

SCLEROBIONTS ON ORGANIC SUBSTRATES FROM THE LATE PALEOCENE CHEHEL-KAMAN FORMATION, KOPET-DAGH BASIN, NE IRAN

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Abstract: Molluscs (oysters and gastropods) of the Late Paleocene Chehel-Kaman Formation, Kopet-Dagh Basin, NE Iran were significantly colonized by sclerobionts. The largest area of the shells studied is covered by various borings. The diversity of macro-bioeroding ichnotaxa is rather high, including *Gastrochaenolites* Leymerie, 1842; *Maeandropolydora* Voigt, 1965; *Trypanites* Mägdefrau, 1932; *Talpina* von Hagenow, 1840, and possibly *Entobia* Bronn, 1837. Some slightly conical borings penetrating the shells could belong to predatory tracemakers of *Oichnus* Bromley, 1981. Encrusters include calcareous polychaetes, cyclostome and cheilostome bryozoans, foraminifera and oysters. Calcareous sabellids [i.e. *Glomerula serpentina* (Goldfuss, 1831)] and serpulids are equally common sclerobionts in the association. Bryozoans cover a slightly larger area of the substrate than the calcareous polychaetes, while encrusting oysters are subordinate. The majority of fossils in the hard-substrate community studied belong to suspension feeders. Sclerobionts are typical of the shallow-marine environment, commonly in warm water. The present study is the first attempt to record the occurrence and diversity of epi- and endobionts in the organic substrates, present in the topmost part of the Late Paleocene Chehel-Kaman Formation, Kopet-Dagh Basin, NE Iran.

Key words: Sclerobionts, Late Paleocene, Chehel-Kaman Formation, Iran.

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INTRODUCTION

In a climatic sense, the Palaeogene was a highly dynamic period and witnessed an abrupt climate warming at the Paleocene/Eocene boundary, known as the Paleocene-Eocene Thermal Maximum (Nicolò *et al.*, 2007; Zachos *et al.*, 2008; Stap *et al.*, 2009).

In the northeastern part of Iran (Kopet-Dagh Basin), the Palaeogene passed through a sequence of sea-level fluctuations (e.g., transgressive and regressive), which allowed the deposition of carbonates (Moussavi and Brenner, 1992; Ahari-pour, 1996; Mahboubi *et al.*, 2001). The Palaeogene rocks of the Kopet-Dagh Basin have been extensively studied, because they host the giant Khangiran and Gonbadli gas fields. Most work focussed mainly on the stratigraphy and foraminiferal content, as well as microfacies and petrogra-

phy (Afshar-Harb, 1979; Rahaghi, 1983; Kalantari, 1987; Rivandi *et al.*, 2013; Rivandi and Moosavizadeh, 2015; VahdatiRad *et al.*, 2016). However, little is known about the macrofaunal content and taphonomy.

The Paleocene rocks of the Kopet-Dagh Basin have a rich and low-diversity macro-invertebrate fauna, dominated by oysters, bivalves, and gastropods. They display many signs of post-mortem processes (e.g., encrustation and macro-bioerosion) and other taphonomical features. The oysters and gastropods provided abundant, hard substrates for the larvae of different organisms, including epi- and endobionts. Many epibionts produced and attached their calcareous tubes, shells or skeletons to the substrates and became fossilized along with them. Therefore, encrustation was a constructive

process. However, encrustation may decrease shell strength (Stachowitsch, 1980) and some encrusters may inhibit the action of bioeroders or protect the host against predation (e.g., Henderson and Styan, 1982; McLean, 1983; Smyth, 1989; Cadée, 1999). On the other hand, bioerosion is an important destructive process. Bioeroders destroy hard substrates by mechanical and chemical means (Lescinsky *et al.*, 2002).

In this context, the aim of this study is twofold: (1) to describe the encrusting sclerobiont assemblages and ichnoassemblages of macro-bioeroding organisms in a hard-substrate community from the Late Paleocene of Iran; and (2) to discuss the palaeoecology of the macro-bioeroders and encrusters.

LOCATION AND STRATIGRAPHIC CONTEXT

The Kopet-Dagh Basin extends along the northeastern corner of Iran, bounded by the Caspian Sea, north Afghanistan and Turkmenistan (Afshar-Harb, 1979; Buryakovsky *et al.*, 2001) (Fig. 1A). It was formed during the Early to Middle Jurassic (Garzanti and Gaetani, 2002) and sedimentation continued into the Neogene (Afshar-Harb, 1979; Kalantari, 1987). This sedimentation was marked by five major transgressive-regressive sequences (Moussavi and Brenner, 1992).

During the Early Paleocene, a thick interval of siliciclastic sediments (widely known as red beds) was deposited in fluvial environments (Pesteligh Formation; Moussavi and

Brenner, 1992). In the late Paleocene, the sea level rose rapidly. This transgression allowed the deposition of carbonate rocks of the Chehel-Kaman Formation (Moussavi and Brenner, 1992; Aharipour, 1996; Mahboubi *et al.*, 2001).

The Shorlukh section is located in the eastern part of Kopet-Dagh Basin (longitude 60°37'1" E and latitude 36°17'5" N; Fig. 1A), in Khorasan Razavi Province, City of Sarakhs, Shorlukh Village (Fig. 1B). In this section, the Upper Paleocene (Thanetian) Chehel-Kaman Formation is principally composed of carbonates, with minor siliciclastics and evaporites. It is conformably overlain by the Khangiran Formation (Eocene), which consists of greenish-grey marl, shale, and nodular limestone (Fig. 2) and is underlain by the Danian Pesteligh Formation.

The present work is focussed on the topmost part of the Chehel-Kaman Formation, which contains a rich macroinvertebrate fauna, dominated by oysters, bivalves and gastropods. These animals hosted various epi- and endobionts.

MATERIAL AND METHODS

The faunal assemblage of the section studied is mainly composed of bivalves (including oysters), gastropods and rare echinoids. The oysters and gastropods display considerable signs of macro-bioerosion and encrustations. The oysters range from exceptionally well-preserved shells, showing microscopic surface characteristics, to occasionally abraded shells. Gastropods mostly occur as well-preserved, complete steinkerns. In the Shorlukh section, oysters constitute 60% of the bivalve remains. Gastropods are the second most common component, accounting for 22% of the total

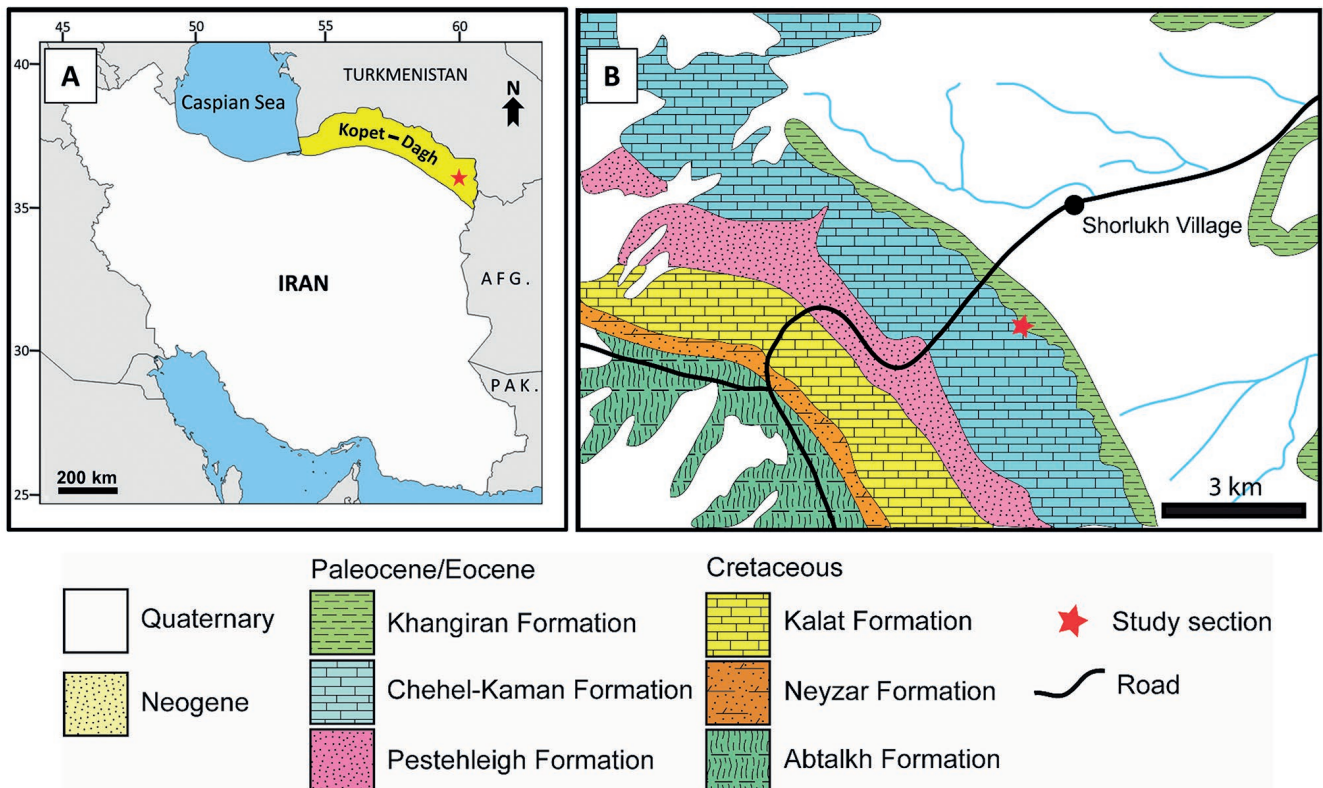


Fig. 1. Location maps. A. Map of the study section. B. Geologic map of the Shorlukh section, eastern part of the Kopet-Dagh Basin, Iran.

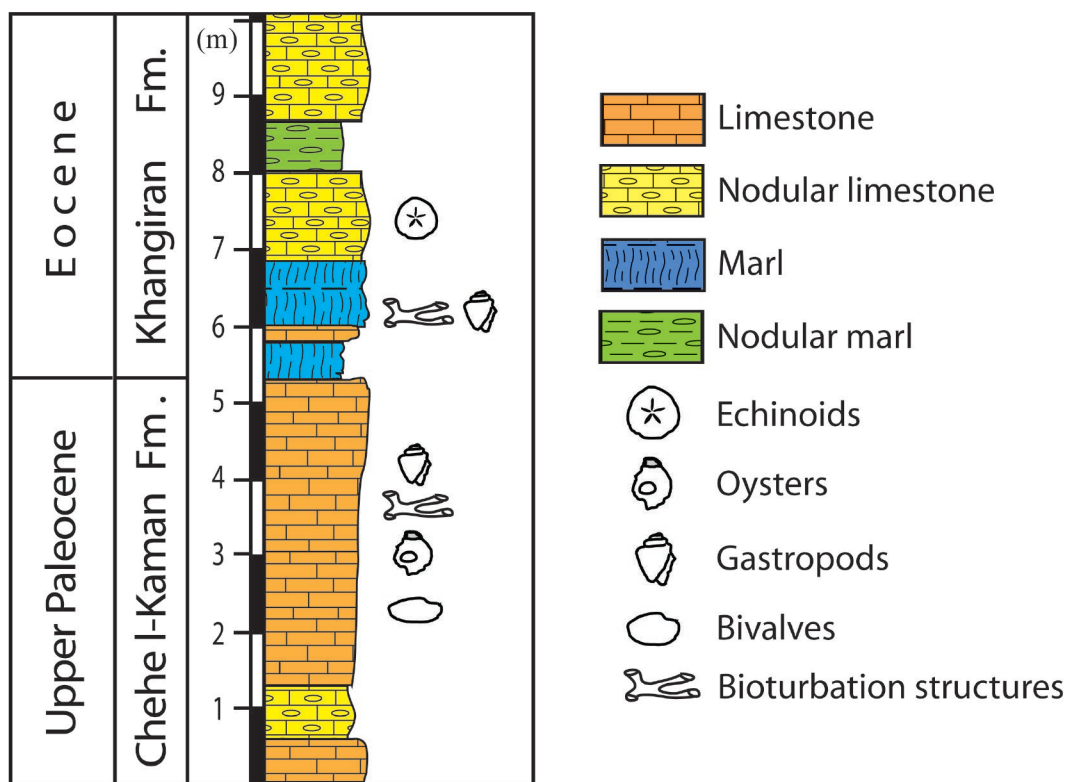


Fig. 2. Stratigraphic column of the topmost part of the Late Paleocene Chehel-Kaman Formation, exposed in the Shorlukh section.

faunal assemblage, while other macrofaunal content makes up the rest.

More than 180 specimens of oyster and gastropod fossils were collected from the Shorlukh Section (N36°36'51"; E60°32'16"), Kopet-Dagh Basin, NE Iran (Fig. 1A, B).

The oyster and gastropod specimens were identified and surveyed for skeleton-encrusting and macroboring organisms on both the internal and external surfaces of the valves. The oysters mainly belonged to *Ferganea ferganensis* (Romanovskiy, 1879), *Flemingostrea hemiglobosa* (Romanovskiy, 1884), *Ostrea (Turkostrea) strictiplicata* (Raulin and Delbos, 1855) and *Pycnodonte* sp. The gastropod steinkerns studied were represented by the ampullinids *Globularia vapincana* (d'Orbigny, 1850) and *Globularia* sp.

In the laboratory, specimens were cleaned by vigorous washing and brushing of the surfaces of the valves. Some of the firmer matrix was removed with a needle. Some specimens were submerged in a 50% acetic acid-water solution to help remove the strongly attached carbonate matrix. The traces of macro-bioeroders and encrusters were identified to the generic and/or specific level. The density of macroborings was determined by counting the surface apertures centred within a grid of four square cm (see Tapanila *et al.*, 2004). The data are expressed as percentages of the total number of bioerosion traces. The aperture size and cavity depth were measured in millimetres, using a digital caliper (accurate to 0.01 mm).

All the materials studied are deposited in the Department of Geology, Ferdowsi University of Mashhad, Iran. The prefix SL distinguishes the registration numbers of specimens.

RESULTS

Encrusting and boring taxa

Encrusting taxa

The oysters and gastropods studied were colonized by different groups of encrusting invertebrates. The preserved encrusters are represented by cheilostome and cyclostome bryozoans, sabellid and serpulid worm tubes, oysters and rare agglutinated foraminifera (Table 1).

Cheilostome and cyclostome bryozoans. Bryozoans represent the most abundant encrusters of the skeletobiont community studied, in terms of abundance and area covered. They almost entirely consist of flat, sheet-like colonies that spread out over the oyster shells (Fig. 3A, B, J–L). Two cheilostome bryozoans (*Conopeum* aff. *paranelsoni* Taylor and McKinney, 2006 (Fig. 3K) and *Rhagasostoma* sp. (Fig. 3L), with two possible cyclostomes (Fig. 3A, B) are reported.

Sabellid and serpulid worm tubes. Polychaete worms are the second main constituent of the substrates studied. Calcareous sabellids and serpulids are nearly equally abundant sclerobionts in the association (Fig. 3A–F).

Sabellid worms are represented by *Glomerula serpentina* (Goldfuss, 1831) (Fig. 3A, B) and *Glomerula* sp. (Fig. 3B). This genus is characterized by single, long tubes with twisted patterns, especially at the beginning of their development (Radwańska, 2004).

Serpulids are represented by thin tubes, circular or nearly circular in cross-section (Fig. 3C–F). They mostly grew as solitary individuals (Fig. 3C, F), but in some cases they

Table 1

Sclerobiont assemblage and ichnoassemblage of macro-bioeroding organisms in the hard-substrate community, with trace producers and ethological categories

| Epibionts | | |
|---|-------------------------------|----------------------|
| Cheilostome and cyclostome bryozoans | | |
| Sabellid and serpulid worm tubes | | |
| Oysters | | |
| Foraminifera | | |
| Endobionts | | |
| Ichnotaxa | Trace producers | Ethological category |
| <i>Gastrochaenolites</i> Leymerie, 1842 | Boring bivalves | Domichnia |
| <i>Maeandropolydora</i> Voigt, 1965 | Polychaete annelid | Domichnia |
| <i>Trypanites</i> Mägdefrau, 1932 | Sipunculid/polychaete annelid | Domichnia |
| <i>Talpina</i> von Hagenow, 1840 | Phoronids | Domichnia |
| <i>Entobia</i> Bronn, 1837 | Boring sponges | Domichnia |
| <i>Oichnus simplex</i> Bromley, 1981 | Predatory gastropods | Praedichnia |

formed rather dense coverings growing across shell margins on internal sides of oysters and most commonly on outer shell surfaces of gastropods (Fig. 3D–E).

Oysters. Oysters are frequent encrusters among the epibionts preserved on shell surfaces (Fig. 3G–I). They are represented by different ontogenetic stages. In terms of relative abundance, oysters are intermediate among the species of the cemented epibiont community. They encrusted either the outside or the inside of the shell (Fig. 3G, H, I). However, they most commonly encrust shell interiors (post-mortem encrustation). The cementing oysters are often penetrated by the traces of macroborings (Fig. 3H). Moreover, because these cementing oysters are the largest and very abundant encrusters in the present assemblage, many overgrowths were recorded (Fig. 3B, I).

Foraminifera. In terms of numbers of individuals, the agglutinating foraminifera represent the least abundant of all encrusters in the section studied. They are only recorded on the exterior surfaces of the left valve of an oyster specimen (Fig. 3J).

Boring ichnotaxa

In this study, the moderately preserved Late Paleocene/Early Eocene oysters display diverse traces of borings produced by endobionts (Table 1). The borings are represented by seven ichnotaxa, dominated by *Gastrochaenolites*, *Oichnus*, *Trypanites* and *Talpina*. Sponge borings are represented by possible *Entobia*. The majority of typical Cenozoic macroboring ichnotaxa were present in the community studied. Thus, one might classify the boring organism of the community as moderately to highly diverse for the Paleocene.

***Gastrochaenolites* Leymerie, 1842.** This ichnogenus is common in the present study; it accounts for about 13% of the total borings observed. All of the *Gastrochaenolites* borings do not contain evidence of the trace-producing organisms or of subsequent occupants. In the present study,

Gastrochaenolites is represented by *G. dijugus* Kelly and Bromley, 1984, *G. torpedo* Kelly and Bromley 1984, and *G. isp. indet.*

***Gastrochaenolites* cf. *dijugus* Kelly and Bromley, 1984** (Fig. 4A, B). This is characterized by a clavate or flask-shaped chamber (up to 21 mm long), with a circular to oval cross-section (0.8 to 12.8 mm wide), with a neck region forming a figure of eight in cross-section. In the neck part, it displays a thick, short calcite syphon lining. The boring surface often shows a prominent xenoglyph (4F). According to Kleemann (2008, p. 11, fig. 3), the pholadid bivalve *Parapholas quadrizonata* (Spengler, 1792) makes borings, which have the diagnostic characteristics of both *Gastrochaenolites dijugus* Kelly and Bromley, 1984 and *G. turbinatus* Kelly and Bromley, 1984. Of these, *G. dijugus* shows a figure-of-eight aperture in cross-section, a characteristic, which was observed clearly in the material studied. The total number of *G. dijugus* identified was 18 in the areas measured, representing about 21% of the total *Gastrochaenolites* specimens identified.

***Gastrochaenolites torpedo* Kelly and Bromley, 1984** (Fig. 4E, F). This occurs as an elongate, torpedo-like chamber, with a neck, which is oval in cross-section. The chamber is commonly at least 12–28 mm long. The maximum diameter (9–17 mm) is located at the centre of the chamber. The neck, in most cases, is not preserved, owing to truncation by erosion. The borings vary in size, indicating different sizes of the producer. The total number of *G. torpedo* identified in the areas measured was 38, representing about 45% of the total *Gastrochaenolites* specimens identified.

Gastrochaenolites isp. (Fig. 4A, B). In the section studied, the presence of *Gastrochaenolites*-like structures affecting the oyster shells is very common. They occur as unlined, deep depressions with rounded to oval apertures in cross-section, 5–7 mm in depth. The poor preservation prevents their assignment at the ichnospecies level. The total number of *G. isp.* was 29 in the areas measured, repre-

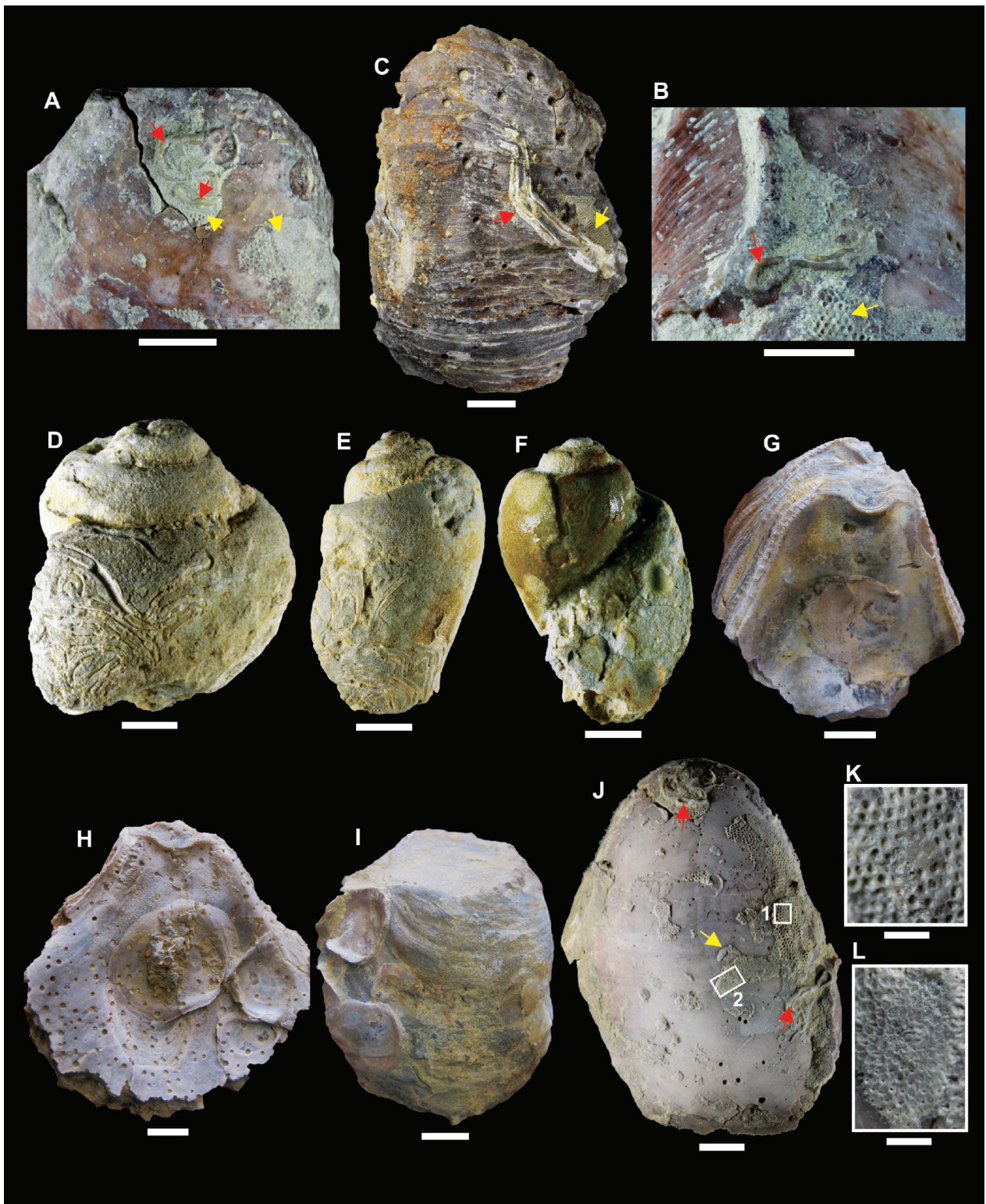


Fig. 3. Encrusting organisms from the Shorlugh section. **A.** Oyster shell encrusted with the sabellid worm *Glomerula serpentina* (Goldfuss, 1831) (red arrows) and a flat-sheet bryozoan colony (yellow arrows). **B.** Oyster shell encrusted with the sabellid worm *Glomerula serpentina* (Goldfuss, 1831) (red arrow) and small bryozoan sheet (yellow arrow). **C.** Internal mould of serpulid worm tubes (partly preserved as undersides of worms; red arrow) and small flat-sheet bryozoan colony (yellow arrow) encrusting the exterior surface of an unidentified oyster shell. Note that the extensive circular or nearly circular openings at the shell surface belong to *Trypanites* isp. **D.** Dense serpulid polychaete *Serpula?* sp. **E.** Serpulid polychaete *Serpula?* sp. **F.** Unidentified serpulid polychaete. **G.** Oyster shell encrusted on the interior of a larger one. **H.** Oyster, both the substrate and the fixed valves are perforated by the sponge boring *Entobia* isp. **I.** Oysters encrusted on the exterior surface of *Flemingostrea? hemiglobosa* (Romanovskiy, 1884). **J.** Sabellid polychaete *Glomerula serpentina* (Goldfuss, 1831; red arrows), bryozoans (cyclostomes and cheilostomes), benthic foraminifera (yellow arrow) and remains of a bivalve. **K.** Close-up of Figure 3J (1), showing colony of the cheilostome *Conopeum* aff. *paranelsoni* Taylor & McKinney, 2006. **L.** Close-up of Figure 3J (2), showing colony of the cheilostome *Rhagasostoma* sp. Scale bar 1 cm for all specimens, except for K and L, where scale bar = 3 mm.

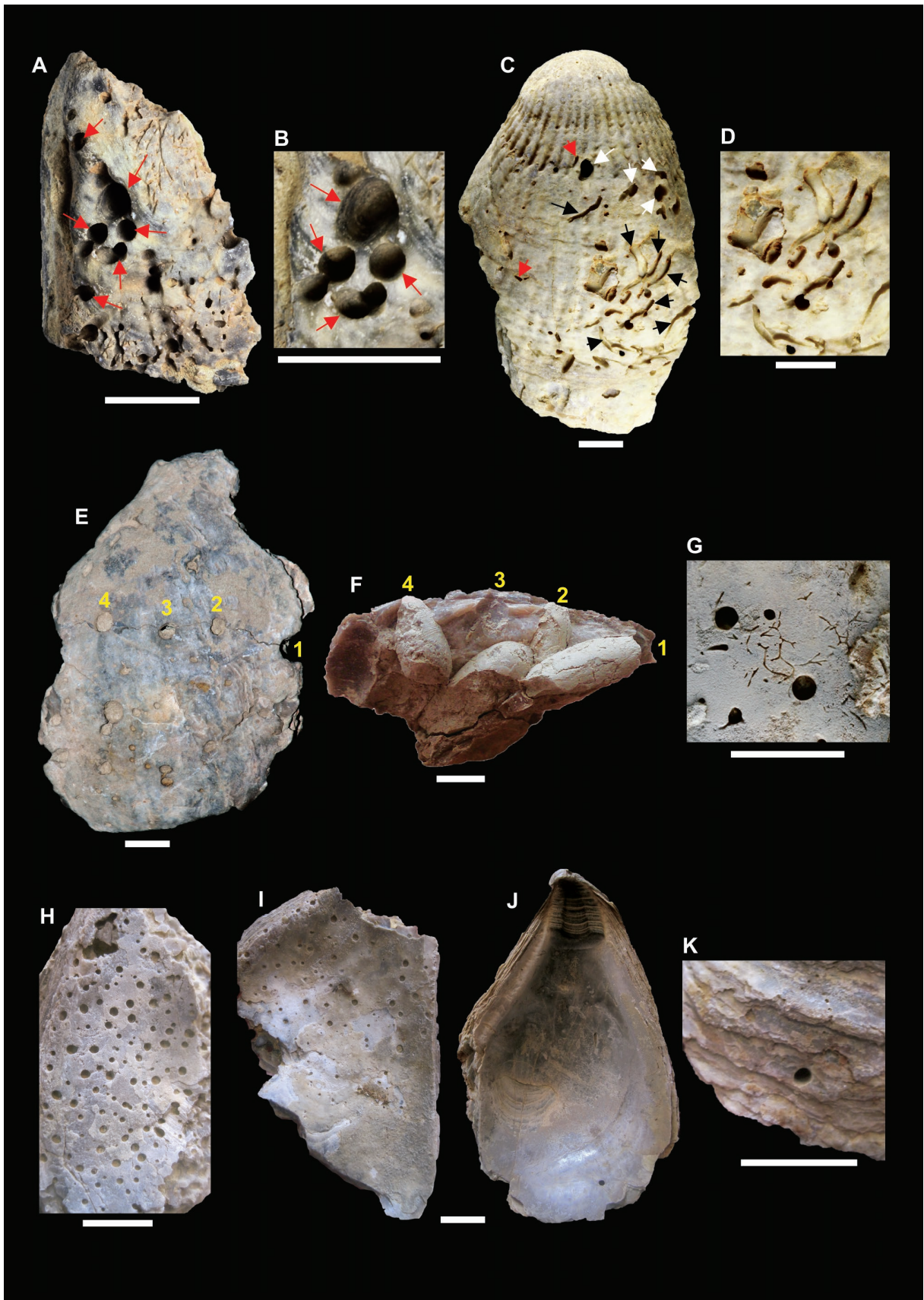


Fig. 4. Traces of bioeroding organisms from the Shorlugh section. **A, B.** *Gastrochaenolites* cf. *dijugus* and some *Gastrochaenolites* isp. **C.** *Maeandropolydora sulcans* in *Ostrea* (*Turkostrea*) *strictiplicata* (Raulin and Delbos, 1855; black arrows); note the presence of the borings *Trypanites* (white arrows) and possible *Rogerella?* isp. (red arrows). **D.** Close-up of Figure 4C. **E, F.** *Gastrochaenolites torpedo* in an unidentified oyster shell. **G.** *Talpina ramosa* and the cylindrical, complete drill hole *Oichnus simplex* in an unidentified oyster. **H, I.** *Entobia* isp. **J.** Cylindrical, complete drill hole (*Oichnus simplex*) in an unidentified oyster. **K.** Close-up of Figure 4J. Scale bar = 1 cm.

senting about 34% of the total *Gastrochaenolites* specimens identified.

***Maeandropolydora sulcans* Bromley, 1981 (Fig. 4C, D).** This occurs as cylindrical galleries with two or more apertures, running parallel and in contact with each other in pairs, with or without fusion. The borings are either sinuous or irregularly excavated on the surfaces of the oyster shells. Loose or tight loops may occur; the limbs of these may be connected by a vane or form a pouch. The size is highly variable; the length ranges from 12 to 28 mm and the width is between 0.7 and 2.5 mm. It has been interpreted as resulting from the activities of several families of polychaetes, mostly Spionidae (Bromley and D'Alessandro, 1983). In the present study, this ichnospecies is common; it accounts for about 19% of the total borings observed.

***Trypanites solitarius* (Hagenow, 1840) (Figs 3C, 4A–C).** This is a simple, smooth, vertically to obliquely oriented boring with an unsculptured surface; it is straight, non-branching and circular in cross-section. Its dimensions vary from 1.5 to 2.8 mm in diameter and 8 to 10 mm in length. *Trypanites* is generally considered to have been produced by sipunculid worms (Bromley, 1992; Pemberton *et al.*, 1980). This trace is typical of carbonate substrates (firm- to hardgrounds, pebbles and skeletal substrates; Bromley and D'Alessandro, 1987; Knaust and Bromley, 2012). This ichnospecies is common and occurs abundantly in the fauna studied. It accounts for about 36% of the total borings observed.

***Talpina ramosa* Hagenow, 1840 (Fig. 4G).** The specimen described herein is characterized by straight to curved tunnels, approximately 0.3 to 0.4 mm in diameter, with circular to semi-circular cross-sections that run primarily parallel to the shell surface. Most tunnels terminate in a circular opening, but a few of the branches taper to a terminus. Branches are roughly evenly spaced in several examples, but in most cases appear to be randomly spaced.

Most of the borings *Talpina* appear to have penetrated the shell very shallowly, possibly at, or just below, the boundary between the periostracum and the ostracum (Zonneveld and Bistran, 2013). This trace fossil is produced mainly by colonial phoronid worms (e.g., Voigt, 1972, 1975, 1978). *Talpina ramosa* is uncommon in this study, accounting for about 11% of the total borings observed.

***Entobia Bronn, 1837* (Fig. 4H, I).** The ichnogenus *Entobia* is a system of round chambers, interconnected by cylindrical galleries bored below the surface of calcium carbonate substrates, made by the sponge *Cliona* (e.g., Bromley and D'Alessandro, 1984).

In the current study, *Entobia* isp. is observed as clusters of rounded to irregular, small (maximum 7 mm across), elongated cavities on the surfaces of the oyster shells; the diameter varies between 0.1 and 1.5 mm and, in some cases, openings of different diameters can be observed in the same specimen (Fig. 4A).

In several specimens, most of the shell surface is covered by chamber openings and in specimens that were subject to considerable abrasion, the external layers of the shell were removed, exposing the internal chamber network (Fig. 4E). In some oyster specimens, fragmentation was mainly due to the presence of great numbers of *Entobia* in their shells (Fig. 4A, I).

In terms of its external/internal occurrence, *Entobia* is more conspicuous externally than internally. On the other hand, it appears on both sides of the oyster valves. *Entobia* isp. is uncommon by comparison with the other ichnospecies. It represents about 6% of the total borings.

***Oichnus simplex* Bromley, 1981 (Fig. 4G, J, K).** This is a small, smooth cylindrical drill hole, circular to sub-circular in cross-section, with an axis oriented perpendicular to sub-perpendicular to the oyster shells, completely penetrating the shell. Diameters range from 1.5–2 mm. After the latest revision of *Oichnus*, made by Wisshak *et al.* (2015), this ichnogenus is diagnosed by complete or incomplete bioerosive penetrations in calcareous, skeletal substrates. These authors follow Zonneveld and Gingras (2014) in synonymizing *Oichnus* and *Fossichnus*. *Oichnus* is interpreted as a praedichnia, produced by many predatory gastropod families, including Naticidae, Muricidae, Tonnacea, Capulidae, Nudibrachia, and Pulmonata (Bromley, 1981; Pickerill and Donovan, 1998). *Octopus* also can be a producer of this ichnogenus (Bromley, 1993). The total number of these drill holes identified was 22 in the areas measured, representing about 15% of the total borings recorded.

DISCUSSION

In the northeastern portion of Iran (Kopet-Dagh Basin), the Palaeogene is characterized by a sequence of sea-level fluctuations. During the Thanetian (late Paleocene), a sequence composed of carbonates with minor siliciclastics and evaporites was deposited. Petrographical examination indicated that these Paleocene sediments were deposited on a shallow carbonate platform of ramp type and they consist of four carbonate lithofacies (fifteen subfacies) (Rivandi *et al.*, 2013). These authors concluded that the carbonate lithofacies have been deposited in open-marine, shoal, lagoon and tidal-flat environmental conditions.

The rocks of this sequence are characterized by a rich and low-diversity macro-invertebrate fauna, dominated by oysters, bivalves and gastropods. After deposition, their shells constituted a secondary hard ground for sclerobionts (bioeroders and encrusters). Bioeroders were significantly more abundant than encrusting organisms.

It is likely that the hard-substrate community studied was dominated by boring organisms, even considering the possibility that some soft-bodied encrusters were not fossilized. The dominance of boring organisms in the community could be due to an abundance of grazers and predators.

Bored shells are very common in the Cenozoic (Taylor and Wilson, 2003), and the bioeroded shells studied are typical of the late Paleocene/early Eocene. Cenozoic shells were mostly bored by clionid sponges, bivalves, polychaetes, phoronids, ctenostome bryozoans and acrothoracican barnacles (Taylor and Wilson, 2003). In the hard-substrate association studied, phoronids produced *Talpina*, polychaetes the *Maeandropolydora* and *Trypanites*, and bivalves made *Gastrochaenolites*. Sponge borings are represented by possible *Entobia*. Thus, one could classify the boring organisms of the community as moderately to highly diverse in the Paleocene.

Moderate to high bioerosion intensities could indicate high nutrient levels in the sea water (Lescinsky *et al.*, 2002). According to Edinger and Risk (1997), borehole size provides a rough estimate of past nutrient availability (palaeo-productivity) in combination with other kinds of data (e.g., facies control), but should not be relied upon alone. Alternatively, high bioerosion can be explained by a long exposure time of the substrates. The high diversity of bioerosional trace fossils would be more consistent with high nutrient levels in the local seawater than with a long exposure time of bored shells. Tapanila *et al.* (2004) found that maximum boring density was as high as 35 borings per 4 cm² in Early Palaeozoic stromatoporoids, but only 1% of substrates showed high boring densities. Among the samples of the present authors, shells with high boring densities are far more common, but this is likely a general characteristic of Cenozoic bioerosion.

The drill holes in the collection described here are confirmed to be of predatory origin as the authors found the distinctive traces of predatory activities, such as a circular outline, an axis perpendicular to the shell surface, sizes being narrowly distributed and with a narrow range of outer borehole diameters (Leighton, 2001; Kelley and Hansen, 2003). Many workers (e.g., Sohl, 1965; Kase, 1984; Fischer and Weber, 1997; Das *et al.*, 1999; Chattopadhyay and Dutta, 2013) considered the ampullinid gastropod *Globularia* to belong to the Naticidae. This genus occurs in considerable numbers in the study section. Taylor (1970) considered *Globularia* as a digger form, due to a morphology similar to that of the naticid forms (Taylor, 1970). On the other hand, the encrusting fauna of the Chehel-Kaman Formation exhibits medium diversity in the Paleocene. At least four types of encrusters were recorded on the hard substrates studied; they are colonies of cheilostome and cyclostome bryozoans, sabellid and serpulid worm tubes, and oysters with scarce benthic foraminifera.

The rather medium diversity of encrusters could be explained by low productivity (low nutrient levels) in the seawater (Lescinsky *et al.*, 2002) or by short exposure time of the substrates (e.g., Nebelsick *et al.*, 1997; El Hedeny, 2005). Pre-occupation of substrate by various boring organisms may have prevented the development of denser encrustation. Abundant grazers could clean substrates of encrusting animals. Numerous predators (e.g., a predatory gastropod, the producer of the ichnospecies *Oichnus*) also may have had a negative effect on encrustation. Moreover, an encrusting fauna also may have been lost due to weathering or simply because of exfoliation. All the above-mentioned reasons may account for the medium diversity of encrusting organisms in the section studied. The presence of some epibionts on the interiors of a number of oysters is related to colonization after the host's death (post-mortem).

Sclerobionts are greatly affected by a number of environmental factors, e.g., depth, turbulence and sedimentation rate in marine environments (Brett *et al.*, 2012). For example, successive bioerosion episodes reflect more productive sites in the ocean, whereas these would decrease with high rates of sedimentation (Lescinsky *et al.*, 2002).

In the present study, most of sclerobionts were suspension feeders. These organisms preferred to live in clear

and oxygenated waters and exhibited a high degree of tolerance to turbidity and sedimentation (Smith, 1995). They are represented by calcareous polychaetes (i.e. *Glomerula serpentina* and serpulids), bryozoans, *Gastrochaenolites*, *Maeandropolydora*, *Trypanites*, *Talpina*, and possibly *Entobia*. *Maeandropolydora* and *Trypanites* makers also were suspension feeders, but a different feeding strategy is also possible. Modern *Polydora* generally feeds on detritus that is removed from the sediment by the two long palps (BIOTIC, 2018). *Polydora* also feeds on suspended particles in the water and on occasions has been observed to eat dead barnacles and other dead invertebrates (BIOTIC, 2018).

Concerning endobionts, most producers of the present ichnotaxa (*Gastrochaenolites*, *Maeandropolydora*, *Trypanites*, *Talpina*, *Entobia* and *Oichnus*) recorded in the section studied invariably have been documented and reported as indicators of shallow, nearshore and shelf deposits. For example, modern phoronids (producers of the boring *Talpina*) are particularly common as shallow borers in the shells of both living and recently dead bivalves, gastropods and barnacles (Ruesink and Trimble, 2010).

The shallow-marine environment is dominated by the bivalve boring *Gastrochaenolites* and the sponge boring *Entobia* (Perry, 2000; Buatois and Mángano, 2011; El Hedeny and El Sabbagh, 2018). In addition, *Trypanites* typically occurred in shallow-marine environments (e.g., Taylor and Wilson, 2003).

The epibionts (bryozoans, polychaetes, oysters and encrusting benthic foraminifera), indicate shallow-marine environment. For examples, bryozoans most commonly encrust hard substrates at shallow shelf depths (e.g., El Sabbagh, 2008). They prefer to live in clean, well oxygenated waters, although some fossil bryozoans tolerate at least some turbidity (Smith, 1995; Taylor, 2005). In modern seas, oysters mostly live in the intertidal zone. This is indicated by their elongated, irregularly shaped shells (e.g., Machalski, 1998; El Hedeny, 2005).

CONCLUSIONS

The Late Paleocene organic substrate of the Chehel-Kaman Formation, Kopet-Dagh Basin, NE Iran, is greatly affected by macro-bioerosion and encrustation. Macro-bioerosion is relatively high, with the presence of *Gastrochaenolites*, *Maeandropolydora*, *Trypanites*, *Talpina* and *Entobia*. Some slightly conical borings penetrating the shells could belong to the predatory tracemaker of *Oichnus*. The trace-fossil assemblage is dominated by the domichnia of suspension feeders, although predation may have been involved as well. Encrustation is usually moderate, despite isolated, small serpulid patch reefs. The most frequent and abundant epibionts were sabellid and serpulid worms, cheilostome and cyclostome bryozoans, oysters and foraminifera. The sclerobiont assemblages in the hard substrates studied indicate that they existed in a low-energy, shallow-marine environment, with a very low rate of sedimentation.

This study is the first attempt to record the occurrence and diversity of epi- and endobionts in the organic substrates present in the topmost part of the Late Paleocene Chehel-Kaman Formation, Kopet-Dagh Basin, NE Iran.

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