Poland. *Cretac. Res.* 13, 539–547.
- Uchman, A., 1995. Taxonomy and palaeoecology of flysch trace fossils: the Marosoarenacea Formation and associated facies (Miocene, Northern Apennines, Italy). *Beringeria* 15, 3–115.
- Uchman, A., 1998. Taxonomy and ethology of flysch trace fossils: a revision of the Marian Książkiewicz collection and studies of complementary material. *Ann. Soc. Geol. Pol.* 68, 105–218.
- Vermeij, G.J., 1978. Biogeography and Adaptation: Patterns of Marine Life. Harvard University Press, Cambridge, Massachusetts, p. 332.
- Villegas-Martín, J., Gibert, J.M., Rojas-Consuegra, R., Belaústegui, Z., 2012. Jurassic *Teredolites* from Cuba: new trace fossil evidence of early wood-boring behavior in bivalves. *J. South Am. Earth Sci.* 38, 123–128.
- Villegas-Martín, J., Rojas-Consuegra, R., 2011. Presencia del icnogénero *Teredolites* en un megabloque de la Formación Peñalver, límite Cretácico–Paleógeno (K/Pg), Cuba occidental. *Rev. Española Paleontol.* 26, 45–52.
- Vossler, S.M., Pemberton, G., 1989. Ichnology and paleoecology of offshore siliciclastic deposits in the Cardium Formation (Turonian, Alberta, Canada). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 74, 217–239.
- Walker, R.G., 1965. The origin and significance of the internal sedimentary structure of turbidites. *Proc. Yorks. Geol. Soc.* 35, 1–32.
- Wetzel, A., 2008. Recent bioturbation in the deep South China Sea: an uniformitarian ichnologic approach. *Palaos* 23, 601–614.
- Wetzel, A., Uchman, A., 1998. Deep sea benthic food content recorded by ichnofabrics: a conceptual model based on observations from Paleogene Flysch, Carpathians, Poland. *Palaos* 13, 533–546.
- Wetzel, A., Uchman, A., 2001. Sequential colonization of muddy turbidites: examples from Eocene Beloveza formation, Carpathians, Poland. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 168, 171–186.