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Depositional Controls on the Ichnology of Ordovician Wave-dominated Marine Facies: New Evidence from the Shirgesht Formation, Central Iran

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Abstract: The Lower Ordovician Shirgesht Formation in central Iran is composed of siliciclastic and carbonate rocks deposited in diverse coastal and marine shelfal environments (tidal flat, lagoon, shoreface, offshore-shelf and carbonate ramp). Five facies associations contain diverse ichnofossil assemblages that show distinct proximal to distal trends formed in a wide range of physical-chemical conditions. The ethological groups of trace fossils in the Shirgesht Formation reflect a gradient of depositional stress conditions across a wave-influenced shoreline and shelf. Deposits of wave-influenced environments make up a significant component of the geological record of shallow marine settings, and the ability to determine paleoenvironments in detail in such successions is critical for reconstruction of depositional histories and sequence-stratigraphic interpretation.

The *Cruziana* ichnofacies of the study shows highly diverse suites that record the establishment of a benthic community under stable conditions and a long-term colonization window. The *Skolithos* ichnofacies recognized is a low diversity opportunistic ichnocommunity suite that resulted from colonization after tempestite deposition in a stressed environment. The strata record an onshore to offshore replacement of the *Cruziana* ichnofacies (with abundant feeding traces of deposit-feeders) by the *Skolithos* ichnofacies (dominated by suspension-feeders and predators). A transitional zone between the two ichnofacies coincides with the offshore-transition/distal lower-surface deposits. The distribution of ichnofacies, the diversity and range of ethological characteristics reflected by the ichnogenera, and the wide range of wave-dominated coastal facies demonstrate the potential to use individual trace fossils and ichnofacies for significantly refined palaeoenvironmental analysis of wave-dominated coastal settings, particularly in Ordovician successions.

Key words: Shirgesht Formation, Ordovician, facies associations, sedimentology, iconology, ichnofacies

1 Introduction

The ichnology of Cambrian–Ordovician wave-dominated shallow marine strata is well-studied (El-Khayal and Romano, 1988; Droser et al., 1994; Mángano et al., 1996; Aceñolaza and Aceñolaza, 2002; Buatois and Mángano, 2003; Knaust, 2004; Weber and Braddy, 2004; Aceñolaza and Milana, 2005; Davies et al., 2007, 2009; Egenhoff et al., 2007; Gibert et al., 2011; Hofmann et al., 2012; Bayet-Goll et al., 2013; Mángano et al., 2013; Singh et al., 2014a, b), but relatively few studies have combined detailed lithofacies analysis with ichnological data. Such integration of data has the potential to significantly increase the paleoecological understanding of Ordovician fauna, and aid in paleoenvironmental analysis. The integration of ichnological with sedimentological analyses provides a useful way of discriminating between lithologically similar facies (Bayet-Goll et al., 2014a). Trace fossils are

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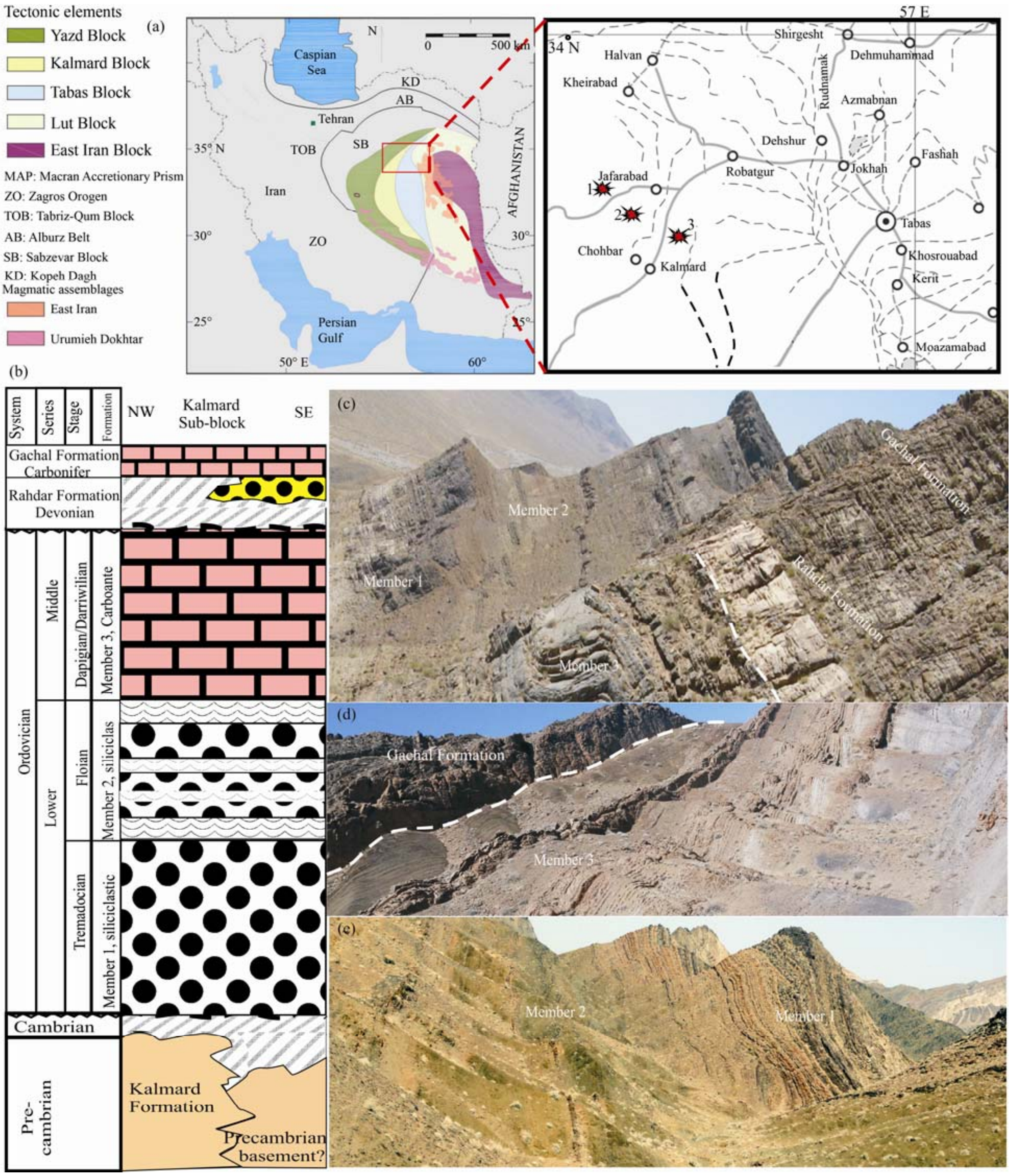

Fig. 1. (a), Generalized tectonic map of Iran (after Alavi, 1991) and index map with location of studied sections. In this map, the Central Iran micro-continent is divided into four blocks. The Kalmard area is located within the Tabas block as an isolated sub-block within Tabas (Kalmard block). Location map of the study area in the Kalmard region about 65 km west of the city of Tabas. Sections: 1) Kuhe Ashghan, 2) Miyugodar, 3) Kuhe Rahdar. (b), Simplfied lithostratigraphy in the Kalmard sub-block. (c), Overview of members 1 to 3 of the Ordovician Shirgesht Formation and the Devonian Rahdar Formation in the Kuhe Rahdar section. (d), Overview of member 3 of the Shirgesht Formation and the Carbonifer Gachal Formation in the Kuhe Ashghan section. (e), Overview of members 1 to 2 in the Kuhe Ashghan section

abundant in the Ordovician siliciclastic deposits of the Shirgesht Formation in the Kalmard block from Central Iran (Fig.1), and herein will be used to illustrate the utility of linked ichnological–sedimentological analysis for the differentiation of ancient depositional settings.

2 Geological Background

Gondwana successions in the Kalmard and Shirgesht areas of central Iran preserve Cambrian through Devonian strata, as summarized by Ruttner et al. (1968), and Bruton et al. (2004). The Lalun (Lower Cambrian), Kalshaneh (Middle Cambrian), Derenjal (upper Cambrian), and Shirgesht (?early to middle? Ordovician) formations (Ruttner et al., 1968) make up the lower part of the Central Iran Gondwana successions (Geyer et al., 2014). Our study is restricted to the Shirgesht Formation in the Kalmard (Fig. 1), here about 260 m thick, and mainly composed of mixed carbonate–siliciclastic deposits. This formation disconformably overlies the Precambrian Kalmard Formation and is underlain by the Gachal (in the northwest part of the basin) and Rahdar (in the southwest part of the basin) Formations. Recent biostratigraphic studies demonstrate an Early/Middle Ordovician age for the Shirgesht Formation (Ruttner et al., 1968; Hamedi et al., 1997; Ghaderi et al., 2009).

In the present study, three stratigraphic sections (NW-SE transects) have been measured, described and sampled in the Kalmard area (Fig. 1). These are located about 65 km west of the city of Tabas (Fig.1). The Shirgesht Formation has been divided into three members dated as Tremadocian, Floian, and Dapinigian/Darriwilian ages, respectively. The lower and middle members are composed of marginal marine siliciclastic strata that contain numerous trace fossils, and these were logged in detail (Fig. 2). No trace fossils were observed in the carbonate facies from the upper member of the Shirgesht Formation. Ichnological attributes involve identification and classification of the present ichnotaxa (Seilacher, 1964, 1967, 2007; Haentschel, 1975; and Monaco and Checconi, 2008); abundance and bioturbation intensities (Taylor and Goldring 1993); estimation of ichnodiversity; identification of trophic types and ethologic groups (Bromley 1996); the toponomy of ichnotaxa (Monaco and Caracuel 2007; ; Monaco et al. 2009) and ichnofacies recognition and subdivision (MacEachern et al. 2007a; MacEachern and Bann 2008; Buatois and Mángano 2011).

3 Siliciclastic Facies and Trace Fossil Content

Ten lithofacies are recognized in the lower to middle siliciclastic members of the Shirgesht Formation and are grouped into five facies assemblages (Table 1).

3.1 Facies association 1 (FA1)

3.1.1 Facies A

This facies consists of black, unbioturbated shale (>80%) with intercalated sandy dolostone (<50% quartz grains). Shale layers are laterally extensive and bed contacts with dolostone and marlstone beds are generally gradational, although basal contacts are locally sharp. The base of the unit is a planar surface with a lag of reworked phosphate nodules (<10 cm thick) (Fig. 3).

Interpretation: Facies A records slow-energy suspension deposition in the absence of waves and currents, based largely on the fine grain sizes and an absence of current-formed sedimentary structures. The absence of bioturbation and grey color suggest oxygen-depleted conditions. This facies is interpreted as having been deposited in a deeper shelf environment. Reworked phosphate nodules are interpreted as a transgressive lag that rests on a ravinement surface.

3.1.2 Facies B

This facies comprises thoroughly bioturbated shale, silty shale, and sandstone beds (<20%). Locally this facies is characterized by unbioturbated shale. Sandstone beds (<5 cm thick) are erosively based and both lenticular and irregular in thickness but laterally continuous (Fig. 4). Internally, sandstone beds exhibit planar lamination, micro-hummocky cross stratification (wavelengths average 5–10 cm), and wave-ripple cross-lamination. In addition, in this facies the relative abundance of sandy interbeds (<40%), the wavelength average (10–25 cm) and thickness (2–20 cm thick) of the HCS also increase upwards. The degree of biogenic reworking of beds of this facies is variable, although bioturbation is commonly uniformly distributed with an intense bioturbated index (BI), ranging from BI4 to BI6 (typically BI5). The two trace fossil assemblages are defined on the basis of their ichnological characteristics from the base to the top of this facies. The lower assemblage is relatively diverse (Table 1) and includes grazing (68%), locomotion (16%), deposit-feeding (9%) and resting (7%) traces (Fig. 4). The thin sandstone beds also locally contain rare suspension-feeding traces. In contrast, the upper assemblage is very diverse and includes locomotion (35%), resting (16%), grazing (18%), and deposit-feeding (14%), dwelling/deposit-feeding to passive carnivory (9%), surface detritus-feeders (4%), deep-tier deposit-feeding (4%) traces (Table 1; Figs. 5–6). Thin sandstone beds contain locally vertical burrows and fugichnia (Table 1).

Interpretation: Micro-HCS and wave-ripple lamination reflect wave action, and thus the sandstone beds are interpreted as tempestites. The lack of bioturbation in some beds, and the presence of sandstone laminae and starved wave ripples in some units suggest episodic very weak wave activity. Facies B contains trace fossil assemblages representing deposit-feeding and grazing or foraging behaviors typical of open marine environments

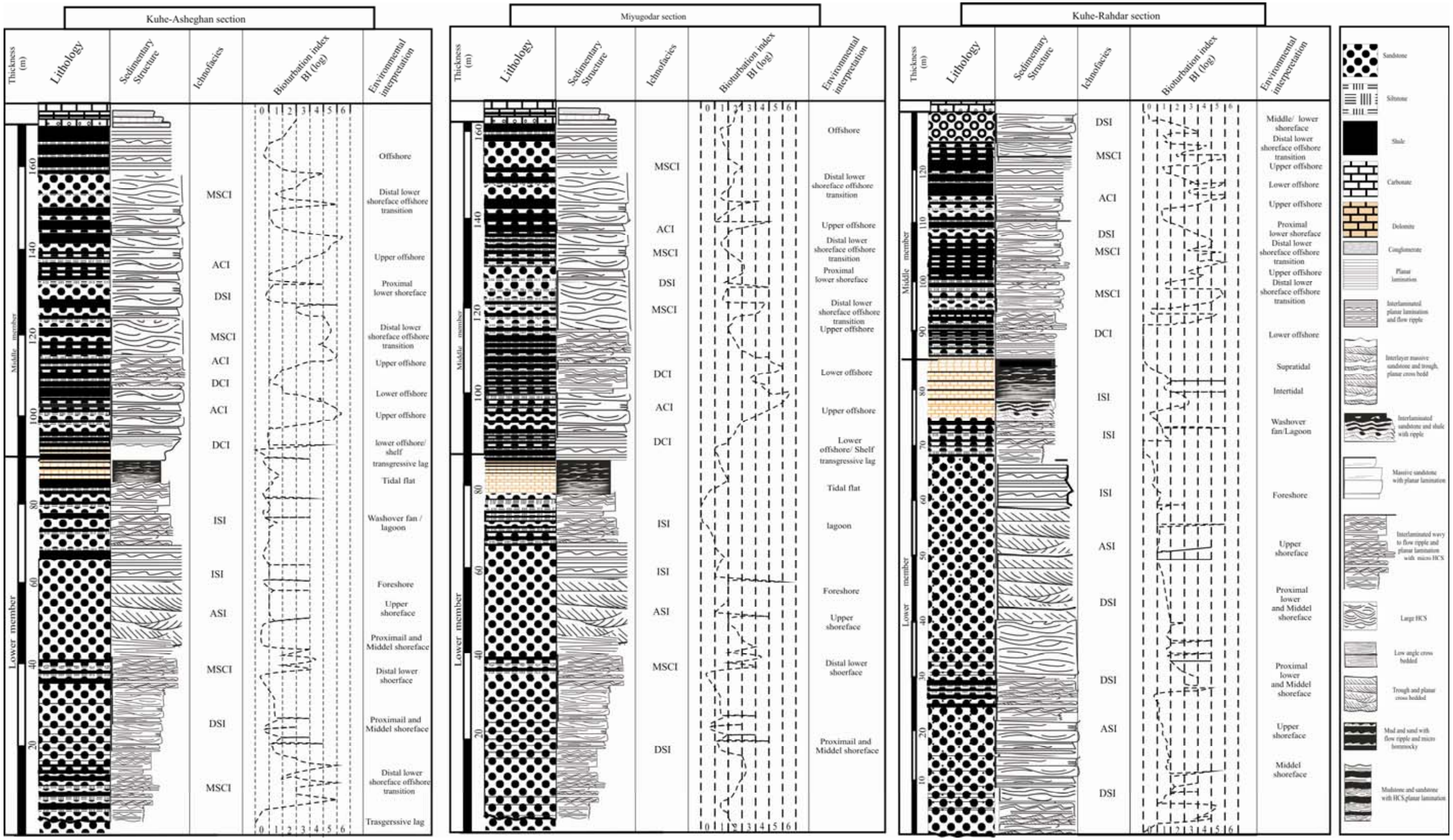

Fig. 2. The three measured stratigraphic sections showing the sedimentological characteristics and interpreted depositional environments for the Ordovician Shirgesht Formation.

DCI= distal *Cruziana* ichnofacies. ACI= archetypical *Cruziana* ichnofacies. MSCI= mixed *Skolithos-Cruziana* ichnofacies. DSI= distal *Skolithos* ichnofacies. ASI= archetypal *Skolithos* ichnofacies. ISI=impoverished expression of the *Skolithos* ichnofacies.

Table 1 Ichnotaxa, sedimentary facies associations and interpreted depositional environments of the siliciclastic succession of the Shirgesht Formation. Ichnotaxa is presented in an abundance order for sedimentary facies

Facies association	Facies	Lithology	Primary Structure	ichnofossil	Ichnofacies	Intertrepation
Facies association 1 (FA1)	Facies A	Gray shale with intercalations from sandy dolomite	massive shale	-	-	shelf
	Facies B	bioturbated shale, silty shale and silty sandstone units, locally fossiliferous	microhummocky cross stratification and current-ripple cross-lamination	*Helminthopsis* (*H. abeli*), *Planolites* (*P. montanus*, *P. annularius*), *Chondrites*, *Gordia*, *Zoophycos*, *Teichichnus* and rare *Cruziana*, *Bergaueria*, *Didymaulichnus*, *Didymaulichnus* (*D. alternates*), and *Lockeia* with *Diplocraterion* in thin sandstone beds.	distal expression of the *Cruziana* ichnofacies	lower offshore
		yellowish green and gray shale with thin (2–20 cm), light gray, laterally extensive, erosive-based, fine-grained sandstone beds, locally fossiliferous	sandstone beds with parallel lamination, wavy ripple cross-lamination and symmetrical to near-symmetrical ripples, rare cross-stratification and planar to low angle lamination	*Cruziana* (*C. furcifera*, *C. goldfussi*, *C. rugosa*, *C. tenella*), *Rusophycus*, *Circulichnus Monomorphichnus*, *Diplichnites* (*D. gouldi*), *Dimorphichnus* (*D. obliquus*), *Trichophycus* (*T. venosus*), *Thalassinoides*, *Cochlichnus*, *Planolites* (*P. beverleyensis*), *Bergaueria* (*B. perata*), *Palaeophycus* (*P. heberti*), *Teichichnus* (*T. rectus*), *Chondrites*, *Arthrophycus* (*A. brongniartii*), *Rosselia*, *Phycodes*, *Gyrochorte?*, *Lockeia*, *Asterosoma*, and *Helminthopsis*, *Didymaulichnus*	archetypical *Cruziana* ichnofacies	upper offshore
Facies association 2 (FA2)	Facies C	Heavily bioturbated facies interlaminated and thinly interbedded shale and sandstone. sandstone beds are generally discrete, thin (10-30 cm) with erosionally based.	Sandstone beds contain HCS, low-angle planar cross-stratification and wave ripples lamination	*Cruziana* (*C. furcifera*, *C. goldfussi*, *C. rugosa*, *C. yini*), *Rusophycus*, *Monomorphichnus* (*M. lineatus*), *Diplichnites* (*D. gouldi*), *Dimorphichnus*, *Trichophycus*, *Arthrophycus* (*A. brongniartii*), *Didymaulichnus*, *Teichichnus*, *Helminthopsis*, *Palaeophycus*, *Bergaueria*, *Chondrites*, *Lockeia*, *Planolites*, *Circulichnus*, *Thalassinoides*, and *Nereites* cf *saltensis* in the fine-grained beds. *Diplocraterion*, *Arenicolites*, *Thalassinoides*, *Palaeophycus*, *P. tubularis*, *Rosselia*, *Skolithos*, *Asterosoma*, *Monocraterion*, and fugichnia in sandstone beds.	mixed *Skolithos*-*Cruziana* ichnofacies	offshore-transition/distal lower shoreface
	Facies D	Amalgamated and usually fine- to medium-grained sandstone, thick (5 to 20 m) with sporadic lenticular clast layers with pronounced concave- up erosional base. Thicker sandstone beds show clast lags (basal and/or top surface)	Thickly amalgamated planar to low angle planar cross-stratified and hummocky cross-stratified and to lesser extant massive to horizontal lamination.	*Thalassinoides*, *Arenicolites*, *Cylindrichnus*, *Palaeophycus*, *Monomorphichnus*, *Diplichnites*, *P. tubularis*, *Bifungites?*, *Teichichnus*, *Planolites* (*P. beverleyensis*), *Helminthopsis*, *Bergaueria*, *Asterosoma*, *Skolithos* (*S. linearis*), *Rosselia* (*R. socialis*), and fugichnia with scratches of *Cruziana*.	proximal *Cruziana* ichnofacies	proximal lower-middle shoreface
Facies association 3 (FA3)	Facies E	10–12 m of highly stratified, well-sorted, coarse sands. It is greyish brown, calcareous, partly dolomite, and sparsely fossiliferous with internal erosion surfaces, gravel lags (basal and/or top surface)	large-scale tabular with high-angle foresets and trough cross-stratified, occasional HCS and symmetrical to near-symmetrical ripples in top layer	*Diplocraterion* (*D. parallelum*), *Skolithos* (*S. linearis*), *Arenicolites*, *Rosselia* (*R. socialis*), *Palaeophycus*, *Macaronichnus*, *Planolites*, *Conichnus*, *Monocraterion* and fugichnia.	archetypal *Skolithos* Ichnofacies	upper shoreface
	Facies F	lateraly persistent subhorizontal sets of light colored, well sorted, parallel-laminated, medium-grained sands, beds show basal and internal erosion surfaces	horizontal to low-angle laminations, planar cross-bedding, trough cross-bedding and current and wave ripples in top layer	*Rosselia*, *Cylindrichnus*, *Macaronichnus*, *Skolithos*, *Monocraterion*, *Palaeophycus*, *Arenicolites*.	impoverished expression of the *Skolithos* ichnofacies	foreshore
	Faceis G	medium- grained, large lenticular sandstone, erosionally based, is up to 3 m thick and variable lateral development	large-scale planar cross-bedding sets interbedded with some horizontal and low-angle individual cross-sets	*Palaeophycus*	No bioturbation observed, scarce	tidal inlet

Table 1 Continued

Facies association	Facies	Lithology	Primary Structure	ichnofossil	Ichnofacies	Intertrepation
Facies association 4 (FA4)	Facies H	Amalgamation of fine-grained, well-sorted sandstone, and dark mudstones with fissile shales, divided of facies K1 and K2. K1 consists of very thinly bedded, dark-maroon mudstone, heavily bioturbated sandy siltstone, K2 consists of interlaminated shale and well-sorted, fine-grained sandstone, chert pebbles and abundant bioclastic material	K1 is highly variable, ranging from homogenous mudstone and bioturbated sandy siltstone to well-laminated shale. In K2 beds show a characteristic upwards evolution with a planar erosional base follows by chert pebbles and massive or horizontal-laminated sand or low angle cross-bedded, capped by symmetrical ripples.	*Skolithos, Palaeophycus, Diplocraterion, Planolites, Arenicolites*, and *Monocraterion*	Sporadically distributed, impoverished expression of the *Skolithos* ichnofacies	washover fan/lagoon
Facies association 5 (FA5)	Facies K	Interlaminated sandy coarse-crystalline dolograinstone and silty dolomudstone. The sandy dolostone consists of an interlocking mosaic of idiotopic dolomite rhombs with abundant sand sized quartz grains. The dolomudstone consists of dense, fine crystalline dolomite with silt-sized quartz grains.	flaser bedding and wavy to planar bedding and rare massive bedding, current, symmetrical-oscillation ripples, polygonal desiccation cracks and kinneyia structure	*Palaeophycus, Skolithos, Conichnus, Diplocraterion, Arenicolites* and *Monocraterion.*	impoverished expression of the *Skolithos* ichnofacies	intertidal-supratidal
	Facies L	consists of dense tightly packed and also very fine to fine crystalline dolomite	intraclasts, scattered detrital quartz grains, and fenestral fabrics	-	-	supratidal

lying well below the fair-weather wave base. Thus, Facies B is interpreted to reflect a distal *Cruziana* ichnofacies to the archetypical *Cruziana* ichnofacies and indicates deposition in offshore and upper offshore environments respectively, above the storm wave base, but only rarely affected by severe storms (e.g. MacEachern et al. 2007; Buatois and Mángano 2011). The shale beds are interpreted as background suspension deposits. Dominance of vertical domichnia such as *Diplocraterion* in some localities suggests that opportunistic, suspension-feeding organisms that preferred a sandy substrate would rapidly colonize the storm beds after deposition.

3.2 Facies association 2 (FA2)

3.2.1 Facies C

Facies C consists of interbedded highly bioturbated shale and siltstone, as well as laminated sandstone (Fig. 7a–b). In contrast to Facies B, this facies, with thicker sandstone beds (<50%), has less abundant and thinner shale beds, although the shale and siltstone component is low (50%). The sandstone generally makes up discrete, 10-30 cm thick beds with sharp erosional bases. They locally contain hummocky cross-stratification (HCS), low-angle planar cross-stratification, wave ripple lamination, and locally, soft-sediment deformation structures. Bioturbation in this facies is intense but not generally uniformly distributed. The shale and sandy siltstone beds are intensely bioturbated (BI4-5) and a diverse suite of trace fossils include locomotion (30%), resting (14%), grazing (12%), deposit-feeding (24%), dwelling/deposit-feeding to passive carnivory (13%), and deep-tier deposit-feeding traces (6%) (Table 1). The laminated sandstone beds range from unbioturbated to mildly bioturbated (BI0 to BI3). These beds contain suspension-feeding (45%), passive carnivore (29%), surface detritus-feeding (15%), and fugichnia traces (11%) (Fig. 7).

Interpretation: The sharp-based sandstone beds in Facies C reflect deposition in a shallow marine environment below the fair-weather wave base. Deposition of bioturbated sandy silt was interrupted by deposition of thin, sharp-based sand beds with HCS and wave-ripple lamination, which reflect combined and oscillatory flows (Myrow and Southard 1996; Myrow et al. 2002; Bayet-Goll et al., 2015a).

This facies is composed of trace fossil suites attributable to the *Cruziana* ichnofacies (a diverse mixture of deposit-feeding and grazing/foraging structures), which alternate with opportunistic elements of the *Skolithos* ichnofacies (dominated by vertical domichnia and resilient surface detritus-feeders) that record post-depositional colonization of the event beds (Pemberton and MacEachern, 1997). Such recurring alternations have been termed the mixed

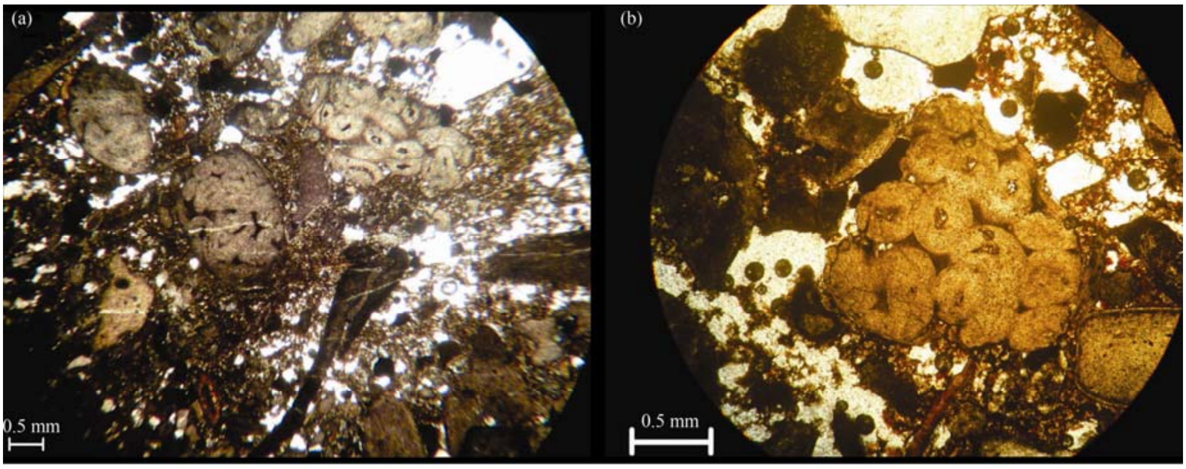

Fig. 3. Thin section slides.
(a) A transgressive lag of phosphorite consisting of phosphatic intraclasts, pellets, and reworked phosphate nodules, interpreted as the deposits of a transgressive lag in the base of Facies A. (b) Close up of phosphate nodules.

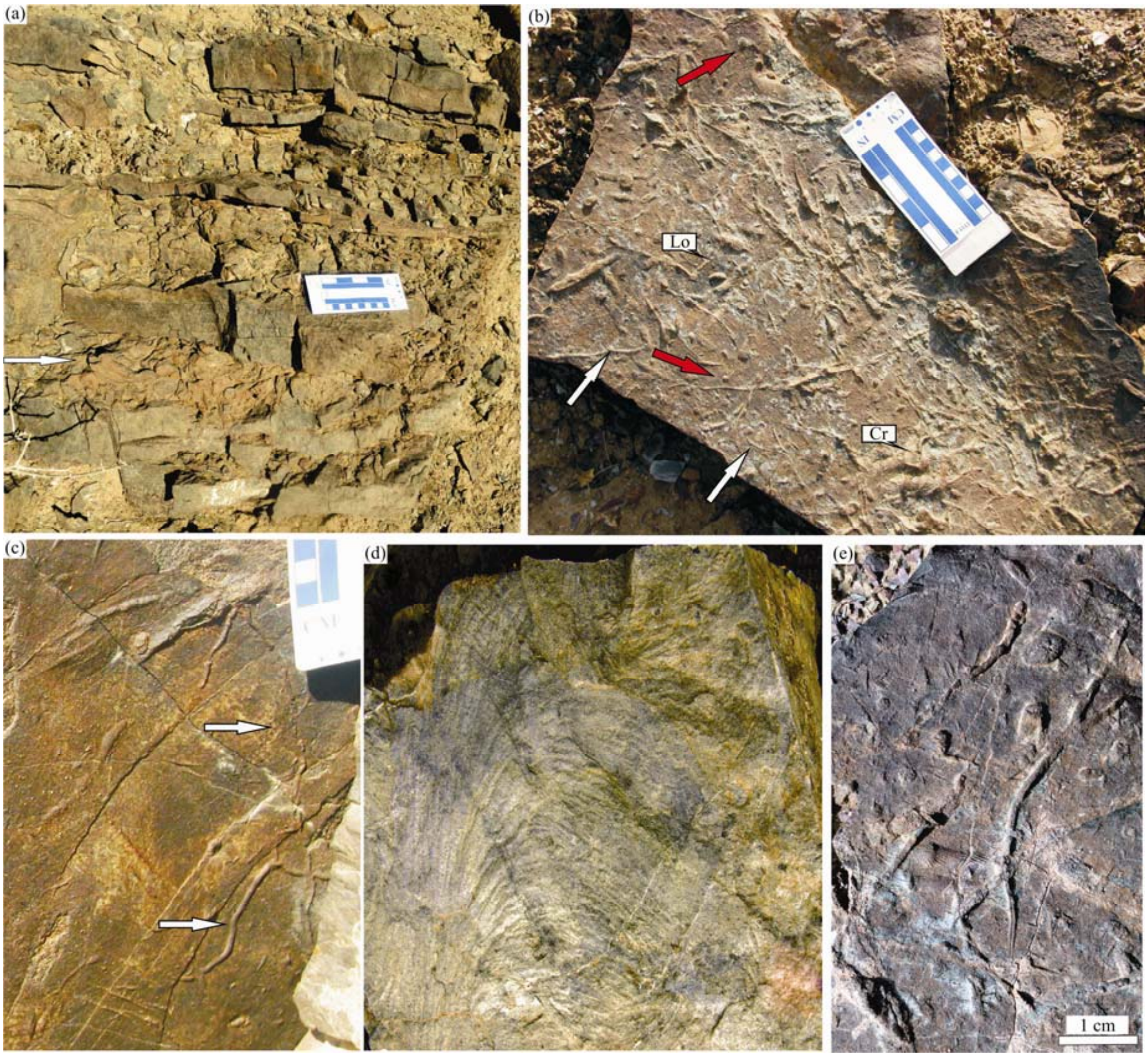

Fig. 4. Outcrop photographs of the siliciclastic facies of the Shirgesht Formation.
(a) Vertical section of heterolithic bedding in fine-grained silty sandstone and mudstone of upper offshore facies, with micro-HCS, and *Teichichnus* cf. *rectus*. with vertical spreite (arrow). Trace fossils of the lower offshore facies. (b) Lower surface of a sandstone bed with *Cruziana* isp. (Cr), *Lockeia* isp.(Lo), *Bergaueria* isp.(red arrows) and *Gordia* isp. with simple meandering form without crossing (arrows). (c) *Helminthopsis* isp. on the lower surface of a fine-grained sandstone bed (arrows). (d) *Zoophycos* isp. in fine-grained sandstone. (e) *Didymaulichnus alternates* (white arrow) and *Cruziana* isp. (yellow arrow) on the lower surface of fine-grained sandstone.

Fig. 5. Trace fossils of the upper offshore facies.

(a) Vertical section of heterolithic bedding in the upper offshore facies, of fine-grained silty sandstone and mudstone, with microhummocky cross-stratification (arrow) and rippled tops (red arrow). These layers show well-developed *Trichophycus* burrows preserved within mudstone. (b) *Chondrites* isp. (arrow) a complexly-branching burrow partly parallel to the bedding plane. (c) *Palaeophycus tubularis* (arrows) specimen on lower surface of fine-grained sandstone with scratches of *Cruziana*. (d) *Cruziana* isp. (white arrow) and *Planolite* isp.(yellow arrow) on the lower surface of fine-grained siltstone. (e) Bedding-plane (lower) view showing well-developed *Teichichnus* isp. Note prominent vertical spreite (arrows). (f) Sandstone with *Cruziana rugosa* (white arrow) and *Rusophycus* isp. (yellow arrow). (g) and (h) *Arthophycus brongniartii*. Note angular segments along the burrow.

Fig. 6. Trace fossils of the upper offshore facies.

(a) The upper offshore facies, showing a well-developed *Trichophycus venosus* burrow preserved within mudstone attached to the overlying sandstone tempestite bed. (b) and (c) *Trichophycus* isp. with micro-HCS (arrow). (d) *Diplichnites gouldi* preserved on fine-grained sandstone as a concave epirelief. (e) *Bergaueria perata* on the lower surface of a fine-grained sandstone bed (arrows). (f) *Phycodes* isp. showing the branches that originate in a palmate form, and the cross-section of branches. (g) *Teichichnus* isp. Note prominent vertical spreite (arrow). (h) Bedding-plane view showing unknown trace fossils.

Skolithos–*Cruziana* ichnofacies (e.g., Pemberton et al., 1992a, b). Facies C is interpreted as the product of sediment accumulation in an open marine offshore-transition to distal lower shoreface. It is difficult to distinguish between offshore-transition and distal lower shoreface deposits due to rapid stratigraphic and spatial variations in physical structures, which result from shifting energy levels. However, variations in thickness and character of HCS strata can be used to tease out proximal–distal trends (e.g., Myrow and Southard, 1996; Ito et al., 2001). Thinner distinct hummocky beds (wave length average up to 30 cm) with rippled tops, separated by mudstone interbeds, represent storm reworking in offshore-transition to distal lower shoreface settings. In contrast, thicker amalgamated low angle cross bedding and hummocky beds (wave lengths average up to 60 cm) represent storm reworking in more

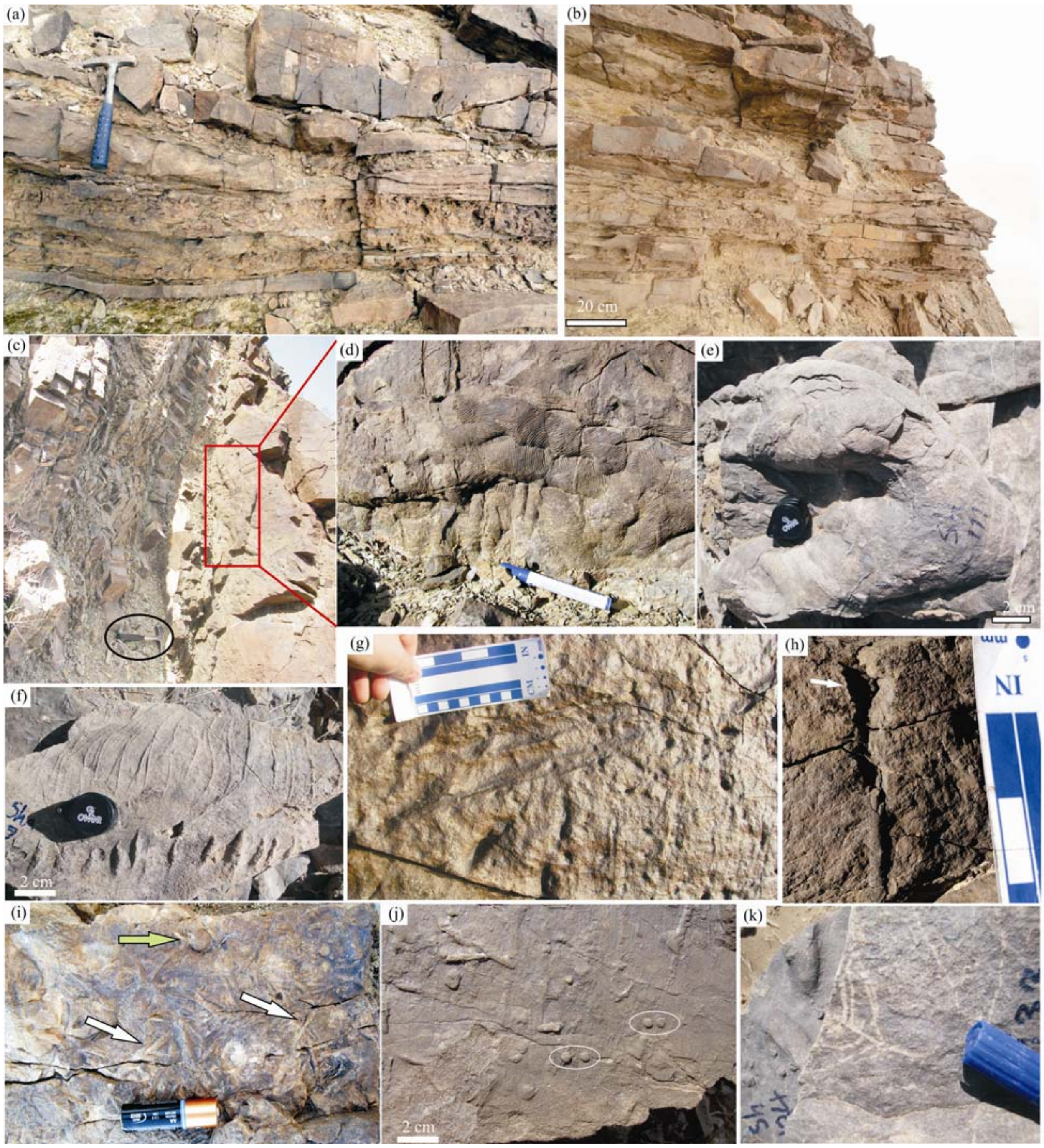

Fig. 7. Sedimentary structures and trace fossils of offshore-transition to distal lower shoreface facies.
(a) and (b) Interlaminated and interbedded highly bioturbated shale, siltstone and sandstone of Facies D. The sandstone beds locally contain HCS, low-angle planar cross-stratification, and wave ripple lamination. The shale and sandy siltstone beds are intensely bioturbated (BI4-5) and the well-laminated sandstone beds are less intensely bioturbated, ranging from BI0 to BI3. (c) Thin beds of sandstone and shale of offshore-transition to distal lower shoreface facies. (d) A lower surface of sandstone with a dense population of *Cruziana yini*. (e) Large *Thalassinoides* isp. branches are Y-shaped, commonly enlarged at the bifurcation point. (f) *Dimorphichnus* isp. Parallel series of sigmoidal or comma-shaped impressions arranged obliquely to the direction of movement. (g) *Nereites* cf. *saltensis*. (h) *Monocraterion* isp. vertical burrow with a wide, funnel-shaped top. (i) Lower surface of fine-grained sandstone bed with *Planolites beverleyensis* (white arrows) and *Bergaueria perata* (yellow arrow). (j) Pairs of tubes without spreiten, which are determined to be *Arenicolites* isp. (k) *Chondrites* isp.

proximal lower shoreface settings. This criterion cannot be applied to the Shirgesht Formation deposits because of the rapid variations in physical structures. Thus it is difficult to distinguish between offshore-transition and distal lower shoreface deposits.

3.2.2 Facies D

Facies D is made of thoroughly amalgamated, medium-grained sandstone units 5 to 20 m thick, which are intergradational with underlying units of facies C (Fig. 8a). This facies consists of thick, amalgamated, cosets of dune-scale cross-bedded sandstone (approximately 40-100 cm thick), as well as parallel- and HCS sandstone (15–40 cm thick). Palaeocurrent data from tabular cross-bed sets give north-east/south-west palaeoflow directions, orientated approximately parallel to the inferred depositional strike (from mapping the lower member sandstones of the Shirgesht Formation by Bayet-Goll, 2008). The hummocks in HCS beds have 2–10 cm amplitude and 1.0–1.5 m wavelength. Locally, the basal parts of units of this facies contain discrete, thin (<5cm thick) mudstone beds, and thin, very fine-grained sandstone laminae and cm-thick wave rippled beds. In general, sedimentary structures in this facies show upward loss of oscillation ripple laminae (wavelength average; 10–20 cm) and muddy interbeds, and increases in thickness and abundance of low-angle lamination, planar lamination, and hummocky cross-stratification (60 cm to 1.0–1.5 m, Figs. 8c, d). This facies is characterized by highly variable bioturbation intensities, generally ranging from BI0 to BI3, although intensive bioturbation (BI4-5) exists locally. The trace fossil assemblage in the sandstone beds is diverse (Table 1) and includes suspension-feeding (32%), passive carnivore (12%), surface detritus-feeding (19%), locomotion (9%), dwelling/deposit-feeding (10%), resting (5%), grazing (3%), and fugichnia (9%) traces (Fig. 8).

Interpretation: Facies D is interpreted as lower to middle shoreface deposits. The facies is characterized by sedimentary structures that reflect deposition in a high-energy, storm-dominated environment, influenced by a longshore current that formed thick, amalgamated tabular cross-beds. The paleocurrent gives additional support to this interpretation. Furthermore, thick, amalgamated HCS beds represent proximal high-energy, storm-generated, oscillatory and combined flows in water depths shallower than the fair-weather wave base (e.g., Cheel and Leckie 1993). The overall trace fossil assemblage, dominated by vertical domichnia and subordinate detritus and deposit feeding traces, is interpreted to reflect a proximal *Cruziana* ichnofacies (e.g., Pemberton and MacEachern, 1997). Considering the above characteristics, Facies D reflects sedimentation in the proximal lower to middle shoreface of a storm-dominated shoreline, above the fair-weather wave base. Palaeocurrent data indicate longshore currents which transported sediment from SW to NE. The transitions from proximal lower shoreface to middle shoreface include the increase of bed thickness of tempestites and the average wavelength of HCS (e.g., Ito et al., 2001; Myrow et al., 2002, 2004).

3.3 Facies association (FA3)

3.3.1 Facies E

Facies E consists of thick bedded (approximately 80-100 cm thick) stratified, well-sorted, coarse-grained sandstone that forms units 10–12m thick. This facies is dominated by thick to very thick bedded (>1m), tabular and trough cross-beds, showing symmetrical to near-symmetrical ripples capping those beds. Cross-strata paleocurrents are mainly oriented towards the northwest, approximately perpendicular to the depositional strike. Most units have little or no bioturbation, with the BI ranging from 0 to 2. Intensive bioturbation (BI4-5) as a pipe-rock ichnofabric of vertical dwelling traces exists locally. The trace fossils suite is characterized by suspension-feeding (46%), surface detritus-feeding (29%), passive predation (12%), dwelling/deposit-feeding (5%), and fugichnia (8%) behaviors (Table 1).

Interpretation: The coarse grain size and the presence of abundant large-scale, trough to tabular cross-stratification suggests that much of this facies was deposited in a storm dominated marine environment above the fair-weather wave base (Bayet-Goll et al., 2015b; Fa et al., 2015). Paleocurrent data taken from trough cross-stratification indicates migration of large three-dimensional dunes within an upper shoreface environment. The trace fossil suite represents an archetypal *Skolithos* ichnofacies (e.g., MacEachern and Bann, 2008). Most of the trace fossils are vertical to subvertical, and represent the domiciles of deeply burrowing suspension feeders or surface feeders.

3.3.2 Facies F

Facies F is characterized by a predominance of laterally persistent, subhorizontal sets of well-sorted, highly mature, parallel-laminated, medium-grained sandstone bedsets (10–15m thick; Fig. 9a). The facies also contains basal and internal erosion surfaces, low-angle lamination to tabular and trough cross-bedding (approximately 50-100 cm thick), and current and wave ripples on bed tops. This facies is not intensely bioturbated and trace fossil diversity is generally very low. Most units have little or no bioturbation, with the BI ranging from 0 to 1. Intensive bioturbation (BI4-5) as a pipe-rock ichnofabric of vertical dwelling traces exists locally. The trace fossil suite is characterized by suspension-feeding (42%), surface detritus-feeding (38%), dwelling/deposit-feeding (9%), and fugichnia (11%) traces (Table 1, Fig. 9 a–b).

Interpretation: The parallel lamination reflects high-energy swash and backwash transport, typical of beach deposits (e.g., Seidler and Steel, 2001). Trough cross-stratification resulted from dune migration under wave-generated onshore-directed sediment transport. The trace

Fig. 8. Facies assemblages from proximal lower to middle shoreface facies.
(a) Panoramic view of the Lower member of the Shirgesht Formation representing the distal lower shoreface to upper shoreface-foreshore deposits. (b) Facies D sandstone beds dominated by vertical dwelling burrows. (c) Thick hummocky cross-stratified bed in proximal to lower-middle shoreface facies. (d) Thickly amalgamated tabular cross-stratified and hummocky beds. The thickness and abundance of tabular cross-stratified beds increases upwards. (e) *Thalassinoides* isp. Y-shaped branches (white arrows) and *Planolites* isp. (red arrows) in highly bioturbated medium-grained sandstone beds. (f) Bedding-plane view of fine-grained sandstone showing well-developed *Thalassinoides* isp. burrows. (g) Large-scale trough-cross stratified upper shoreface facies with tabular cross-stratification towards the top of the layer.

Fig. 9. (a) Well-developed horizontal lamination in Facies F with *Rosselia* (yellow arrow) and fugichnia (light arrow). (b) *Rosselia* isp. in Facies F, transverse cross-sections showing alternating concentric sandstone and mudstone laminae. (c) Oppositely dipping cross-strata is present in superimposed beds, resulting in a bidirectional pattern (white arrow), with gravel lags on basal surfaces (yellow arrow) in Facies G. (d) Bioturbation in Facies H (highly variable), ranging from homogenous mudstone and bioturbated sandy siltstone (BI4–5) to well-laminated shale (BI0). (e) Sandstone beds containing *Monocraterion* isp. (in Facies H, arrows) in vertical section with planar lamination (e). (f) *Conichnus*--like structures (arrows) in Facies K, consists of vertical, conical, v-shaped burrows with chaotic internal structure. Note irregular fill and chevron laminae. (g) Facies K consists of fine-grained deposits with wavy to planar bedding, dominated by vertical dwelling burrows.

fossil suite represents an impoverished expression of the *Skolithos* ichnofacies (e.g., MacEachern et al., 2007). Most of the trace fossils represent the domiciles of deeply burrowing suspension-feeding organisms, indicative of relatively high levels of wave or current energy in the foreshore environment.

3.3.3 Facies G

This facies consists of laterally discontinuous, lens-like units of thick bedded (~50–100 cm), medium grained to poor-sorted, coarse-grained sandstone. The facies is dominated by thick tabular and trough cross-bedsets, which are interbedded with horizontally laminated and cross-bedded sandstones, showing low-angle lamination and a finer grain size. In some cases, the angle-of-repose of cross-bed sets show oppositely dipping foresets in superimposed beds, resulting in a bidirectional pattern (Fig. 9c). Locally, superimposed beds show basal and internal erosion surfaces with gravel lags on basal surfaces (Fig. 9c). This facies is generally in erosional contact with underlying deposits of Facies E, F and D. The only trace fossil found in Facies G is *Palaeophycus*.

Interpretation: This facies is interpreted as recording deposition in a tidal inlet setting. The pervasive tabular cross-bedding reflects the transport of coarse grained dunes in a deep channel, and the moderate to poor sediment sorting, bidirectional paleocurrents, together with the lenticular geometry and erosive bases paved by gravel lags, also support the interpretation of this facies as a tidal inlet. The lack of trace fossils may indicate a paucity of organisms, probably due to high energy currents and high sedimentation rates in tidal inlet settings.

3.4 Facies association (FA4)

3.4.1 Facies H

Facies H is composed of interbedded fine-grained, well-sorted, medium bedded (20–30 cm thick) sandstone (<40%), and dark mudstone, siltstone, and shale. The sandstone is massive and occurs as thick units of sandstone beds separated by very thin shale beds. Individual beds pinch out within a few hundred meters along strike. Finer-grained lithologies consist of very thinly bedded (1–3 cm thick), generally dark-maroon mudstone, highly bioturbated sandy siltstone, and shale. The degree of bioturbation in the fine-grained lithologies is highly variable, ranging as high as BI4–5 in the homogeneous mudstone and bioturbated sandy siltstone, to BI0 in well-laminated shale (Fig. 9d). Wrinkle marks and synaeresis cracks are preserved locally. Units of this facies have basal erosional contacts, with chert-pebble-bearing sandstone, massive to horizontal-laminated sandstone, and low-angle cross-bedded sandstone, the latter of which is locally capped by symmetrical ripples. Load structures are common. The sandstone contains a low-diversity trace fossil assemblage consisting of suspension-feeding (72%), dwelling/deposit-feeding (11%), and grazing (17%) structures (Table 1; Fig. 9e), and is characterized by low levels of bioturbation (BI1-2).

Interpretation: In general, facies H, which is the only facies in facies association FA (4), reflects deposition in a lagoonal environment that was periodically flooded by storm events. This facies association is interpreted as an interfingering of washover fan sandstone beds with fine-grained lagoonal deposits behind a barrier island. The turbid water and likely fluctuating salinity from inflows may have made a poor habitat for most organisms. As a result, bioturbation is much less intense here than in shoreface facies. The sandstone beds have features indicating single-event deposition, such as normal grading. The low-diversity trace fossil assemblage in this facies is diagnostic of deposition in environments subject to periodic salinity and oxygenation stresses, as common in lagoonal settings (Pemberton et al., 1992a).

3.5 Facies association (FA5)

3.5.1 Facies K

Facies K is composed of interlaminated sandy coarse dolograinstone and silty dolomudstone. Facies K is characterized by flaser and wavy to planar bedding (Figs. 9g). Physical sedimentary structures include massive bedding, current-ripple cross-stratification, symmetrical ripples, polygonal desiccation cracks and wrinkle marks. The dolomudstone contains planar lamination and subordinate wavy lamination and massive bedding. Most units have little or no bioturbation, with the BI ranging from 0 to 2. The assemblage is composed of suspension-feeding (61%), dwelling/deposit-feeding (21%), and passive predation (18%) traces (Fig. 9f–g). Small to medium burrow sizes are dominant in the assemblages. Intensive bioturbation (BI4-5) as a pipe-rock ichnofabric of vertical dwelling traces also exists locally.

Interpretation: This facies represents deposition within intertidal to supratidal environments, based on the trace fossil assemblage and the presence of sedimentary features such as desiccation cracks and flaser, lenticular and wavy bedding. The sedimentological differences between sandy dolograinstone and interlaminated dolomitic mudstone indicate that sediment accumulation occurred in various intertidal flat subenvironments (Zonneveld et al., 2001). The trace fossil suite includes vertical to sub-vertical forms, and represents the domiciles of deeply burrowing suspension-feeders. This trace fossil assemblage is indicative of an impoverished expression of the *Skolithos* ichnofacies (MacEachern et al., 2007).

3.5.2 Facies L

This facies consists of dense, very-fine- to fine-grained dolostone. The main features of this facies are subtly-preserved depositional textures, such as intraclasts, scattered detrital quartz grains, and fenestral fabrics.

Interpretation: The fine-grained nature of this facies, the presence of scattered detrital silt-size quartz grains and fenestral fabrics, suggest that deposition occurred in a supratidal environment (e.g., Bayet-Goll et al., 2014b; Nowrouzi et al., 2015). The absence of fossils or trace fossils in this facies likely reflects an ecologically-stressed setting in which subaerial exposure and extended periods of hypersalinity made it hard for colonization.

4 Depositional Model

A depositional model and history is given below for the siliciclastic succession of the Shirgesht Formation in the Kalmard area, including the lower (Tremadocian) and middle (Floian) members.

4.1. Lower member

The up to 70 m thick coarsening- and thickening-upward succession of the lower member is interpreted to record a prograding shoreface/foreshore system (Fig. 10). The energy level appears to have been sufficient for transportation and deposition of sand and gravel, and the prograding of a shoreface/foreshore system during deposition of the lower member. Sedimentological and ichnological data indicate that the shoreface deposits have distinct progradational stacking patterns.

The facies distributions indicate that tidal flats developed at the landward margin of lagoons behind the protective barrier islands. The barrier margin of the

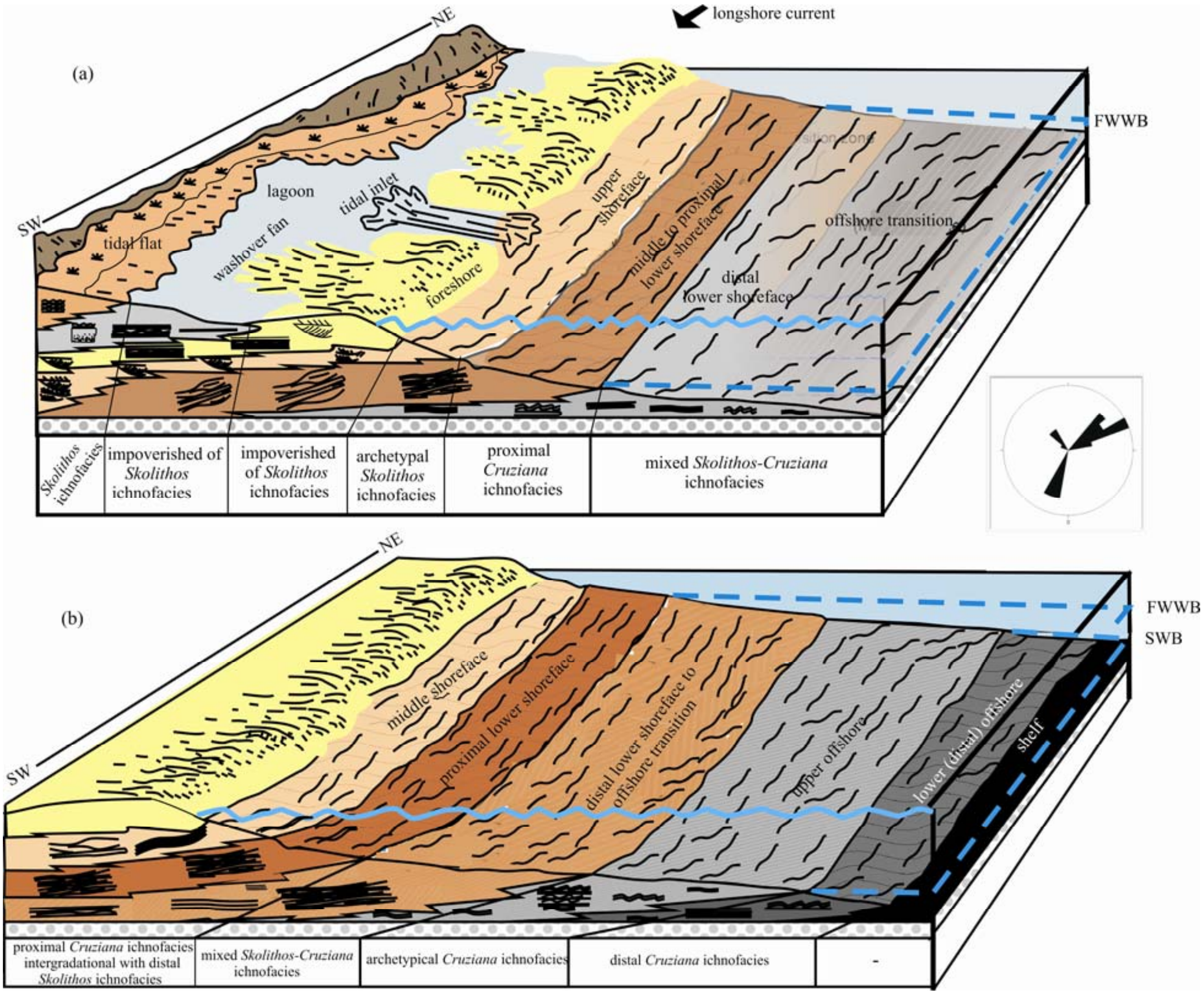

Fig. 10. A schematic paleosedimentological model of the Shirgesht Formation, showing onshore-offshore ichnofacies gradients related to paleoenvironments of the siliciclastic deposits from lower member (a) and middle member (b). Rose diagram of 42 true dip azimuths representative of longshore bedform migration directions, suggest a NE–SW paleoshoreline orientation. Tabular sets were deposited from longshore currents (NE paleocurrents) while the trough cross-bed sets were deposited from breaking waves (northerly paleocurrents). FWWB = fair-weather wave base; SWB = storm wave base.

lagoon was strongly influenced by storm washover sand destruction of the barrier, which was apparently the main source of sandy sediment to the lagoon. The development of the barrier may have been aided by the influx of sediment by an earlier fall of sea level and reworking into barriers during the subsequent Tremadocian transgression. Under such conditions, an onshore transport of sediment would have re-established an equilibrium profile of the beach after storm events (Stapor and Stone, 2004). Lithofacies data, paleocurrent analysis, and hydrodynamic interpretations of sedimentary structures indicate that the wave- and storm-dominated coastal zone was also influenced by longshore currents. Paleocurrent data for FA3 and FA2 (42 true dip azimuths) suggest a shoreline orientation of NE–SW for the lower member sandstone. In general, it can be stated that tabular sets were deposited from longshore currents (NE paleocurrents), while the generally trough sets were deposited from shoaling and breaking waves (northerly paleocurrents) (Fig. 10).

4.2. Middle member

The progradationally-stacked lower member barrier–lagoonal facies grade upward to transgressive, siliciclastic, open shelf deposits of the middle member (Fig. 10). This transition represents the establishment of an open shallow marine, low-gradient, storm-dominated platform. Deposition of the transgressive middle member may have been aided by increased subsidence caused by movement along the Kalmard fault at this time (Hosseini-Barzi and Bayet-Goll, 2009).

In this member, the inferred paleoenvironments range from middle–lower shoreface to shelf. The progressive landward shifting of facies suggest that the strongly heterolithic succession of the middle member represents shoreface/offshore-shelf systems tracts formed during the rise of sea level in the Early Ordovician (Floian). The middle member shows retrogradationally-stacked sets from offshore-shelf environments (FA1, facies A, B) and offshore-transition to distal lower shoreface environments (FA2, facies C), and in turn grades upwards into progradational packages from offshore-transition to distal lower shoreface environments (FA2, facies C) and proximal lower to middle shoreface environments (FA2, facies D). Fair-weather bioturbated shale and storm-generated event beds dominate the middle member facies, and these comprise heterolithic deposits that grade from mudstone dominated (facies A, B) to sandstone dominated (facies C, D), with an upward increase in grain size and sandstone bed thickness.

5 Implications and Factors Regulating Ichnofaunal Distribution

Proximal and distal facies of lagoon–offshore successions of this study start from the archetypal ichnofacies and show marked reductions upwards in bioturbation intensity, sporadic distribution of burrowed intervals, and impoverished assemblage. Resolving the ichnological signature of these sedimentary settings will provide a template for reconstructing the depositional environments of other ancient successions (MacEachern and Gingras, 2007; MacEachern and Bann, 2008; Buatois and Mángano, 2011). The archetypal ichnofacies (MacEachern et al. 2007a) are diagnostic of a limited range of environmental stress parameters. Departures from the norm are well-documented for deltaic and estuarine settings (Pemberton et al., 2001; MacEachern et al. 2007b; MacEachern and Gingras, 2007; Bann et al. 2008), but departures from wave-dominated coastal settings, which are extremely abundant in the rock record, are poorly known.

Ichnofacies of storm-dominated offshore to shoreline depositional systems reflect, in part, depth-dependent changes in hydrodynamic conditions. In this study, six trace fossil assemblages are identified in the Shirgesht Formation, from distal to proximal ichnofacies including (1) the distal *Cruziana* ichnofacies, (2) the archetypical *Cruziana* ichnofacies, (3) the mixed *Skolithos–Cruziana* ichnofacies, (4) the distal *Skolithos* ichnofacies intergradational with proximal *Cruziana* ichnofacies, (5) the archetypal *Skolithos* Ichnofacies, and (6) an impoverished expression of the *Skolithos* ichnofacies (Fig. 10).

Storm-dominated settings generally yield biogenically reworked substrates with ichnological suites that represent opportunistic colonization of storm beds, which are overprinted by a fair-weather suite characteristic of an equilibrium community (e.g., Pemberton et al., 2001; Buatois and Mángano, 2003; MacEachern et al. 2005; Buatois and Mángano, 2011; Angulo and Buatois, 2012; Buatois et al., 2012). The fair-weather trace fossil assemblage is the most diverse and includes more varied behavioral strategies, representing elements of the *Cruziana* ichnofacies (Buatois and Mángano, 2011). Ethologically, this assemblage includes locomotion, grazing deposit-feeding, deep-tier deposit-feeding, dwelling/deposit-feeding to passive predation, and dwelling structures of deposit-feeders or surface detritus-feeders (e.g., Mángano et al., 2005; Buatois and Mángano, 2011) (Table 2). The storm-related assemblage produced after deposition by opportunistic organisms (r-strategists),

Table 2 Ichnotaxa of the Shirgesht Formation, their ethology and relation to sedimentary facies beds. Description of ethological groups referred in the text

ichnogenera	Ethological category	Pre-, post-depositional origin	shelf	lower offshore	upper offshore	offshore-transition/ distal lower shoreface	proximal lower-middle shoreface	upper shoreface	foreshore	washover fan/lagoon	intertidal-supratidal
Arenicolites	suspension-feeding structures	Post				R	C	A	A	C	C
Arthrophycus	deposit-feeding	Pre		A	A	C	C	A	C	R	A
Arthrophycus brongniartii	deposit-feeding	Pre		A	A	R					
Asterosoma	surface detritus-feeders	Pre		A	A	R					
Bergaueria	resting, passive carnivores	Pre and post		R	C	A	R				
B. perata	resting, passive carnivores	Pre and post		R	R	A					
Bifungites?	dwelling/deposit-feeding to passive carnivore	Pre					C				
Cruziana	locomotion	Pre		C	C	A	R				
C. furcifera	locomotion	Pre			C	A	R				
C. goldfussi	locomotion	Pre			C	A	R				
C. rugosa	locomotion	Pre			C	A	R				
C. tenella	locomotion	Pre			C		R				
C. yini	locomotion	Pre			C	A	R				
Chondrites	deep-tier deposit-feeding	Pre		A	C	C					
Circulichnus	deposit-feeding	Pre and post			C	C					
Cochlichnus	grazing	Pre			R	C					
Conichnus	passive carnivores	Post						A			C
Cylindrichnus	surface detritus-feeders	Pre and post					A	R	A		
Didymaulichnus	locomotion	Pre		R	C	A					
D. alternates	locomotion	Pre			C	A					
Dimorphichnus	grazing	Pre		C	C						
Dimorphichnus obliquus	grazing	Pre		R	C						
Diplichnites	locomotion	Pre		R	A	A	R				
D. gouldi	locomotion	Pre		R	C	A					
Diplocraterion	suspension-feeding structures	Post		R	R	C		A	R	C	C
D. parallelum	suspension-feeding structures	Post			R	C		C		R	
fugichnia	escape structures	Post				C	A	C	C		
Gordia	grazing	Pre		C	R						
Gyrochorte	locomotion	Pre			R						
Helminthopsis	grazing	Pre		C	A	A	R				
Lockeia	resting	Pre		R	C	C					
Macaronichnus	passive carnivores	Post						C	A		
Monocraterion	suspension-feeding structures	Post				C		A	C	R	C
Monomorphichnus	locomotion	Pre		R	A	C	R				
M. lineatus						C					
Palaeophycus	dwelling/deposit-feeding to passive carnivore	Post		R	C	A	C	C	R	C	R
Palaeophycus tubularis	dwelling/deposit-feeding to passive carnivore	Post				A	C				
Phycodes	deposit-feeding	Pre			R						
Planolites	grazing	Pre		R	A	A	C	R		C	

Table 2 Continued

ichnogenera	Ethological category	Pre-, post-depositional origin	shelf	lower offshore	upper offshore	offshore-transition/ distal lower shoreface	proximal lower-middle shoreface	upper shoreface	foreshore	washover fan/lagoon	intertidal-supratidal
Planolites beverleyensis	grazing	Pre		R	C	C	R				
Nereites cf *saltensis*	grazing	Pre				C					
Rosselia	surface detritus-feeders	Pre and post			R	R	C	A	A		
R. socialis	surface detritus-feeders	Pre and post					C	A	R		
Rusophycus	resting	Pre		R	C	C	R				
Skolithos	suspension-feeding structures	Post				C	C	A	A	C	A
S. linearis	suspension-feeding structures	Post					C	A			
Teichichnus	dwelling/deposit-feeding to passive carnivore	Pre		C	A	A	R				
T. rectus	dwelling/deposit-feeding to passive carnivore	Pre			C						
Thalassinoides	dwelling/deposit-feeding to passive carnivore	Pre and post			C	A	A				
Trichophycus	deposit-feeding	Pre			A	A					
T. venosus	deposit-feeding	Pre			A						
Zoophycos	deposit-feeding	Pre and post		C							

Fodinichnia=feeding traces. Pascichnia= grazing traces. R= rare; C=common; A= abundant.

represents elements of the *Skolithos* ichnofacies (Buatois and Mángano, 2011). Ethologically, this assemblage includes suspension-feeding structures, passive carnivores, escape structures (fugichnia), and dwelling structures of deposit-feeders (e.g., Mángano et al., 2005; Buatois and Mángano, 2011; Buatois et al., 2012) (Table 2).

Ichnofossil assemblages and their features (size, diversity, bioturbation intensity, distribution style) that hold the greatest potential to enhance paleoenvironmental interpretations allow the development of a conceptual model (Figs. 11–12) that permits significantly more refined recognition and differentiation of shoreface lithofacies and successions in storm-/wave-dominated regimes.

5.1 Lower offshore/shelf

Bioturbation is absent in shelf facies, presumably due to oxygen-depleted depositional conditions. Shelf facies generally grade upward into storm-dominated offshore successions that mostly consist of shale and bioturbated silty sandstone (Fig. 12, Diagram 1). These facies contain suites that resemble distal *Cruziana* ichnofacies (Fig. 11), with high bioturbation ranging up to 5. In the basinward direction (in lower offshore/shelf environments), due to the high concentrations of deposited organic matter, the trace fossil suites are dominated by deep-tier deposit feeding and grazing organisms. Generally, grazing reflects superficial foraging and is common to the offshore, although it is more prevalent in lower offshore settings. Low-diversity suites in these settings can also result from the presence of substrates that mainly favor surface grazing and deep-tier deposit feeding (e.g., MacEachern and Bann, 2008; Gingras et al., 2011a, b; Buatois and Mángano, 2011; Angulo and Buatois, 2012). In contrast to shelfal facies, wave aeration and consequent suppression of anoxia in lower offshore settings is the root cause for the existence of the habitable zone (Fig. 11). Here, suites record the activity of simple infaunal burrows and epifaunal trails, and commonly belongs to the distal *Cruziana* ichnofacies (e.g., MacEachern and Bann, 2008; Angulo and Buatois, 2012; Buatois et al., 2012). However, the low diversity, scattered or irregular burrowing and small size of the burrows may suggest a low oxygen content and soft to soupy substrates in lower offshore facies (Savrda, 1992; Buatois et al., 2002; Angulo and Buatois, 2012). In contrast to the upper offshore and the lower shoreface facies, low oxygen concentrations in bottom and interstitial waters of lower offshore facies influence trace fossil size, burrow diameter, abundance, and diversity; as oxygen content decreases in the substrate there is a noticeable reduction in the size of the burrows and the diversity of the organisms (Figs. 11–12). Substrate control (texture and consistency) most strongly influence the burrowing behavior in a sedimentary environment (Goldring, 1995). The emplacement and preservation of distinct burrow structures are reduced dramatically in very soft to soupy substrates. From the viewpoint of ecological strategies, the absence of large burrows and complex trace systems or behavioural complexity and a dominance of deposit-feeding burrows with an open conduit to the sediment–water interface (such as *Zoophycos*, *Chondrites*, and *Teichichnus*; see Gingras et al., 2011a, b) are considered characteristic of soft to soupy substrates with a low oxygen content and present in lower offshore facies.

5.2 Upper offshore

In contrast to mudstone-dominated heterolithic facies of lower offshore facies, bioturbated, fair-weather, silty and sandy mudstone of the upper offshore show lower proportions of grazing structures and deep-tier deposit-feeding structures (Figs. 11–12, Diagram 2). The presence of behavioral complexity with the great variety in forms and the numerous ichnospecies, and sophisticated feeding strategies, is characteristic of the archetypical *Cruziana* ichnofacies (e.g., MacEachern and Bann, 2008; Buatois and Mángano, 2011; Bayet-Goll et al., 2015b). Our observations indicate that these suites typify depositional settings characterized by cohesive soft substrates, reduced

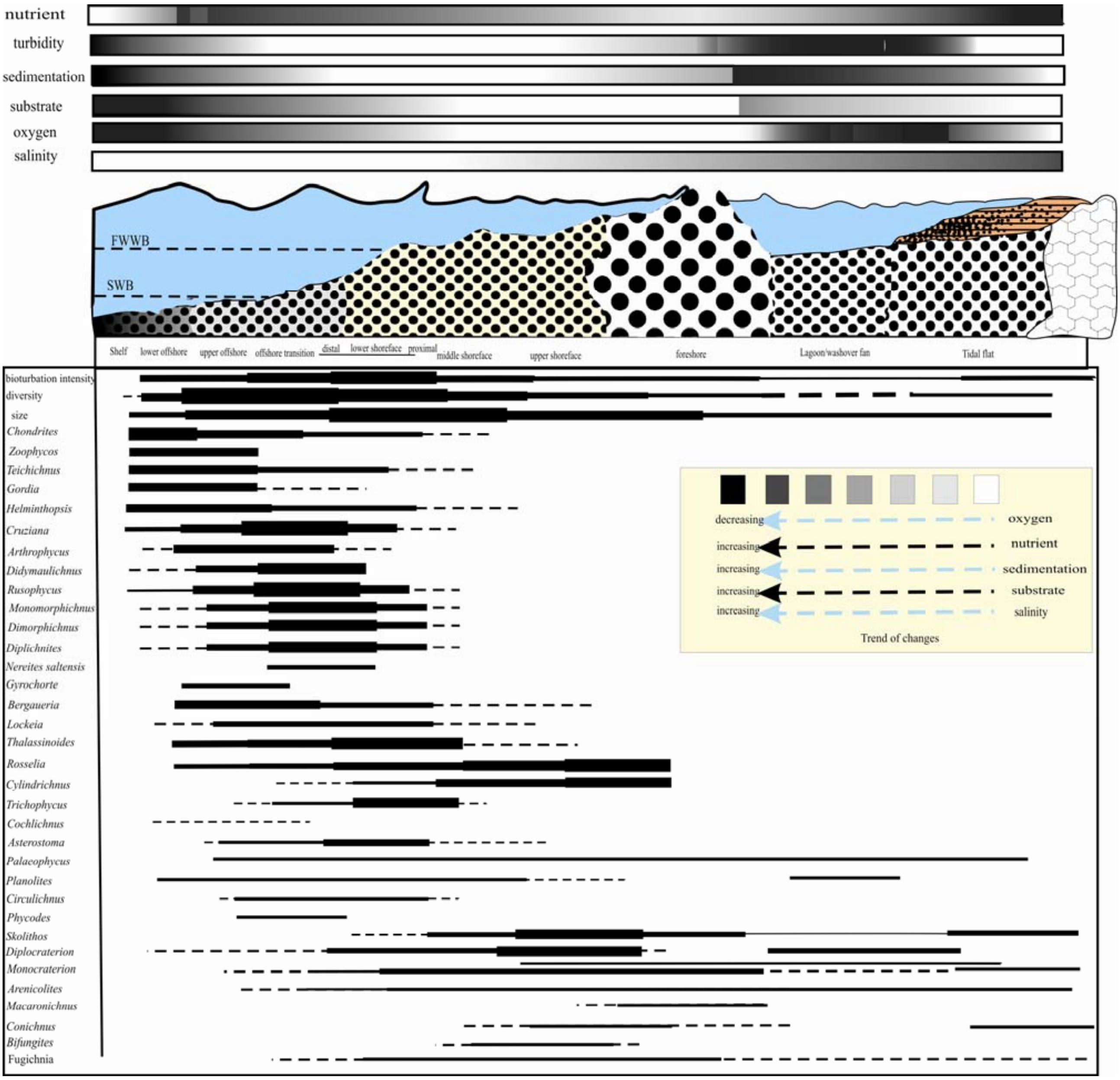

Fig. 11. The range of occurrence and maximum cited abundance for each ichnotaxon cited in the core literature is plotted against the onshore–offshore transect of the Shirgesht Formation. The habitable zone is depicted with respect to the shoreface position, infaunal diversity peak, oxygen level, and wave stress.

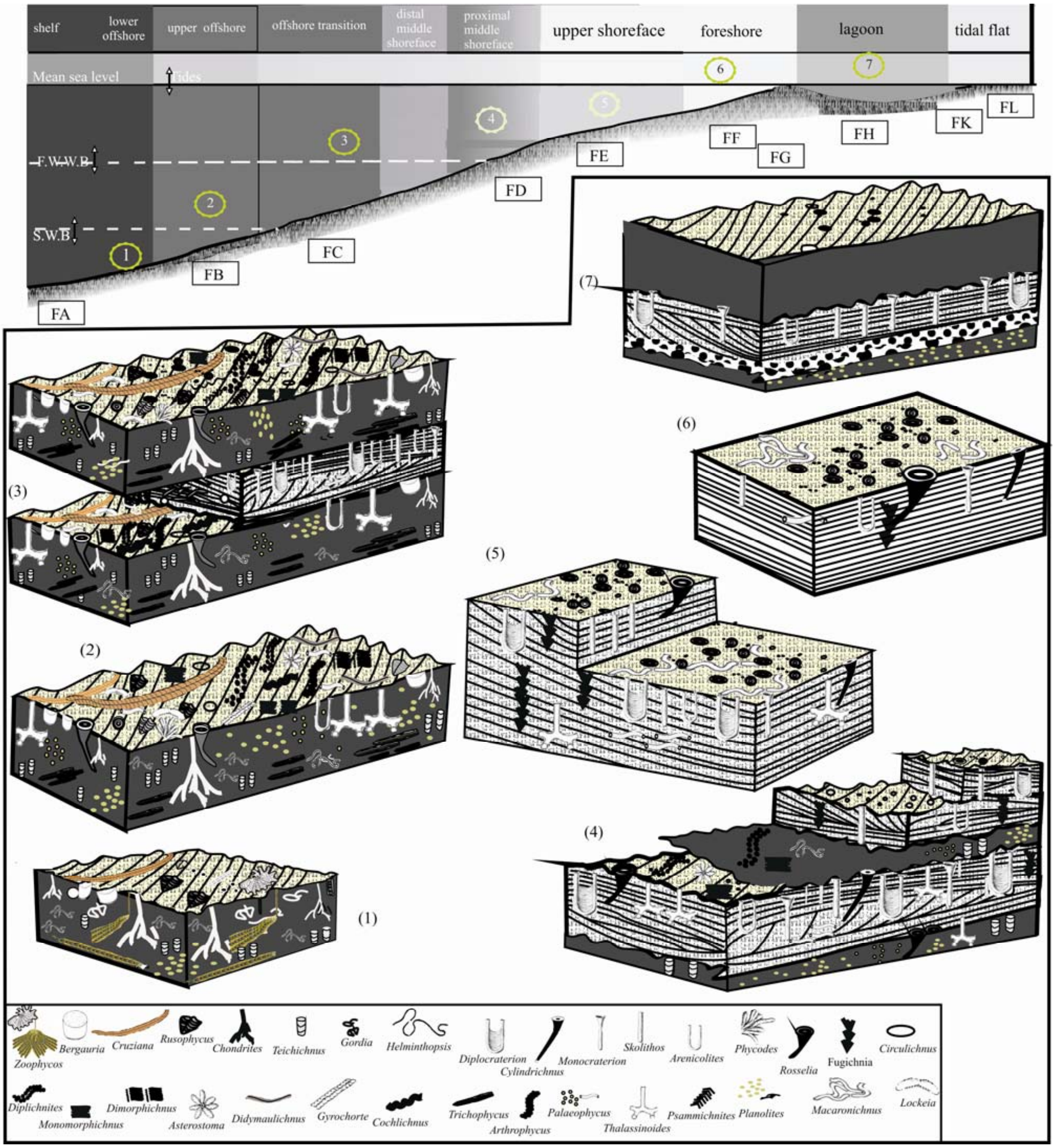

Fig. 12. Graphical representation of the characteristic sedimentological features and ichnogenera of facies with general position (i.e., proximal–medial–distal) of each ichnofacies related with different sub-environments. Some symbols for trace fossils used in this study, on the basis of schematic split-core expression (Pemberton et al. 1992; MacEachern et al., 2007a; Seilacher, 2007; MacEachern and Bann, 2008).

deposition rates, and variable but abundant food resources typical of quiet-water, fully marine conditions lying well below the fair-weather wave base. High diversity of trace fossils and uniform bioturbation in the upper offshore reflects a homogeneous distribution of food, normal salinity, and oxygenated water due to persistent wave agitation, and hence, a wide colonization window (*sensu* Pollard et al., 1993). The intensity and uniformity of burrowing in the archetypical *Cruziana* ichnofacies, and the scarcity of preserved primary sedimentary structures, suggest considerable time breaks between storms, during which the fair-weather fauna reworked the substrate. According to this model, a high proportion of the facies has been completely homogenized by the repeated reworking during fair-weather by a diverse infaunal assemblage. The presence of behavioral complexity associated with a rapid increase in the abundance and depth of infaunal structures of archetypical *Cruziana* ichnofacies indicates slow, continuous deposition under quiescent, fully marine conditions (e.g., Pemberton et al., 2001; MacEachern et al., 2007a; MacEachern and Bann, 2008; Buatois and Mángano, 2011; Bayet-Goll et al., 2015b). Generally, a high degree of bioturbation indicates that the sedimentation rate was relatively low, giving burrowing organisms enough time to keep up with the accumulation rate and reworking of any previously-deposited sediment (Pemberton et al., 1992a; Buatois and Mángano, 2011).

5.3 Offshore-transition to distal lower shoreface

Facies attributed to deposition in these settings are heterolithic and dominated by bioturbated silty and sandy mudstones, but contain fissile, unburrowed mudstone, and thin parallel-laminated to oscillation-ripple-laminated fine-grained sandstone. Ichnological suites attributable to the *Cruziana* ichnofacies in the mud-dominated beds with cohesive soft substrates, alternate with opportunistic suites of the *Skolithos* ichnofacies, recording colonization of the event beds with shifting non-cohesive substrates (Figs. 11–12, Diagram 3). Bioturbation is characterized by highly variable intensities, from BI2 (sandstone beds) to BI6 (total reworking of finer-grained interbeds). Highly variable ichnological signatures reflect alternating and contrasting energy conditions due to episodic storm events and the physical character of a substrate, including its geotechnical properties. On the basis of the sedimentological data, bioturbation intensity (BI) was linked to environment and component lithology. Bioturbation is generally well-developed in siltstone and shale (BI4–6). Ichnological data such as burrow size, burrow systems or behavioural complexity, and the presence of behavioral complexity with the great variety in forms and the numerous ichnospecies, indicate a stable and long-term colonization window for fair-weather suites.

Bioturbation is absent or low in sandstone (BI0–3), except at the top of beds, which record recolonization behavior (post-event). Burrows in storm-generated sandstone beds with large-scale HCS and internal erosion surfaces reflect the generation of communities of opportunistic organisms in an unstable and high stress environment. The periodic generation of a community of opportunistic organisms in the event beds suggest a physically-controlled environment with shifting non-cohesive substrates (e.g., Pemberton and MacEachern, 1997). More intense biological reworking of tempestites is the product of an abundance of suspended organic matter, the escape behavior of resident organisms simultaneous with storm-sand accumulation, deeper vertical penetration by deposit feeders, and a higher abundance of vertical burrows. In this case, depositional energy impacts substrate sediment grain size, as well as the distribution and availability of organic matter. From the viewpoint of ecological strategies, epifaunal life habits (such as locomotion and grazing/foraging traces) are expected to be more sensitive than infaunal ones (such as suspension-feeding structures and the dwellings of carnivores) under high-energy conditions in shifting non-cohesive substrates. The absence or scarcity of epifaunal deposit-feeding, grazing structures in non-cohesive substrates, reflects the rapid deposition of sediment and turbidity in these substrates that may have left trace makers little time to significantly bioturbate the sediment before overlying beds were deposited.

5.4 Proximal lower shoreface to middle shoreface

Progradation of these settings produce higher depositional energies, accumulation rates, and frequencies of episodic sedimentation, as reflected by the upward-coarsening grain size trend, increasing sandstone bed thickness, and greater degree of bed amalgamation. Trace fossil assemblages attributable to the distal *Skolithos* ichnofacies are intergradational with proximal *Cruziana* ichnofacies (e.g., MacEachern et al., 2007a), and show markedly variable distributions of burrowing and generally-reduced bioturbation intensities (Fig.12, Diagram 4). Trace-fossil suites in these deposits are characterized by the dominance of suspension-feeding structures (e.g., *Skolithos*, *Diplocraterion*), and both escape structures (fugichnia) and burrows of dwelling/deposit-feeders and carnivores (e.g., *Thalassinoides*, *Palaeophycus*, *Bergaueria*) (Figs. 11–12). Nonetheless, some dwelling structures of deposit-feeders (surface detritus-feeders), such as *Asterosoma*, *Rosselia*, and *Cylindrichnus*, are very common. Spreiten-bearing feeding burrows are represented only by the extremely rare *Teichichnus*. Bioturbation shows highly variable intensities, ranging from BI0 to BI3. Variability in storm intensity and frequency strongly affected the character of shoreface facies, both sedimentologically and ichnologically, including marked differences in the diversity of deposit-feeding structures in intermediate to proximal shoreface facies (Angulo and Buatois, 2012; Buatois et al., 2012). Amalgamated beds with more intense and uniform bioturbation indicate less extensive storm influence or a longer time between storms, during which the fair-weather assemblage reworked the substrate (e.g., MacEachern et al., 2005). Variable sedimentation rates associated with storm reworking of shoreface deposits typically cause scattered or irregular burrowing (e.g., Gingras et al., 1998; MacEachern and Gingras, 2007). Thus, intensely physically reworked amalgamated beds record shallower vertical penetration by dwelling/ deposit-feeding, a decrease in size and abundance of vertical burrows, and a decreased time between storm events, that hinders complete colonization and the development of deeply penetrating structures (Fig. 11).

5.5 Upper shoreface to foreshore

Facies deposited in these settings contain a low diversity burrow suite attributable to the archetypal *Skolithos* ichnofacies (e.g., MacEachern et al., 2007a; upper shoreface, Fig. 12, Diagram 5), and impoverished expression of the *Skolithos* ichnofacies (foreshore, Fig. 12, Diagram 6), including mostly vertical domichnia, passive carnivore-related burrows, escape structures, and surface detritus-feeder traces. Strata display either a bioturbation index (BI) of 0-2, or BI5–6, the latter produced by opportunistic colonization of substrates by large pipe-rock-producing communities of vertically-burrowing suspension feeders. Ichnotaxonomic composition, ichnodiversity levels, burrow depth, complexity, and bioturbation levels in these settings are indicative of harsh conditions in the sedimentary substrates due to traction, frequent wave reworking, and intermittently-high current velocities that prevent extensive colonization by organisms (e.g., Pemberton et al., 2001; Bayet-Goll et al., 2015b). The paucity of deposit-feeding structures in these deposits is attributed to the abundance of well-winnowed sand, and the general paucity of endobenthic food for deposit feeders (e.g., MacEachern and Bann, 2008). In general, relatively constant mixing of the water column by waves and/or currents results in coarser grained substrates, normal marine salinities, and predominantly oxic bottom waters (Fig. 11). These conditions favor suspension-feeding trace-makers, which produce vertical dwelling burrows (MacEachern, et al., 2005, 2007a).

5.6 Back barrier

This facies records the interfingering of washover fans with lagoonal deposits, and it contains low diversity suites of trace fossils. Bioturbation in this facies is characterized by a highly variable intensity. Homogeneous mudstone and bioturbated sandy siltstone exhibit BI4–5, sandstone with lower diversity ichnofauna have BI0–1, and well-laminated shale show BI0. The low-diversity trace fossil assemblage in these deposits may reflect strong fluctuations in salinity, nutrients and oxygen (Figs. 11–12, Diagram 7). Synaeresis cracks and depauperate ichnofaunal suites support salinity fluctuations and brackish-water conditions (e.g., MacEachern and Gingras, 2007). In these settings, the low diversity and small size of the burrows correlate with low oxygen levels. In addition to the above factors, depositional rates and water turbidity may have had an important effect on both sedimentological and ichnological features (degree of bioturbation, diversity of trace fossils, etc.) in this facies. Enhanced water turbidity may have at times decreased the degree of bioturbation, and if coupled with the rapid deposition typical of washovers, may have led to completely unburrowed deposits. In contrast, at other times, re-establishment of lower energy conditions under low rates of deposition, coupled with well-oxygenated water, might have favored the increase in the degree of bioturbation in muddy sediments. Thus, instability in physical-chemical conditions is reflected in the spatial distributions of trace fossils, and ethological departures from the archetypal *Skolithos* ichnofacies (MacEachern et al., 2007) in these back barrier facies.

5.7 Tidal flat

Sedimentary features, such as desiccation cracks and flaser, lenticular and wavy bedding evidenced in these facies suggest tidal flat deposition with regularly fluctuating flow velocities and periodic exposure. In general, tide-dominated deposits contain low diversity trace fossil faunas. Tidal flats are characterized by numerous ecological constraints on potential trace-making organisms, including parameters such as low salinity, and short-term fluctuations in salinity levels related to precipitation, discharging groundwater, low oxygen levels, desiccation, and temperature fluctuations (e.g., Cadée, 1998; Wang and Hu, 2015). Trace-fossil assemblages (i.e., elements of the *Skolithos* ichnofacies) result from the establishment of an unstable benthic community. Such associations, which are regarded to be resource-limited, occur in habitats having high physical-chemical stress. Elements of the *Skolithos* ichnofacies are thought to represent a community of opportunistic organisms persisting in an unstable, high stress environment.

6 Conclusions

The trace fossil assemblages from various facies of the Ordovician Shirgesht Formation, central Iran, suggest that physical-chemical stresses were variable across the wave-dominated shallow-marine setting. Identification and interpretation of departures from the archetypal ichnofacies presented herein are used to further refine sedimentary interpretations of parameters such as wave energy, substrate properties, nature of the available food supply, salinity, dissolved oxygen content, and variability in sedimentation rates.

The following important conclusions can be drawn as a summary of the newly-accomplished ichnological-sedimentological study and presented synopsis of the siliciclastic succession of the Shirgesht Formation: (1) Low oxygen concentrations in bottom and interstitial waters of lower offshore facies influenced trace fossil size, burrow diameter, abundances, and diversity. (2) Low sedimentation rates, relatively stable substrate, sufficient nutrient supply and the presence of oxygen near the sediment-water interface caused by mixing of water by waves led to a highly diverse trace fossil suite, dominated by a mixture of complex deposit-feeding, detritus-feeding, grazing and foraging structures in upper offshore–lower shoreface environments. (3) Monospecific suites of vertical domiciles, and low levels of bioturbation in the thin sandstone event beds within upper offshore-lower shoreface environments, correspond to post-event opportunistic colonization and an ichnologically-stressed environment during deposition, which is typical of tempestites. (4) Low diversity of ichnogenera and low levels of bioturbation within the upper shoreface and foreshore successions is interpreted as the result of high-energy conditions in the surf and beach zones, due to persistent wave agitation and water swash and backwash. (5) Lagoon ichnological suites are characterized by impoverished trace diversity and reduced burrow size. The lagoon environment is characterized by numerous ecological stresses on potential trace-making organisms, including low salinities, fluctuating salinity levels, high water turbidity, and low oxygen levels in bottom and interstitial waters. (6) Low salinity, and short-term fluctuations in salinity levels related to precipitation, temperature fluctuations, low oxygen levels, discharging groundwater, and episodes of desiccation, induce inhospitable infaunal living conditions in tidal flat settings.

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