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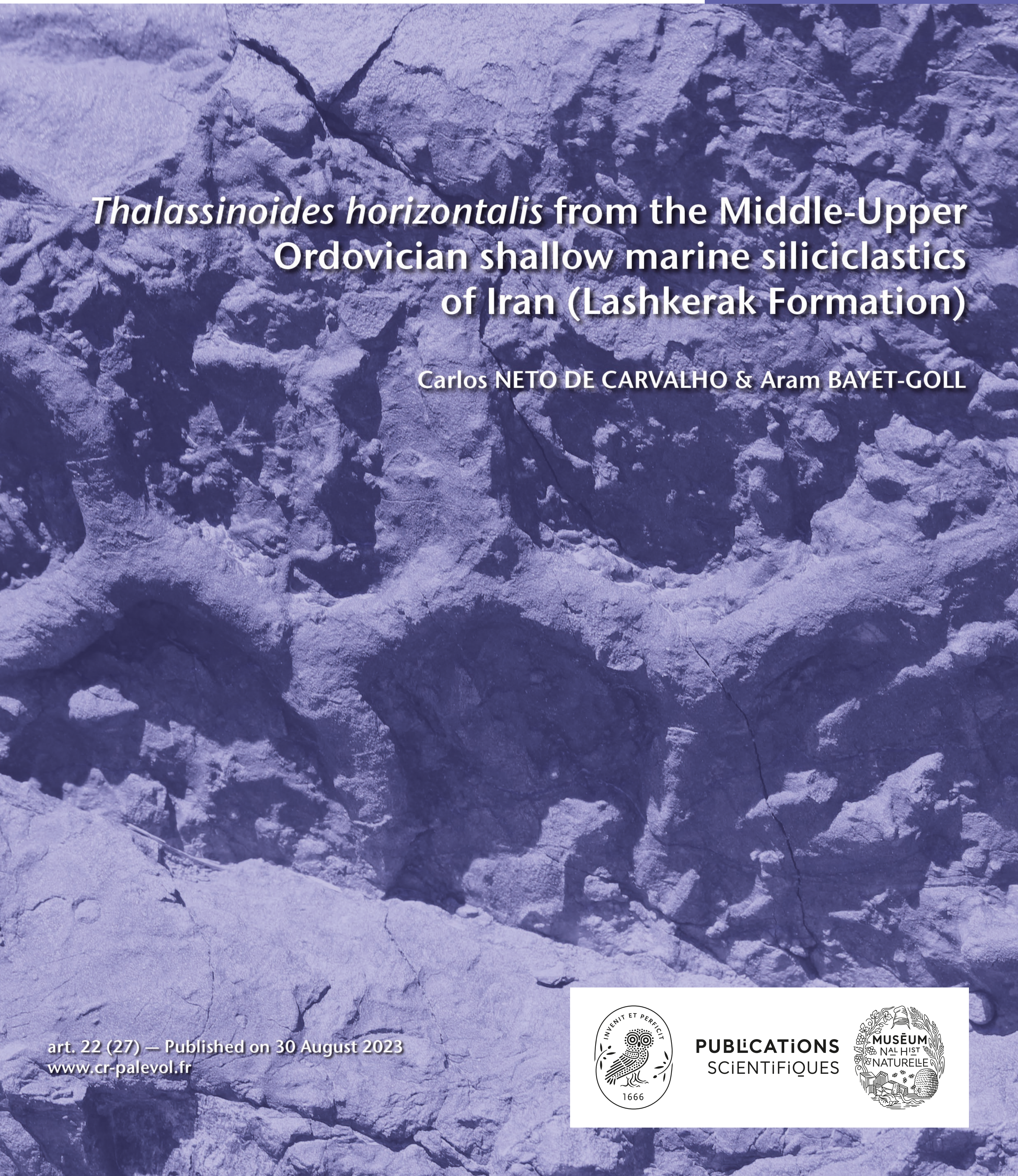

Thalassinoides horizontalis from the Middle-Upper Ordovician shallow marine siliciclastics of Iran (Lashkerak Formation)

Carlos NETO DE CARVALHO & Aram BAYET-GOLL

art. 22 (27) — Published on 30 August 2023
www.cr-palevol.fr

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MUSÉUM NAL HIST NATURELLE

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Thalassinoides horizontalis, Middle Ordovician, Lashkerak Formation, northern Iran. Credits: Carlos Neto de Carvalho.

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Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

ISSN (imprimé / *print*) : 1631-0683/ ISSN (électronique / *electronic*) : 1777-571X

Thalassinoides horizontalis Myrow, 1995 from the Middle-Upper Ordovician shallow marine siliciclastics of Iran (Lashkerak Formation)

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Submitted on 31 August 2022 | Accepted on 5 January 2023 | Published on 30 August 2023

urn:lsid:zoobank.org:pub:63F467A3-6B15-4477-94CA-ED1CE216D8B2

Neto de Carvalho C. & Bayet-Goll A. 2023. — *Thalassinoides horizontalis* Myrow, 1995 from the Middle-Upper Ordovician shallow marine siliciclastics of Iran (Lashkerak Formation). *Comptes Rendus Palevol* 22 (27): 569-583. https://doi.org/10.5852/cr-palevol2023v22a27

ABSTRACT
Thalassinoides Ehrenberg, 1944 are relatively common bioturbational structures in carbonate shallow marine successions from the early Paleozoic. Much rarer is the reference to this ichnogenus in siliciclastic formations from the same age. In the Ordovician Lashkerak Formation cropping out at the Central Alborz mountains, Iran, *Thalassinoides* is a common trace fossil in wave-dominated shoreface complex and prodelta-mouth bar environments of a fluvial-dominated delta. We compare the Middle-to-Upper Ordovician branching networks of the Unit 2 of the Lashkerak Formation with the ichnospecies *Thalassinoides horizontalis* Myrow, 1995 emphasizing the almost entire bedding-parallel orientation, regular branching and lack of constrictions and swellings. The eodiagenetic halos developed from mucus-lining walls, or by change of the original sediment fabric, typical of this and other ichnospecies of *Thalassinoides* in carbonate settings are not found in sandstones. The almost polygonal mazes from the Lashkerak Formation are also compared with the recently erected *Protopaleodictyon aitkeni* Morgan, Henderson & Pratt (2019), considered as a giant graphoglyptid in an early evolutionary stage of these forms in shallow marine environments. Both trace fossils are similar in morphology, size, preservation, ichnofacies and interpreted function, thus being *P. aitkeni* a junior synonym of *Thalassinoides horizontalis*.

KEY WORDS
Thalassinoides, *Protopaleodictyon*, fluvial-dominated delta, Middle-to-Upper Ordovician, Lashkerak Formation.

RÉSUMÉ
Thalassinoides horizontalis *Myrow, 1995 des siliciclastiques marins peu profonds de l'Ordovicien moyen-supérieur d'Iran (Formation de Lashkerak).*
Les *Thalassinoides* Ehrenberg, 1944 sont des structures bioturbationnelles relativement courantes dans les successions marines carbonatées peu profondes du Paléozoïque précoce. Les références à cet ichnogenres dans les formations siliciclastiques du même âge sont beaucoup plus rares. Dans la

formation ordovicienne de Lashkerak, qui se développe dans les montagnes de l'Alborz central, en Iran, *Thalassinoides* est une trace fossile commune dans les environnements du complexe de la surface littorale dominée par les vagues et de la barre de l'embouchure d'un delta dominé par les cours d'eau. Nous comparons les réseaux de ramification de l'Ordovicien moyen à supérieur de l'unité 2 de la formation de Lashkerak avec l'ichnospèce *Thalassinoides horizontalis* Myrow, 1995, en soulignant l'orientation presque entièrement parallèle au litage, la ramification régulière et l'absence de constrictions et de renflements. Les halos éodiagénétiques développés à partir de parois tapissées de mucus, ou par changement du tissu sédimentaire d'origine, typiques de cet ichnotaxon et d'autres ichnotaxons de *Thalassinoides* dans des environnements carbonatés, ne sont pas trouvés dans les grès. Les labyrinthes presque polygonaux de la formation de Lashkerak sont également comparés au *Protopaleodictyon aitkeni* Morgan, Henderson & Pratt (2019) récemment érigé, considéré comme un graphoglyptide géant à un stade précoce de l'évolution de ces formes dans les environnements marins peu profonds. Les deux traces fossiles sont similaires en termes de morphologie, de taille, de préservation, d'ichnofaciès et de fonction interprétée, ce qui fait de *P. aitkeni* un synonyme junior de *Thalassinoides horizontalis*.

MOTS CLÉS
Thalassinoides,
Protopaleodictyon,
delta à dominante fluviale,
Ordovicien moyen à supérieur,
Formation de Lashkerak.

INTRODUCTION

As a component of the *Nereites* Murchison & MacLeay, 1839 Ichnofacies, graphoglyptids are regular, highly patterned predepositional burrows preserved as erosional casts mainly on the soles of turbidites (e.g. Seilacher 1977; Uchman 2003; Seilacher 2007; Monaco 2008; Monaco & Checconi 2010; Checconi & Monaco 2013). They all share the same kind of preservation and normally occur associated to deep-sea turbidites, being characterized by the usual small, submillimeter to millimeter-sized burrows (see Uchman 1995). However, as it is known from the bibliography, some exceptions to these generalized rules may be found, i.e., taken the most popular *Paleodictyon* Meneghini, 1850, both for the environmental range where this trace fossil can be found (e.g. Fürsich *et al.* 2007; Lan & Chen 2010) and for the size of the burrows (Wetzel 2000; Uchman 2003). *Protopaleodictyon* Książkiewicz, 1970 was recently considered to be an exception in environmental range and size as well (Morgan *et al.* 2019).

Protopaleodictyon is defined as an uniramous and birramous hypichnial graphoglyptid consisting of wide first-order meanders and sine-shaped, more or less regular second order meanders, with one or two appendages usually branching from the apex of the second-order meanders (Uchman 1998). No mesh structure is usually attributed to this ichnogenus. The new ichnospecies *Protopaleodictyon aitkeni* Morgan, Henderson & Pratt (2019) was named by Morgan *et al.* (2019) from the middle Cambrian (Series 3) of the transition between Stephen and Eldon formations in Alberta, Canada. It is diagnosed as a horizontal trace with a central Y-branching (zigzag) second-order angular meanders forming two rows of mostly open, but occasionally closed network with hexagonal and equidimensional polygons. This trace fossil occurs within an ichnoassemblage representing the *Cruziana* d'Orbigny, 1842 Ichnofacies, in a dolomitic lime mudstone bed deposited in a relatively-shallow water environment within a carbonate platform (Morgan *et al.* 2019). The dimensions of *P. aitkeni* are unexpectedly large for graphoglyptids in general and the preservation and depositional environment contrasting with the turbidite siliciclastic settings in which these kind of trace fossils usually occurs. Notwithstanding, *Protopaleodictyon* is referred by Gierlowski-Kordesch & Ernst (1987) in shallow-water deposits of Cretaceous age in East Africa. On the other hand, Bendella & Mehadji (2015) describes the association of *Protopaleodictyon submontanum* Crimes & Crossley, 1991 (synonym of *Megagrapton* Książkiewicz, 1968: Uchman 1998) and *Thalassinoides suevicus* (Rieth, 1932) in the Upper Devonian deep-sea turbidite deposits of southwestern Algeria.

Protopaleodictyon aitkeni was compared by Morgan *et al.* (2019) with other ichnogenera, such as burrow networks attributed to the work of crustaceans, namely *Ophiomorpha* Lundgren, 1891 and *Sinusichnus* Gibert, 1996. However, this trace fossil was not compared with other, more common burrow network in the Lower Paleozoic, the ichnogenus *Thalassinoides* Ehrenberg, 1944. *Thalassinoides* are cylindrical to elliptical burrows in cross section that form a three-dimensional to horizontal branching polygonal network, with or without connecting shafts to the surface; burrows may evidence regular branching with Y- or T-shaped bifurcations, that may or may not show enlargement of the branching area (e.g. Bromley & Frey 1974; Fürsich 1981; Myrow 1995; Schlirf 2000). Mainly horizontal forms of *Thalassinoides* are typical from lower Paleozoic shallow carbonate successions since the early Cambrian (Miller & Byers 1984; Sheehan & Schiefelbein 1984; Droser & Bottjer 1988; Myrow 1995; Ekdale & Bromley 2003; Jin *et al.* 2012; Zhang *et al.* 2017). High-latitude, shallow marine siliciclastic occurrences of *Thalassinoides* has only been rarely described, namely in the Lower Ordovician of the Alborz Mountains of northern Iran (Bayet-Goll & Neto de Carvalho 2017). In the present paper we describe regular branching networks which we attribute to *Thalassinoides horizontalis* Myrow, 1995, and that are relatively common in the Middle-to-Upper Ordovician siliciclastic successions of the Lashkerak Formation, at the Alborz Mountains. We describe and compare the diagnostic morphology of these *Thalassinoides* with *Protopaleodictyon aitkeni* and conclude that they are the same trace fossil, and not related to graphoglyptids.

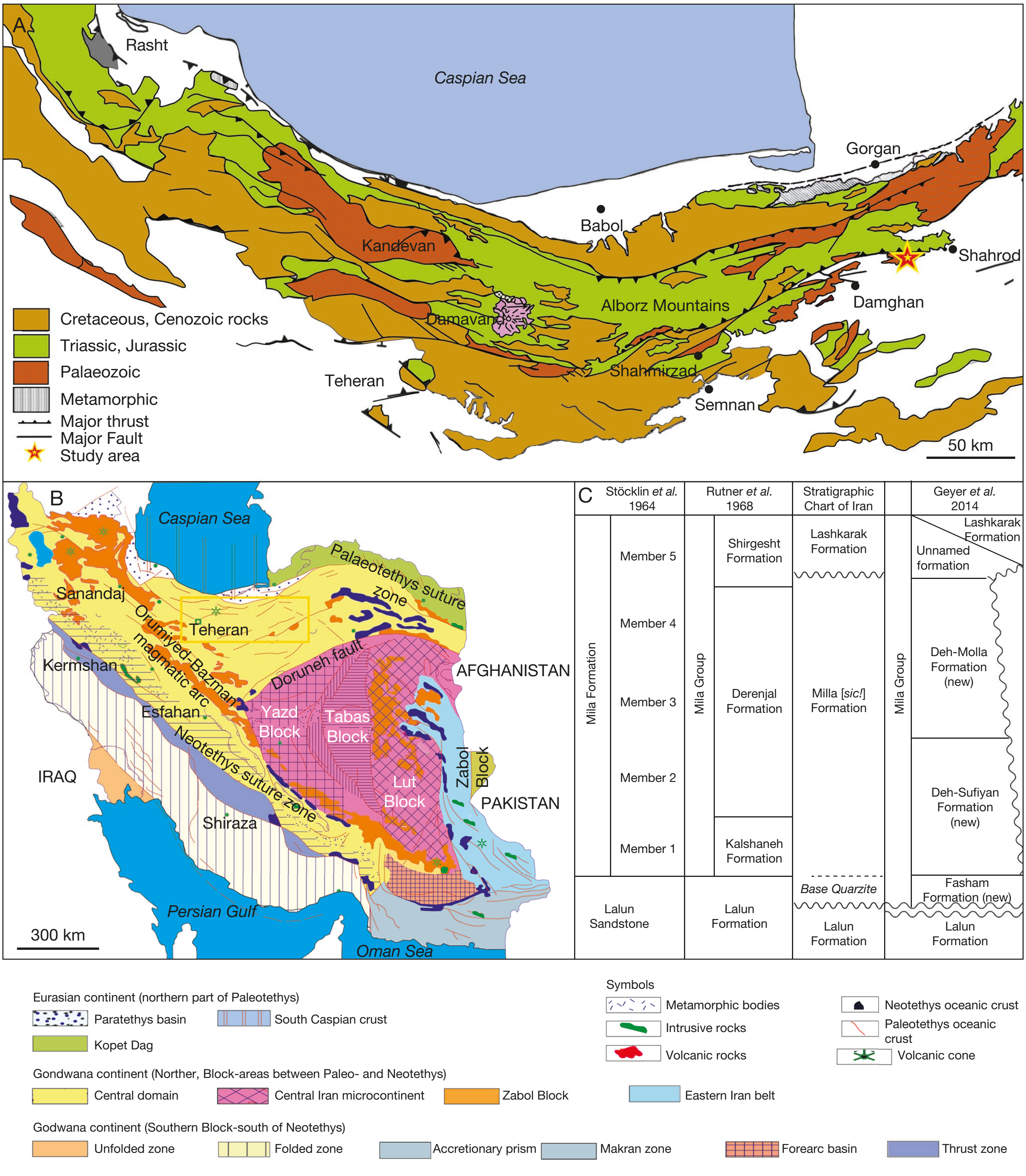

FIG. 1. — **A**, Simplified geological map of the eastern part of the Alborz Mountain Range (modified after Aghanabati 2004; Bayet-Goll & Neto de Carvalho 2017; Bayet-Goll *et al.* 2022a); the **star** indicates the location of the study area; **B**, geological map of Iran with its structural provinces (modified from Aghanabati 2004); **C**, general lithostratigraphy of the Alborz Mountains (modified from Geyer *et al.* 2014).

METHODS

Two sections of the Lashkerak Formation separated by 3 km were studied in the Central Alborz (Deh-Molla area at 15 km from West of Shahrud city (see also Bayet-Goll *et al.* 2022a) (Figs 1; 2). The stratigraphic columns of this formation were constructed using data from sedimentology and ichnology. The sections were measured, logged and evaluated integrating sedimentology and ichnology to interpret the depositional processes (facies) and the depositional systems (facies successions).

The most important sedimentologic characteristics used in the identification of facies include grain size, sorting, bedding contacts, bed thickness, physical sedimentary structures, lithological constituents, fossils, and important stratigraphic surfaces. Trace fossils were described and measured in a conventional way, and compared with bibliography. Special attention was devoted to the preservational variants of *Thalassinoides* networks, the main focus of this paper. Twenty specimens were used for this study occurring in different bedding planes. No trace fossils were collected due to the large size of the exposed beddings planes; they were photographed in the field and remain there for subsequent studies. Exact location coordinates may be provided by the authors upon request.

Abbreviations

BHD	bay head delta;
BI	biotubation index;
CB	central bay;
Dmb	distal mouth bar;
EMC	estuary-mouth complexes;
FO	foreshore;
FS,	fluvial sandstones;
FTD	flood tidal delta;
FWWB	fair weather wave base;
HCS	hummocky cross-stratified;
LOF	lower offshore;
LS	lower shoreface;
MS	middle shoreface;
Pd	prodelta;
Pmb	proximal mouth bar;
SB1	sequence boundary 1;
Sh	shelf;
SWB	storm wave base;
TI	tidal inlet;
trs	transgressive ravinement surface;
UOF	upper offshore;
US	upper shoreface;
WF	washover fan.

GEOLOGICAL SETTING

The Cambro-Ordovician deposits of northern, central and eastern Iran form a very comprehensive succession in comparison with neighboring Middle East regions (Stöcklin *et al.* 1964), and thus are critical for understanding the geological history of this region (Geyer *et al.* 2014). The Ordovician rocks of Iran, in most places, consist of green-colored shales, siltstones, and sandstones. The consistency of the lithofacies is related to continental margin shallow-marine environments across Iran. These rocks range in age from the Tremadocian to the early Hirnantian (see Ghavidel-Syooki & Vecoli 2007; Bayet-Goll *et al.* 2022a; and references therein).

The Lashkerak Formation is the uppermost unit of the Cambro-Ordovician Mila Group. This formation is divided into two units based on lithologic properties (Geyer *et al.* 2014) (Fig. 2). The Unit 1 with an Early Ordovician (Tremadocian-Floian) age is composed of thick-bedded sandstones with thin shale interbeds. The upper unit (Unit 2) is dated from the Middle-to-Late Ordovician (Darriwilian-Katian, Ghobadi Pour & Turvey 2009; Ghobadi Pour 2019) and is composed of thick-bedded shales with sandstone and siltstone interbeds. The lower boundary of the Lashkerak Formation is defined by Unit 1's channel-filled sandstone with trough cross-bedding overlying unconformably the uppermost carbonates of the Deh-Molla Formation (Figs 2; 4A).

STRATIGRAPHIC AND PALEOENVIRONMENTAL CONTEXTS OF THALASSINOIDES AT DEH-MOLLA

After the global sea-level fall at the Cambro-Ordovician boundary (Geyer *et al.* 2014), incised valleys were developed in the central Alborz. Subsequent to this incised valley system representing the Lower Ordovician basal deposits of the Lashkerak Formation, shallow marine and estuarine sediments were accumulated in the lower part of the first sequence during the succeeding sea-level rise. The lateral patterns of facies transitions and the paleogeographic context indicate that the incised valley-fill system was mostly located toward the eastern part of the basin (Deh-Molla area). The same incised valley-fill system is absent in the western area of this basin (Shahmirzad section; Bayet-Goll & Neto de Carvalho 2017; Bayet-Goll *et al.* 2022b).

Field observations and petrographic analysis carried out on the siliciclastic strata of Unit 1 of the Lashkerak Formation recognized two facies associations including, from bottom to top: 1) wave-dominated estuary; and 2) open marine (wave-dominated shoreface-offshore complex) (Figs 3; 4C). The estuarine depositional system of the Lashkerak Formation is subdivided in three zones: 1) an inner zone involving facies being under the influence of fluvial channel currents where the marine processes were minimized, including bay-head delta and fluvial channel facies (Fig. 4A, B); 2) a low energy central zone where marine processes are balanced by fluvial processes (a mixture of waves and tides); the facies of this zone include central bay or lagoon and washover or flood tidal delta (Fig. 4A, D); and 3) a high energy outer zone where marine processes had a stronger influence than fluvial ones.

This last zone includes estuary-mouth complexes and tidal inlets. Bioturbation in the wave-dominated estuary system of Unit 1 is sporadically distributed (Biotubation Index (BI) 0 to 3), and many beds are not burrowed. In few beds, intensively burrowed centimeter-thick intervals with BI values up to 3/4 may occur. The trace fossil assemblage is of very low-to- moderate diversity and is usually dominated by *Planolites* isp., *Cruziana furcifera* d'Orbigny, 1842, *C. goldfussi* Rouault, 1850, *Rusophycus* isp., *Monomorphichnus* isp., *Skolithos* isp., *Palaeophycus* isp., *Diplocraterion* isp., *Bergaueria* isp., *Diplichnites* isp., and fugichnia. Trace fossils are typically small in size, though more robust traces are observed locally. The overall sedimentological and ichnological characteristics of the estuary system strongly support a highly stressed depositional environment when compared to the wave-dominated shoreface-offshore complex.

The upper part of Unit 1 is composed of shallow-marine facies deposited under the influence of FWWB and SWB.

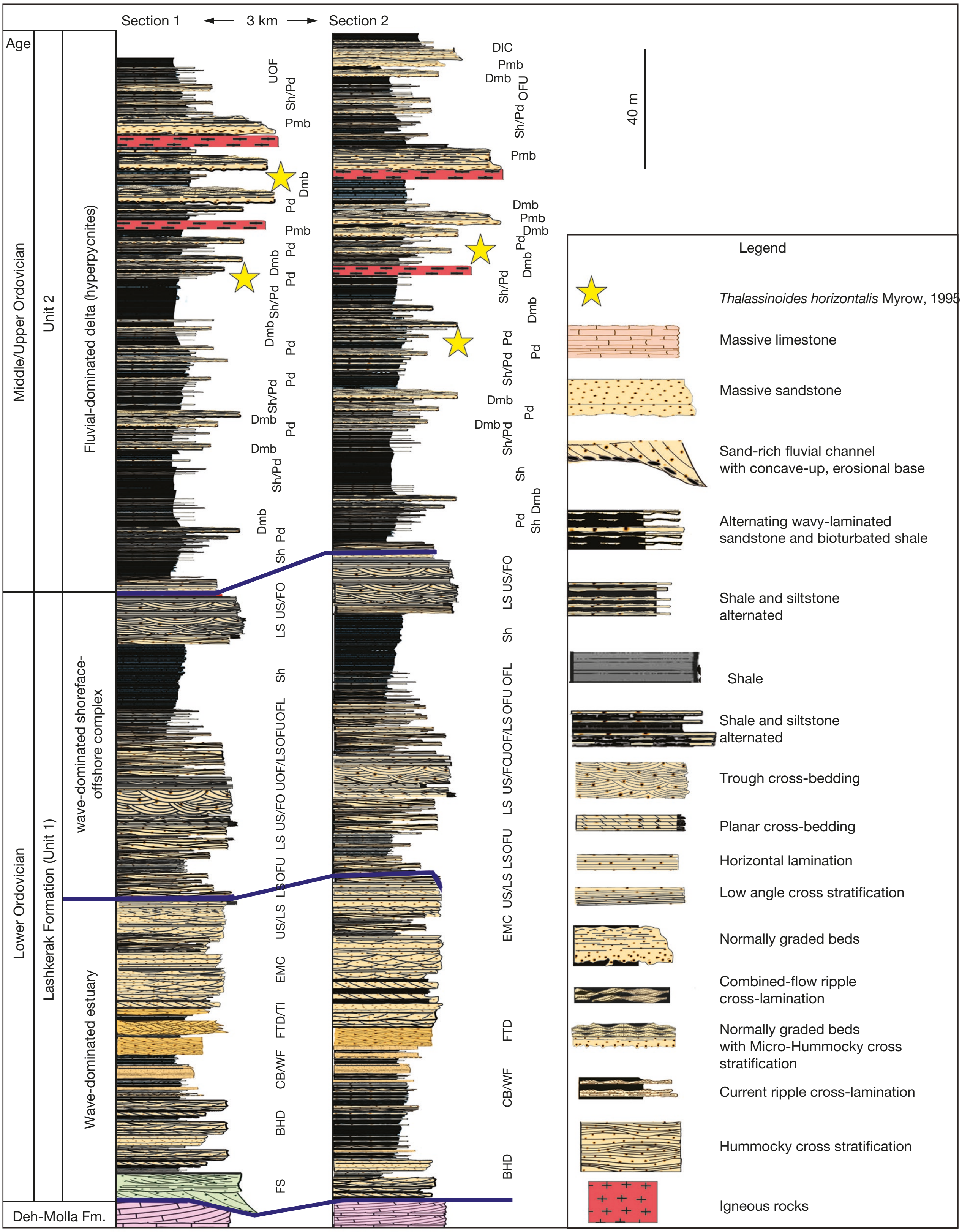

Fig. 2. — Composite log of the two studied sections of the Lashkerak Formation in the Central Alborz (the Deh-Molla area), including sedimentological features indicative of wave-dominated estuary, wave-dominated shoreface-offshore complex, and fluvial dominated delta facies (modified from Bayet-Goll & Neto de Carvalho 2017; Bayet-Goll *et al.* 2022a, b). Abbreviations: **BHD**, bay head delta; **CB**, central bay; **Dmb**, distal mouth bar; **EMC**, estuary-mouth complexes; **FO**, foreshore; **FS**, fluvial sandstones; **FTD**, flood tidal delta; **LOF**, lower offshore; **LS**, lower shoreface; **MS**, middle shoreface; **Pd**, prodelta; **Pmb**, proximal mouth bar; **Sh**, shelf; **TI**, tidal inlet; **UOF**, upper offshore; **US**, upper shoreface; **WF**, washover fan. The **yellow stars** are the location of the studied trace fossils in the sedimentary logs.

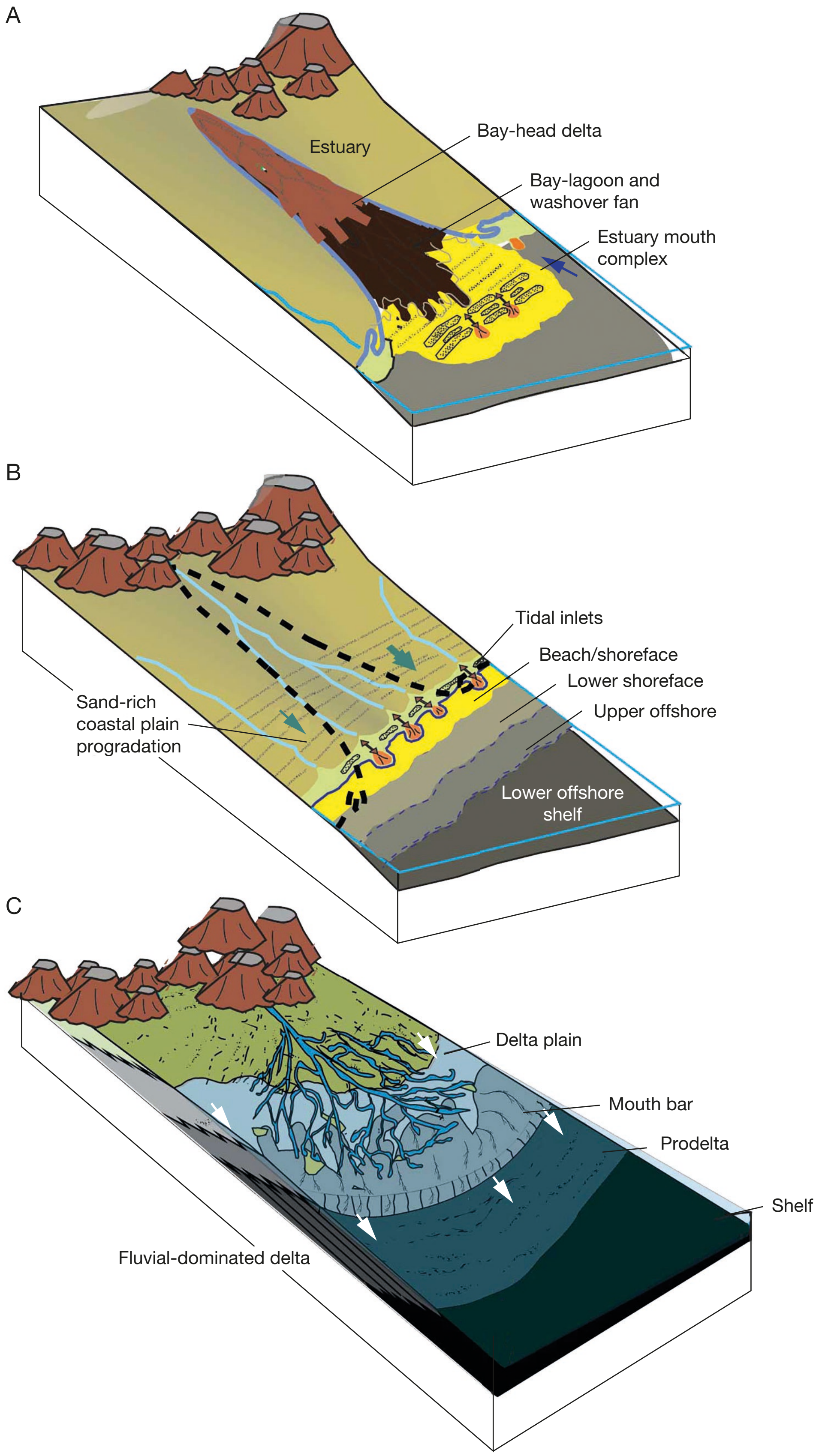

FIG. 3. — Schematic depositional evolution of the Lashkerak Formation described with sedimentological models: **A**, wave-dominated estuary; **B**, wave-dominated shoreface-offshore complex; **C**, flood-dominated fluvio-deltaic systems with hyperpycnal flows (see text for detailed explanation). **Blue arrows**, marine transgression; **brown arrows**, tidal inlets; **green arrows**, coastal progradtion.

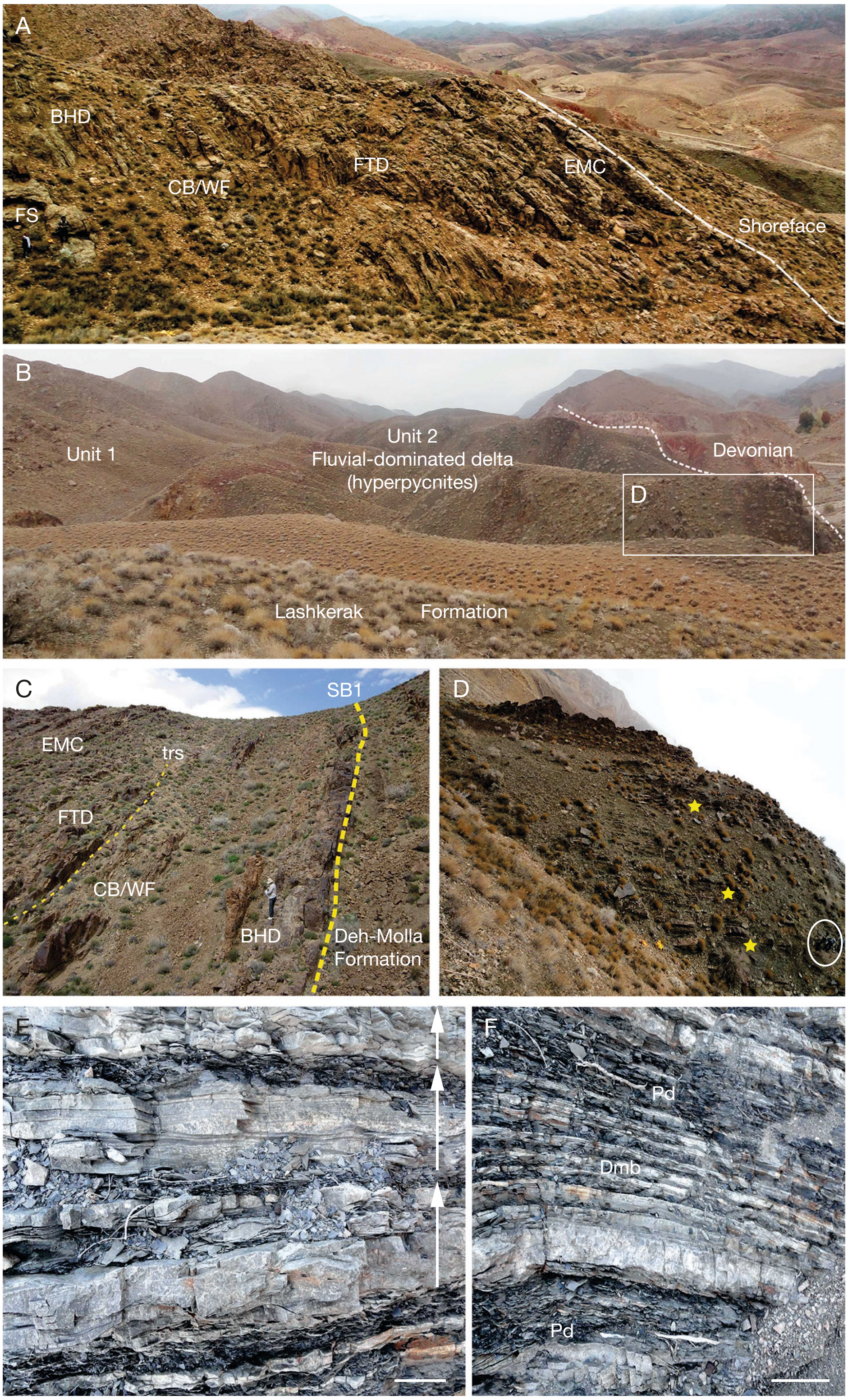

FIG. 4. — Field aspects of recognized third-order depositional sequences of the Lashkerak Formation in the Central Alborz: **A**, fluvial channel facies association with concave-upward erosional bases and flat top boundaries, in contact with deposits of BHD grading upward into wave-dominated barrier estuary successions, with CB, WF, FTD, and EMC onlapped by transgressive (fining-upward) shoreface deposits; section 1; **B**, panoramic view of the siliciclastic strata of Unit 1 and Unit 2 of the Lashkerak Formation; section 2; **C**, panoramic view of the wave-dominated estuary and wave-dominated shoreface-offshore complex; section 2; **D**, prograding stacked package of shallowing-upward cycles in prodelta and mouth bar facies within the fluvial-dominated delta. The **yellow stars** show the location of beds with *Thalassinoides horizontalis* Myrow, 1995; section 2; **E**, heterolithic beds of Pd and Dmb represented by the sandstone-dominated heterolithic units with graded beds, **arrows** indicate sandy hyperpycnite cycles (three cycles); section 2; **F**, thickening- and coarsening-upward successions, from heterolithic beds of Pd and Dmb into amalgamated, thick, tabular, bedsets of medium-grained sandstones of Pmb; section 2. Abbreviations: **BHD**, bay head delta; **CB**, central bay; **Dmb**, distal mouth bar; **EMC**, estuary-mouth complexes; **FS**, fluvial sandstones; **FTD**, flood tidal delta; **Pd**, prodelta; **Pmb**, proximal mouth bar; **SB1**, sequence boundary 1; **trs**, transgressive ravinement surface; **WF**, washover fan. Scale bars: E, 5 cm; F, 10 cm.

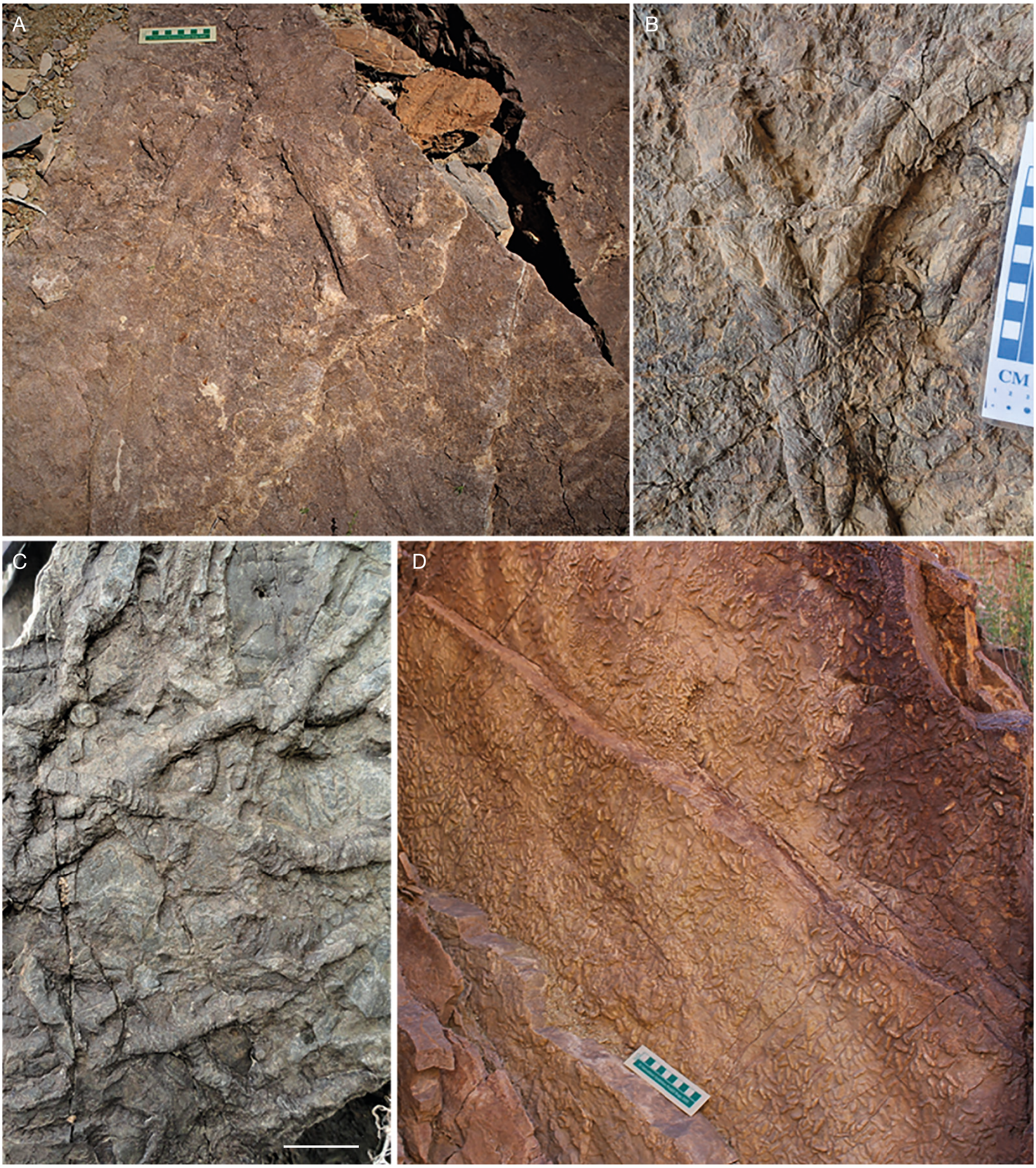

Fig. 5. — Trace fossils from Units 1 and 2 of the Lashkerak Fomation: **A**, **B**, *Cruziana furcifera* d'Orbigny, 1842 and *C. goldfussi* Rouault, 1850, 30 to 60 mm wide, from facies 2 of the Unit 1; **C**, *Arthrophycus brongniartii* Harlan, 1832 in the Unit 2; **D**, pervasive monoichnospecific bioturbation by *Lockeia* isp., facies 2 from Unit 1. Scale bar: C, 5 cm.

They include shoreface-foreshore facies deposited above the FWWB, offshore transition facies deposited between FWWB and SWB, and low-energy distal shelf-offshore deposited below SWB (Fig. 4d). The facies consist of well-sorted, fine to medium-grained, thick, amalgamated sandstones, as well as tabular to low-angle planar cross-stratified, and hummocky cross-stratified (HCS), or wave ripple laminated sandstones that typically coarsen upwards. Rhythmically bedded, fine-to-medium grained sandstones with mm-to-cm thick mudstone-siltstone are intercalated. The wide occurrence

Fig. 6. — *Thalassinoides horizontalis* Myrow from the Middle Ordovician of the Lashkerak Formation: **A**, sole bed perspective of the entirely bedding-parallel orientation of the pseudo-polygonal network of burrows; **B**, **D**, regular alternating branching network with burrows bending slightly upwards (**D** is a detail of **B**); **C**, **E**, change of orientation of the burrows during their development make them slightly winding. No swelling in the branching points are evident; **F**, regular branching pattern with the development of mostly open, to occasional five-sided polygons and homogeneous diameter of the burrows along the whole network. Scale bars: 10 mm.

of wave/storm-induced structures, such as HCS, implies deposition of beds during storms, while mudstone interbeds were formed during intervening fair-weather phases. Wave-dominated shoreface-offshore complex is characterized by highly variable bioturbation intensities, ranging from BI0 to BI3. Moreover, intensive bioturbation (BI4-5) can be found locally. The trace fossil assemblage in the sandstone beds (BI0-3) includes *Arenicolites* isp., *Diplocraterion* isp., *Skolithos* isp., *Rosselia* isp., *Palaeophycus* isp., *Bergaueria* isp. and fugichnia. The shale and siltstone beds are usually intensely bioturbated (BI3-5) by *Rusophycus* isp., the *Cruziana rugosa* group, *Helminthopsis* isp., *Planolites* isp., *Psammichnites* isp., *Lockeia* isp., *Thalassinoides* isp., *Rosselia* isp., *Bergaueria* isp., and *Diplocraterion* isp. (Fig. 5A, B, D). Moderate diversity of trace fossils, high bioturbation and the existence of suites typical of the archetypal *Cruziana*/*Skolithos* Ichnofacies are characteristic of a wave-dominated shoreface complex with wide colonization window (MacEachern *et al.* 2007a, b).

The Unit 2 (Middle-to-Upper Ordovician; Ghobadi Pour & Turvey 2009) is mostly composed of multiple stacks of coarsening-upward packages (Fig. 4C, E). The packages in their lower part consist of mudstone-dominated heterolithic units whereas sandstone-dominated heterolithic units with flat bedded-tabular bedsets comprise the upper part. These packages are regarded as deposited between prodelta and mouth bar of a fluvial-dominated delta neighboring the distributary channels, which were occasionally under the influence of marine waves. The building blocks of this unit are muddy hyperpycnites and sandy hyperpycnites (Mulder *et al.* 2003) (Fig. 4F, G). Commonly, the presence of normal-and/or inverse-graded beds, the close relationship between soft-sediment deformed beds and composite graded bedsets, muddy drapes, and the sporadic distribution of burrowed intervals with overall scarcity of bioturbation are considered as evidence for hyperpycnal and/or hypopycnal flows, common in flood-dominated fluvio-deltaic systems (see also Bayet-Goll & Neto de Carvalho 2017). The lower part of this unit is characterized by the heterolithic associations, being attributed to periods of very rapid mud accumulation in prodelta/distal mouth bar environments of a river-dominated delta. The occurrences of unbioturbated, structureless, mud-dominated units point to muddy sediment-gravity (hyperpycnal) flows or mud flocculation from hypopycnal (buoyant) mud plumes. However, in a thickening-upward trend with progradational stacking pattern, they show an increase in the thickness and abundance of sandstone beds with evidence of river-derived, unidirectional waning and/or waxing flows (e.g. Bouma-like sequences), which are considered as high concentration currents or sandy hyperpycnal currents. Upward in the succession, the decrease in muddy beds associated with evidence of higher degrees of erosion and amalgamation of sandstone beds are regarded as flood-generated mouth-bars deposited by high-density hyperpycnal flows. In these sediments, the existence of features pointing to high accumulation rates such as massive beds, convolute lamination, ball and pillow structures and climbing ripples imply the existence of quasi steady hyperpycnal currents (Mutti *et al.* 1996, 2003; Mulder *et al.* 2003).

Bioturbation structures occur sporadically throughout the Unit 2, and comprise a very low abundance, and low-diversity suite of trace fossils. Many intervals are totally lacking bioturbation structures. In addition, composite graded bedsets and deformed intervals are unburrowed. The trace fossil suite is punctually dominated by *Thalassinoides horizontalis* networks (Fig. 6), including also *Taenidium* isp., *Planolites* isp., *Palaeophycus* isp., *Rosselia socialis* Dahmer, 1937, *Arthrophycus brongniartii* (Harlan, 1832) (Fig. 5C), *Phycodes* isp., *Gordia* isp., *Helminthopsis* isp., and *Bergaueria* isp. Overall, the facies displays the sporadic distribution of bioturbation structures, small sizes of trace fossils attributable to a “stressed” environment, which is commonly regarded as non-archetypal expression of the *Cruziana* Ichnofacies (MacEachern *et al.* 2005; MacEachern & Gingras 2008). In general, the vertical passage from bioturbated and more heterolithic bed sets of the lower portion of the Unit 2 to amalgamated massive beds reflects rapid dumping of the turbulent and energetic flows near the mouth of river responsible for sand transport and deposition in the forms of bedload and coarse suspended material along with the erosion of the mud layers that strongly limited the activities of many trace makers. The studied *Thalassinoides horizontalis* occur in fine-to-very fine sandstones alternating with silty sandstones, shales and silty mudstones deposited in these prodelta environments under the influence of storms and river discharges (Bayet-Goll *et al.* 2022a).

SYSTEMATIC ICHNOLOGY

Ichnogenus *Thalassinoides* Ehrenberg, 1944

Thalassinoides horizontalis Myrow, 1995 (Fig. 6)

Thalassinoides horizontalis Myrow, 1995: 62-63, figs 6, 7a, b. — Blissett & Pickerill 2004: 360, pl. 10, fig. A. — Tiwari, Majkonwar, Malsawma, Malte & Patel 2011: 1139, pl. 4d. — El-Hedeny, Hewady & Al-Kalitany 2012: 728, figs 6A, B. — El-Sabbagh, El-Hedeny & Ferraj 2017: 11, 12, figs 4c, 5, 6d, e, 7e, f. — Darngawn, Patel, Joseph & Shitole 2018: 176, pl. 3, figs 3, 4. — Bendella, Benyoucef, Mikuláš, Bouchemla, Martinell & Feri 2021: 539, fig. 5E.

Protopaleodictyon atkeni Morgan, Henderson & Pratt, 2019: 217, figs 3, 5, 6.

Thalassinoides isp. Bayet-Goll, Buatois, Mángano & Daraei, 2022a: 17, fig. 6f.

Material. — Numerous field observations; 20 specimens were measured.

Diagnosis. — Horizontal, branching network of smooth-walled, unlined burrows, lacking vertically oriented shafts. Burrow diameter identical within individual specimens; constrictions or swellings at both junctions and inter-junction segments are absent (emended by Blissett & Pickerill 2004, after Myrow 1995).

Description

Thalassinoides from Lashkerak Formation consists of mainly horizontal, sole bed preserved, branching networks and pseudo-polygonal networks, with mainly horizontal Y-shaped branching burrows (Fig. 6). Burrows have a rounded cross section in and show passive filling. The persistent diameter of the burrows ranges between 5 and 10 mm. They have variable length and are straight to winding (Fig. 6D, E). The margin is smooth with no lining. Branching occurs regularly every 2-3 cm (Fig. 6B, F). Angle of branching varies between 100-120°.

Remarks

In the description of the ichnogenus *Thalassinoides*, Ehrenberg (1944) stated that it is composed by cylindrical-to-elliptical burrows that form a three-dimensional to horizontal branching polygonal network with vertical shafts connected to the surface, where branching is regular and swells are found at the branches and elsewhere. According to the original diagnosis of *Thalassinoides horizontalis* by Myrow (1995), these networks are mostly horizontal, regularly branching of unlined burrows lacking vertical shafts, with tunnels straight to curved showing almost constant burrow diameter (no swellings). So, the main ichnotaxobases for *T. horizontalis* are the lack of vertical offshoots, lack of swellings, regular branching and almost constant burrow diameter, also in accordance to the emended diagnosis of Blissett & Pickerill (2004). In his controversial revision of the ichnogenus *Thalassinoides*, Schlirf (2000) included *T. horizontalis* in his *Spongeliomorpha suevica* (Reith), which diagnosed as mainly horizontal, but sometimes partly vertical to oblique burrow systems with unlined, smooth lined or ornamented walls with Y- and T-shaped branches, typically enlarged at junctions or elsewhere, and variable diameters within a given system. This diagnosis is too broad as includes different burrow systems with different expressions of behavior and preservation in substrates with different consistencies. We do not intend in this paper to revise the ichnogenus *Thalassinoides*, or raise again the discussion about the usefulness of keeping *Spongeliomorpha*, *Thalassinoides* and *Ophiomorpha* as separate ichnogenera. However, the ichnotaxobases of *T. horizontalis* as defined originally by Myrow (1995) were included in this broad diagnosis or were not taken into account by Schlirf (2000), such as the constant diameter along the tunnels, and therefore the characteristic lack of swellings, or turning chambers, in the branching areas and elsewhere, in a burrow network recognized by the lack of vertical shafts by all the subsequent authors that described this as a valid ichnospecies (Blissett & Pickerill 2004; Tiwari *et al.* 2011; El-Hedeny *et al.* 2012; El-Sabbagh *et al.* 2017; Darngawn *et al.* 2018; Bendella *et al.* 2021; this paper), allows to maintain *T. horizontalis* as valid distinctive ichnotaxon.

The small diameter burrows in Lashkerak Fm. do not swell at branching areas and do not show constrictions (Fig. 6), and they are organized in regularly branching, mostly horizontal burrow systems, matching with the diagnosis by Myrow (1995) for *Thalassinoides horizontalis*. Some oblique burrows could have been the connection of the burrow system in a lower level with the water-substrate interface (Fig. 6D), making them closer in morphology to the Zhushadong specimens from Cambrian Age 4 (Zhang *et al.* 2017). According to Myrow (1995), this pattern may have had the function of conduits through which water would be pumped during filter-feeding, or as a feeding structure, in case of an agrichnial burrow. In the examples of *Thalassinoides* described by Myrow (1995), it is frequent the presence of an "outer wall" resulting from a diagenetic halo. This kind of preservation in carbonates is particularly evident for *Thalassinoides* from different ages (e.g. Fürsich 1981; Ekdale & Bromley 2003), and the eodiagenetical processes and dolomitization (Jin *et al.* 2012) inside and in the vicinities of the disturbed sediment ultimately develop a nodular fabric. The diagenetical processes are usually different in siliciclastic settings and for this reason the halo typical of *Thalassinoides horizontalis* in carbonates cannot be found in the unlined burrows from the Lashkerak Formation, as it is not found in the examples described by, e.g. El-Sabbagh *et al.* (2017) and Bendella *et al.* (2021).

DISCUSSION

Some of the earliest *Thalassinoides* networks, similar to *Thalassinoides horizontalis* from the Lashkerak Formation, occur in lower Cambrian nearshore carbonate sediments (Zhang *et al.* 2017). *Thalassinoides* occurs profusely in late Cambrian and Ordovician shallow marine limestones all over the world (Miller & Byers 1984; Droser & Bottjer 1988; Sheehan & Schiefelbein 1984; Ekdale & Bromley 2003; Jin *et al.* 2012), being the two-dimensional forms dominant, at least until the Middle Ordovician (Myrow 1995, and this new occurrence). They form discrete small two-dimensional networks, and more rarely, tridimensional boxworks, with low impact in the level of bioturbation. Examples of these two-dimensional networks are the *Thalassinoides horizontalis* described by Myrow (1995) and Blissett & Pickerill (2004). The Upper Ordovician already shows pervasive deep burrowing *Thalassinoides* (Sheehan & Schiefelbein 1984; Jin *et al.* 2012). The earliest boxworks, assigned to *Thalassinoides bacae* Ekdale & Bromley, 2003, were developed in the Lower Ordovician shallow marine carbonates of Sweden. These burrows were originally described by Ekdale & Bromley 2003) as irregularly anastomosing horizontal tunnel mazes with highly variable branching angles, accompanied by numerous closely spaced and short vertical shafts that must have provided a large number of burrow openings to the sea floor, supporting the interpretation as agrichnial behavior. According to these authors, the main difference between *T. horizontalis* and *T. bacae* is that the later shows the presence of numerous vertical shafts, which are entirely absent from *T. horizontalis*. The ichnogenus *Balanoglossites* Mägdefrau, 1932 only superficially resembles the 3D, dense nodular ichnofabrics of *Thalassinoides* (Knaust 2021). It is typical from shallow-marine carbonates and can be found in limestones from the Volkhov Fm., Russia, similar in age to Lashkerak Fm. (Knaust & Dronov 2013). Despite some similarities, *Balanoglossites* vertical and horizontal tunnel sizes vary within a single gallery system (Knaust 2008, 2021), which is different from the low bioturbation, network systems found in the Lashkerak Formation.

The ichnogenus *Protopaleodictyon* occurs almost exclusively in flysch deposits (Uchman 1995) as pre-depositional forms, preserved as erosional casts on the soles of turbidites, which is a typical feature of the graphoglyptids (Seilacher 1977; Uchman 1995, 1998, 2003; Monaco 2008). They are meanders with appendages developed in the background mud rather than hypichnial networks, which lead us to exclude the new ichnospecies *P. aitkeni* by Morgan *et al.* (2019) from the ichnogenus *Protopaleodictyon*. In effect, *Protopaleodictyon aitkeni* was described by these authors as convex hyporelief forms exhibiting straight to gently curving strands with a "zigzag" shape; strands are regular and with uniform diameter, branching every 25-30 mm, with branching angles of 110-120°, occasionally producing closed hexagonal polygons arranged alternatively along the specimen's axis. Hexagons are 25-40 mm wide and burrows widths are 5-10 mm. (Morgan *et al.* 2019). Moreover, *P. aitkeni* may develop open and closed polygons (Morgan *et al.* 2019). The ichnogenus *Protopaleodictyon* was previously redefined by Uchman (1998) as

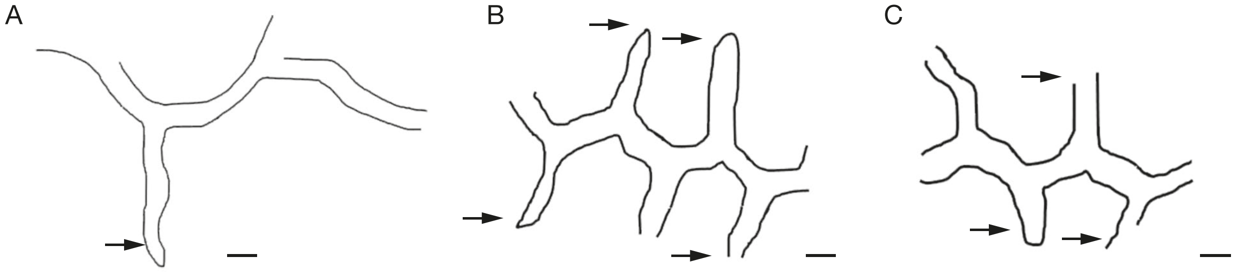

Fig. 7. — Line drawing for comparison: **A**, type material of *Thalassinoides horizontalis* (Myrow 1995: fig. 7b); **B**, type material of *Protopaleodictyon aitkeni* Morgan, Henderson & Pratt (2019) (Morgan *et al.* 2019: fig. 3b); **C**, *Thalassinoides horizontalis* Myrow, 1995 from Lashkerak Fm. (Fig. 6D). **Arrows** indicate oblique tunnels. Scale bars: 1 cm.

horizontal traces with two orders of "string" meanders, one encompassing the entire burrow and the second developed in smaller curves with "string" protrusions extending from the apex of each individual bend. Branching graphoglyptids usually split into two or more burrows repeatedly. The branches do not reconnect these to the main burrow or any other branch, except for *Paleodictyon* and *Megagrapton* Książkiewicz (Lehane & Ekdale 2013). The forms of Morgan *et al.* (2019) are diagnosed with first-order meandering absent thus not comparable with one of the main diagnostic ichnotaxobases of *Protopaleodictyon*. Nevertheless, the authors also compare with *P. spinata* which also has a zigzag secondary meander and lacks primary meandering (Uchman 1998). In fact, they are remarkably similar with the specimens redrawn by Uchman (1998: fig. 102) without scale.

Morgan *et al.* (2019) included *P. aitkeni* as part of a possible taphoseries having *Protopaleodictyon spinata* (Geinitz, 1867) and *Paleodictyon* as end terms. The main differences to *P. aitkeni* are: 1) *P. spinata* is found in the typical flysch facies for graphoglyptids starting already from Cambrian (Uchman 1998); 2) they are one order of magnitude smaller than *P. aitkeni*, thus having the typical minute scale of most of the *Protopalaeodyction* ichnospecies; and, most important 3) they do not develop polygons. Giant *Paleodictyon gomezi* Azpeitia Moros, 1933 was described by Wetzel (2000) in the Lower Eocene flysch near Zumaya, indicating other similar forms occurring in the Silurian flysch. Again, this giant graphoglyptid, consisting in a regular polygonal network, shows the typical preservation in its deep-sea turbidite facies. Ichnospecies of *Megagrapton* are defined by Uchman (1998) as hypichnial irregular nets. *Megagrapton submontanum* corresponds to networks bordered by distinctly winding strings. Unlike *Protopaleodictyon*, however, this ichnospecies define meshes with branches making acute angles and winding strings.

P. aitkeni was also compared by Morgan *et al.* (2019) with the non-graphoglyptid burrow networks *Sinusichnus* and *Ophiomorpha*. The authors used as example *Ophiomorpha* from a Paleogene deep-sea setting (Cummings & Hodgson 2011), which differs by the distinctive presence of a pelletal outer wall in this ichnogenus, and by the absence of vertical shafts in their *P. aitkeni*, which is an ichnotaxobase of *Ophiomorpha* (Morgan *et al.* 2019). The morphotype 1 of Cummings & Hodgson (2011) could in fact be assigned to *Thalassinoides suevicus*, with smooth burrow walls, although Uchman (1995) noted that some horizontal segments of *Ophiomorpha* lack the knobby texture at the bottom of turbidites.

Unlike the miniaturized graphoglyptids in general which are pre-depositional (Uchman 2003; Monaco & Checconi 2010), *Thalassinoides* is mostly a post-depositional large burrow system that may be preserved by passive filling by coarser sediments in sole beds. As *P. aitkeni*, the *Thalassinoides* described from the Lashkerak Formation are open burrow systems of alternating branching (the "zigzag meandering" of *P. aitkeni*) showing similar size, uniform diameter with no swelling at branching points, regular branching length and angle, forming open and occasionally closed polygons (Fig. 7). Although Morgan *et al.* (2019) point out the hexagonal shape of the polygons in *P. aitkeni*, as in *Thalassinoides horizontalis* those are clearly 5 to 6-side polygons (see Morgan *et al.* 2019: figs 6A, B). Both burrows have smooth margins with no lining or wall, roughly rounded to somewhat flattened by compaction in the case of some *P. aitkeni*. In the case of *P. aitkeni*, they are preserved as sole casts of a marly limestone bed being passively filled at the interface with a marl bed (Morgan *et al.* 2019). This is the typical preservation of *Thalassinoides* in carbonate systems. The incomplete development of polygons could be due to differential scour or variable depth of the burrow (Morgan *et al.* 2019) or, more likely by our interpretation, just the oblique connection with the upper substrate interface as in *Thalassinoides horizontalis* (Myrow 1995) (Fig. 7).

Thalassinoides are often preponderant elements of the *Glossifungites* Ichnofacies as Myrow (1995) rightly pinpoints, occurring frequently in firmgrounds resulting from erosional or omission surfaces. However, as in the typical preservation of *Thalassinoides*, as 2D networks during early Paleozoic or 3D boxworks after Middle Ordovician, the structure complexity of the burrow depends mainly on its purpose and tier depth, which may be related with several interdependent factors, such as trophic structure and ecospace competition, food availability and distribution, oxygen and substrate cohesiveness (e.g. Uchman 2003; Bromley *et al.* 2007; MacEachern *et al.* 2007b).

Myrow (1995) hypothesized that *T. horizontalis* could be an agrichnion burrow. Similar behavioral purposes of microbial farming, or microbial trapping, were justified for *P. aitkeni* by Morgan *et al.* (2019). These authors discuss that some string terminations bend upwards, serving the burrows as home and trapping systems. Some of the preservational variants of

Thalassinoides horizontalis found in Lashkerak Fm. show the development of upward bending shafts from the branching points, presumably connecting with the sea bottom. As in *Thalassinoides horizontalis* from Lashkerak Formation, also *P. aitkeni* shows burrow terminations bending upward to the sediment surface, representing conduits through which water may have been pumped during filter-feeding, farming (Myrow 1995), ventilation or trapping prey. This agrichnial or irretichnial ethology in neritic environments, which has been interpreted for *Thalassinoides*, is unusual in the context of graphoglyptids, as stated for *P. aitkeni* by Morgan *et al.* (2019). Because of all the morphological, ethological, environmental and evolutionary time frame similarities with the *Thalassinoides* forms from the Middle Ordovician of the Lashkerak Formation, *Protopaleodictyon aitkeni* erected by Morgan *et al.* (2019) must be considered as a junior synonym of *Thalassinoides horizontalis*.

CONCLUSIONS

Thalassinoides is usually interpreted as a feeding burrow typically produced by infaunal deposit feeders (Bromley & Frey 1974; Fürsich 1981). Being relatively common in low-latitude carbonate settings since the early Cambrian, the presence of *Thalassinoides horizontalis* in siliciclastic fluvial-dominated delta units from the Middle Ordovician Lashkerak Formation allows to expand the paleogeographic distribution of this ichnogenus to high latitudes. Unlike the deep-tier, three-dimensional *Thalassinoides* boxworks developed after the Middle Ordovician, the earliest forms developed discrete small, two-dimensional branching and pseudo-polygonal horizontal networks, which produced a low bioturbational impact (Zhang *et al.* 2017) at a relatively shallow tier level only. This pattern of *Thalassinoides* would thrive until the Middle Ordovician, with the examples from the Lashkerak Formation being included in the paleogeographical distribution climax. The persistence of shallow tiering typical from the Cambrian, well into the Ordovician, is well known in high latitudinal settings (see Mángano & Buatois 2017), and *Thalassinoides* and the associated ichnoassemblage from Lashkerak Formation follow this timing. Still in the Lower Ordovician, *T. bacae* represents the increase of the *Thalassinoides* tier depth during the Great Ordovician Biodiversification Event (Sheehan & Schiefelbein 1984; Jin *et al.* 2012), the so called "beaded *Thalassinoides* ichnofabric" (Ekdale & Bromley 2003), which subsequently lead to the complete disruption of sediments showing the typical nodular appearance, so common for the large crustacean boxworks in neritic carbonate environments from the Mesozoic and Cenozoic. The morphology of the alternating branching and pseudo-polygonal burrows found in *Thalassinoides* from the lower Cambrian of Henan, middle Cambrian of Alberta, upper Cambrian and Ordovician of Colorado, and the Middle Ordovician of Lashkerak Formation seem to correspond in similar approaches to the domicile, ventilation and deposit feeding purposes of their shallow-tiered earliest producers. Finally, the preservational, morphological, ethological, environmental and evolutionary time frame similarities pointed out in this paper between *Thalassinoides horizontalis* from the Middle Ordovician of the Lashkerak Formation, and the recently described *Protopaleodictyon aitkeni* from Colorado, allow us to consider the later as a junior synonym of *Thalassinoides horizontalis* Myrow.

Acknowledgements

Financial support to CNC was provided by Naturtejo, EIM, through the programme for international scientific partnerships under the UNESCO Naturtejo Global Geopark. CNC thanks the support of José António Anacleto (Geological Museum of Lisbon, Laboratório Nacional de Energia e Geologia) during the fieldwork in Iran. IASB of Zanjan is greatly acknowledged for the financial and logistical support to the fieldwork and development of this paper. We thank to George Mustoe (Western Washington University) for reading an early version of the manuscript and provide detailed comments. We acknowledge Jin Jisuo (University of Western Ontario) and an anonymous reviewer for their hints to improve this paper. We also thank the associated editor, Annalisa Ferretti, and the editor-in-chief, Michel Laurin.

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Submitted on 31 August 2022;
accepted on 5 January 2023;
published on 30 August 2023.