

## Bioerosional structures from the Late Pleistocene coral reef, Red Sea coast, northwest Saudi Arabia

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**Abstract:** Herein, 20 ichnospecies belonging to 8 ichnogenera were identified in bivalves, gastropods, and corals (n = 701) from the Late Pleistocene coral reef along the Red Sea coast, northwest Saudi Arabia. The trace fossils were produced by clionid sponges (47.39%), endolithic bivalves (42.17%), polychaete annelids (5.42%), vermetid gastropods (3.81%), and acrothoracican barnacles (1.21%). The recognized ichnotaxa were *Entobia geometrica*, *E. ovula*, *E. cf. goniodes*, *E. cf. retiformis*, *E. cretacea*, *Entobia* isp., *Gastrochaenolites torpedo*, *G. lapidicus*, *G. cf. dijugus*, *Gastrochaenolites* isp., *Oichnus paraboloides*, *O. simplex*, *Oichnus* isp., *Caulostrepis taeniola*, *Caulostrepis* isp., *Maeandropolydora cf. sulcans*, *Maeandropolydora* isp., *Renichnus* isp., *Centrichnus* isp., and cf. *Rogerella* isp. Most bivalves and gastropods contain *Entobia* rather than *Gastrochaenolites*, which is commonly found in the larger and thicker corals. The content of the trace fossils indicated an *Entobia* ichnofacies formed in the coral reef during transgression. The habitat conditions changed gradually, from well-oxygenated, shallow, high-energy back-reef and reef crest bioeroding polychaetes and bivalves, to deep, low-energy reef slope dominated by boring sponges.

**Keywords:** Bioerosional structures, coral reefs, Pleistocene, Red Sea coast, Saudi Arabia

### 1. Introduction

Coral reefs are known as the most biologically diverse ecosystems in the world, and many organisms include high species diversity within the reefs. They normally weaken the reef framework, and turn their massive reef structures into rubble, sand, and silt. The various activities of reef species causing coral and coralline algal erosion are commonly known as bioerosion (Glynn and Manzello, 2015). Bioerosion was identified for the first time by Neuman (1966) to explain every form of biological erosion of hard substrates, including lithic and woody substrates (Bromley, 1992).

The study of bioerosion has revealed significant information about the ecological interactions between organisms and strata for the geological past history. Therefore, trace fossils also present useful data for paleoecological analyses (e.g., Belaústegui et al., 2017). Bioeroders attack living and dead shell material alike, although some of them are highly selective (Santos and Mayoral, 2008). Their diversity and abundance increase with biogenic productivity and decrease with higher rates of sedimentation (Lescinsky et al., 2002). The diversity

of micro and macroborers in intertidal and shallow sublittoral environments is usually quite high (Santos and Mayoral, 2008). Molluscan shells can provide the only hard substrate available for larval settlement and ontogeny development by different types of boring and encrusting organisms in soft-bottom areas (Parras and Casadío, 2006; Lopes, 2011; El-Sorogy, 2015; El-Sorogy et al., 2018). Based on the reduction or lack of sedimentation, rocky shorelines offer exceptional conditions for colonization by boring and encrusting organisms (Santos et al., 2011). The best confirmation of a rocky paleoshore and reconstruction of the paleoenvironments related to sedimentary discontinuities is the existence of an assemblage of marine fossils on a hard substrate, either as direct encrustations on the unconformity surface or as borings into it (Ghibaudo et al., 1996; Johnson 2006; Santos et al., 2008).

Extensive environmental, sedimentological, and faunal studies have been conducted on both coasts of the Red Sea (e.g., Anan, 1984; Ziko and El-Sorogy, 1995; Abd El-Wahab and El-Sorogy, 2003; Ostrovsky et al., 2011; Pan et al., 2011; Ziko et al., 2012; El-Sorogy et al., 2012, 2013a, 2013b, 2015; 2019; El-Sorogy, 2008; 2015; Ruiz-Compean

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et al., 2017; Alharbi et al., 2018; Kahal et al., 2018, 2020; Youssef et al., 2020). El-Sorogy et al. (2019) identified 24 foraminiferal species, 67 corals, 79 gastropods, and 63 bivalves from the same Late Pleistocene coral reef unit in the present study area. The identified scleractinians indicated a deepening upward pattern for the studied Late Pleistocene reef unit.

Bromley and Asgaard (1993) stated that careful study of preserved bioerosional structures may provide information on the extent of the nondepositional period, the nature and duration of hiatuses at hardgrounds, initial marine flooding event, rate of transgression across limestone surfaces, and general bathymetry. Ichtnological studies on the Red Sea coast are scarce (El-Sorogy, 2015). In this context, the present study aimed to: a) document the taxonomy of the bioeroders affecting the bivalves, gastropods and corals from the Late Pleistocene coral unit along the Red Sea coast, northwest Saudi Arabia, b) study the distribution of bioerosional structures upon the studied hard substrate, and c) interpret the relationship between the investigated bioerosional structures and the sea level during the formation of the reef unit.

## 2. Geological setting

The geological setting of the Pleistocene coral reefs along the Red Sea coast has been studied in detail over recent decades (e.g., Berry et al., 1966; Gvirtzman and Friedman, 1977; Hötzel, 1984; Mathews, 1984; Vail et al., 1984; Dullo, 1990; Hoang and Taviani, 1991; Gvirtzman et al., 1992; Strasser et al., 1992; El-Sorogy, 1997a, 1997b; Plaziat et al., 2008; Kahal et al., 2018; El-Sorogy et al., 2019; Taviani et al., 2019). In general, the Pleistocene coral reefs, 500–800 m wide and up to 26 m above the present sea level, are represented by 3 obvious units. They were developed during the interglacial highstands (El Moursi et al., 1994; El-Sorogy 1997b; Plaziat et al., 1998). A block faulting by tectonics, constructive onlap during different sea levels, and differential erosive flattening were the 3 possibilities for their morphology (Dullo, 1990).

The present study concentrated on the lower reef unit of the Late Pleistocene age, which extends all over the study area and is interrupted only in the wadi entrances. It exhibits 2 terraces (3 and 10 m above the present sea level) that may be attributed to small-scaled changes of sea level or sea-level high stands (Mathews, 1984; El-Sorogy et al., 2019). The lower reef unit is formed of coralline limestone with scleractinian corals, milleporids, red algae, bivalves, gastropods, and echinoids, and rests on a conglomeratic bed of basement clasts. The lower unit exhibits a vertical transgressive pattern, starting from a coral assemblage and back-reef zone at the base, followed by a reef crest, and an upper reef slope community. It developed during the last interglacial times (Oxygen isotope stage 5 of deep-sea cores) (El-Sorogy et al., 2019).

## 3. Materials and methods

The study area lies along the Red Sea coast, northwest of Saudi Arabia, between 27°30'04"N–35°75'07"E and 27°78'52"N–35°39'88"E (Figure 1). A total of 285 bivalves, 243 gastropods, and 173 corals were collected from 10 sites from the Late Pleistocene reef unit between Duba and Sharma. Their preservation ranged from well-preserved to slightly abraded materials. Specimens of 95 bivalves, 90 gastropods, and 84 corals, with evidence of bioerosion, were washed and identified. The studied material comprised 8 species of bivalves (*Anadara antiquata*, *Quidnypagus palatam*, *Tridacna maxima*, *Ctena divergens*, *Asaphis violascens*, *Chama aspersa*, *Acrosterigma lacunose*, *Arca ventricosa*), 10 gastropods (*Hexaplex kuesterianus*, *Conus virgo*, *C. flavidus*, *Magilus antiquus*, *Cymatium aquatile*, *Turbo radiatus*, *Strombus erythrinus*, *S. persicus*, *Nerita albicilla*, *Cypraea grayana*), and 12 corals (*Stylophora pistillata*, *Porites lutea*, *P. solida*, *Favites pentagona*, *Goniastrea pectinata*, *Platygyra daedalea*, *Fungia klunzingeri*, *Favia stelligera*, *F. pallida*, *Favia* sp., *Acropora* sp., *Pocillopora damicornis*). The bioerosional structures were examined, identified, and then photographed. All of the examined specimens were housed in the Museum of the Department of Geology and Geophysics, College of Science, King Saud University, Saudi Arabia, under KSUM numbers.

## 4. Results

The most common bioerosional structures were produced by clionid sponges (47.39%), followed by endolithic bivalves (42.17%), polychaete annelids (5.42%), drilling gastropods (3.81%), and acrothoracican barnacles (1.21%) (Figure 2). Based on their morphology, 20 ichnospecies belonging to 8 ichnogenera were identified, comprising clionoid sponges (*Entobia geometrica*, *E. ovula*, *E. cf. goniodes*, *E. cf. retiformis*, *E. cretacea*, *Entobia* isp.), duraphagous drillers (*Oichnus paraboloides*, *O. simplex*, *Oichnus* isp.), endolithic bivalves (*Gastrochaenolites torpedo*, *G. lapidicus*, *G. cf. dijugus*, *Gastrochaenolites* isp.) and polychaete annelids (*Caulostrepsis taeniola*, *Caulostrepsis* isp., *Maeandropolydora cf. sulcans*, *Maeandropolydora* isp.), vermetid gastropods (*Renichnus* isp.), anomiid bivalves (*Centrichnus* isp.), and acrothoracican barnacles (cf. *Rogerella* isp.). The abundance of the identified ichnotaxa among the 3 investigated groups of hard substrate were recorded (Figure 3). Some bioerosional structures in coral colonies were observed in the field (Figure 4).

### 4.1. Systematic paleoichnology

Ichnofamily Entobiaidae Wisshak, Knaust and Bertling, 2019

Ichnogenus *Entobia* Bronn, 1837

*Entobia geometrica* Bromley and D'Alessandro, 1984 (Figures 5A–5D, 6C, 6G, and 6I)

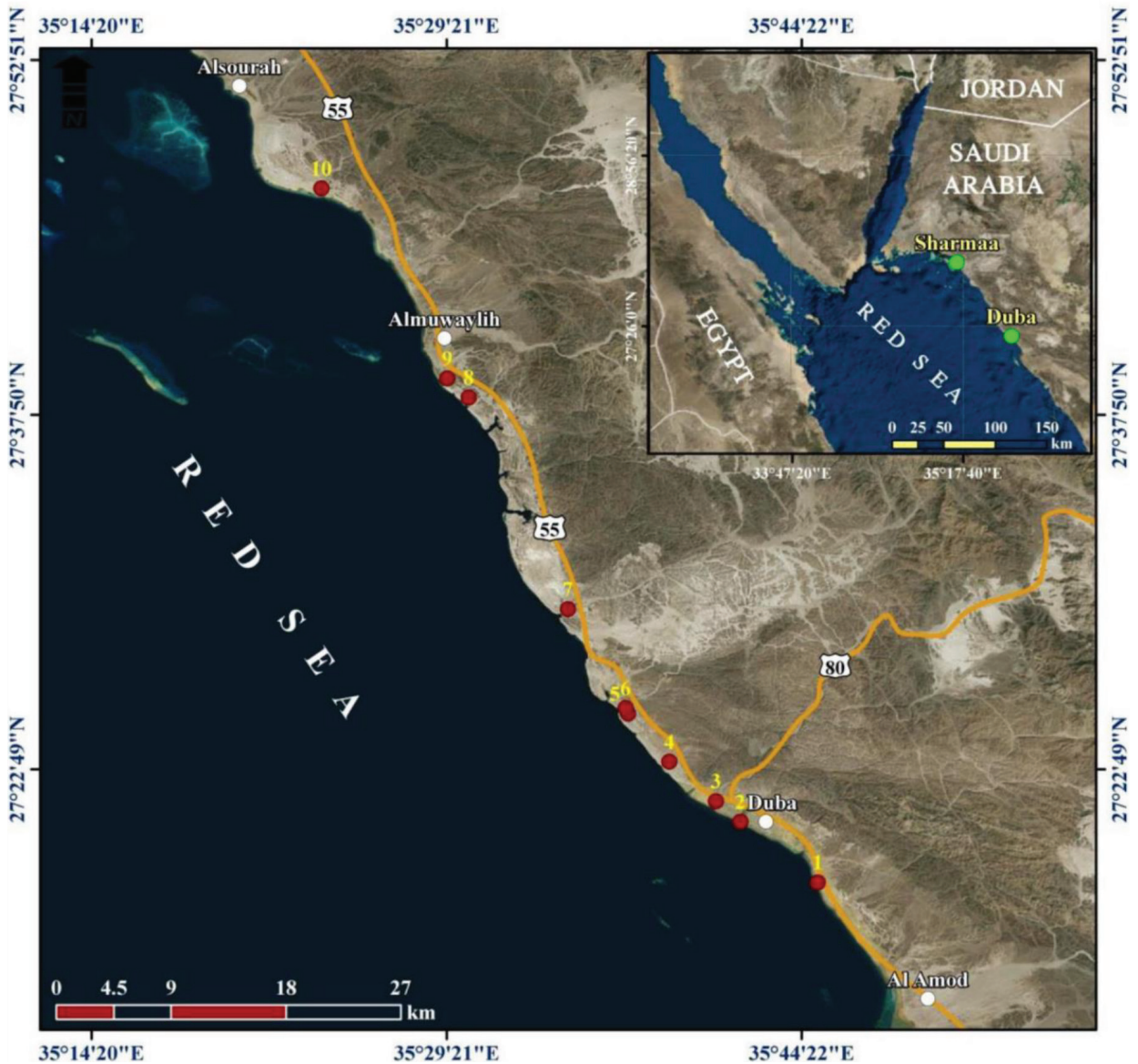


Figure 1. Location map of the study area and collection sites.

2010 *Entobia geometrica* Bromley and D'Alessandro, Johnson et al., Figure 7D.

2011 *Entobia geometrica* Bromley and D'Alessandro, Santos et al., 537, pl. 1, Figure 5.

2012 *Entobia geometrica* Bromley and D'Alessandro, Demircan, 339, pl. 2, Figures G and H.

Substrate: Bivalves (*T. maxima*, *Ch. aspersa*), gastropods (*C. virgo*, *M. antiquus*, *C. aquatile*, *N. albicilla*), and corals (*P. damicornis*, *S. pistillata*).

Description: Networks of chambers, with large circular apertures (2.5–3 mm in diameter), and small apertures (1–2 mm in diameter), and 1.5–2.5 mm deep. The chambers are interconnected by irregularly distributed cylindrical galleries.

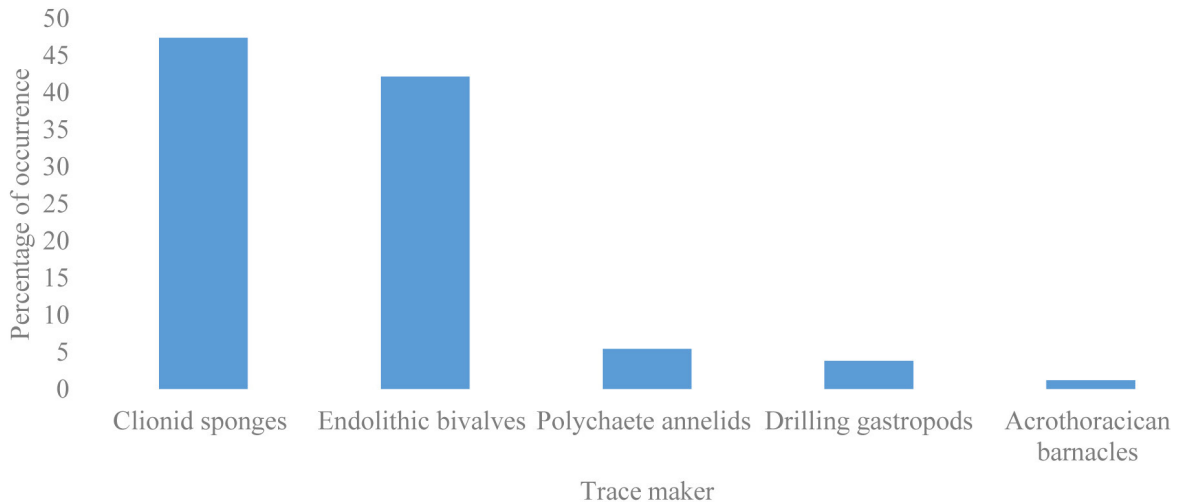
Remarks: It was interpreted as produced by *Cliona celata*. This ichnospecies occurred in gastropods, bivalves, and corals, and in all 3 cases, involved the entire shell, resulting in stenomorphic borings (Bromley and D'Alessandro, 1984).

Occurrences: *E. geometrica* represented 18.64% of the entobian traces (55% on bivalves, 40% on gastropods, and 5% on corals).

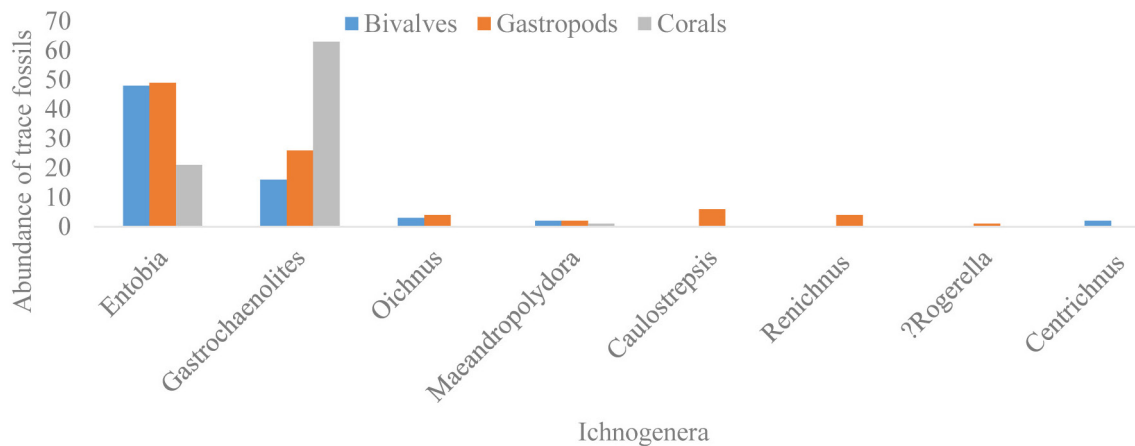
*Entobia ovula* Bromley and D'Alessandro, 1984 (Figure 5E)

2004 *Entobia ovula* Bromley and D'Alessandro, Blissett and Pickerill, 175, Figure 5/4.

2007 *Entobia ovula* Bromley and D'Alessandro, El-Hedeny, 277, pl. 2, Figure 6.



**Figure 2.** Trace makers and their percentages in the present work. The most common bioerosional structures were produced by clonid sponges and endolithic bivalves.



**Figure 3.** Distribution abundance of the identified ichnogenera among the investigated bivalves, gastropods, and corals.

2011 *Entobia ovula* Bromley and D'Alessandro, Santos et al., 537, pl. 1, Figure 6.

2017 *Entobia ovula* Bromley and D'Alessandro, Gurav and Kulkarni, 5, Figures 3E and 3F.

2018 *Entobia ovula* Bromley and D'Alessandro, El-Hedeny and El-Sabbagh, 7, Figure 7B.

Substrate: Bivalve, *Ch. aspersa*, and gastropods *C. virgo* and *N. albicilla*.

Description: Borings of stage A occur as a system of narrow tunnels, which are less than 1 mm in diameter, and branched tunnels, about 1 mm in diameter, with indistinct swellings and enlargements at the branching point. Stage B consists of curved rows of elongated chambers, 2–3 mm long, 1.8–2.2 mm wide, connected by constrictions. Stage C is poorly developed and composed of oval, closely spaced chambers, which are up to 3.5 mm wide. Borings in stage D are composed of small spherical to ovoid chambers, with an average diameter of about 3 mm.

Remarks: The ichnogenus *Entobia* was mostly produced by *Cliona schmidtii* (Ridley, 1881), *C. vermifera* Hancock 1867, and *C. vastifica* Hancock, 1849 (Bromley and Asgaard, 1993a) in the Mediterranean Sea. Its taxonomy was discussed by Bromley and D'Alessandro (1984).

Occurrences: *Entobia ovula* represented 8.03% of the entobian trace fossils, on bivalves (25%) and gastropods (75%).

*Entobia* cf. *goniodes* Bromley and Asgaard, 1993 (Figures 5H and 6L)

1993 *Entobia* cf. *goniodes* Bromley and Asgaard, 97, Figures 9 and 10.

2002 *Entobia* cf. *goniodes* Bromley and Asgaard, Uchman et al., 265, Figures 5A and 6.

Substrate: The coral *Acropora* sp.

Description: It is represented by a system of small, camerate to nodular chambers, up to 3 mm in diameter.





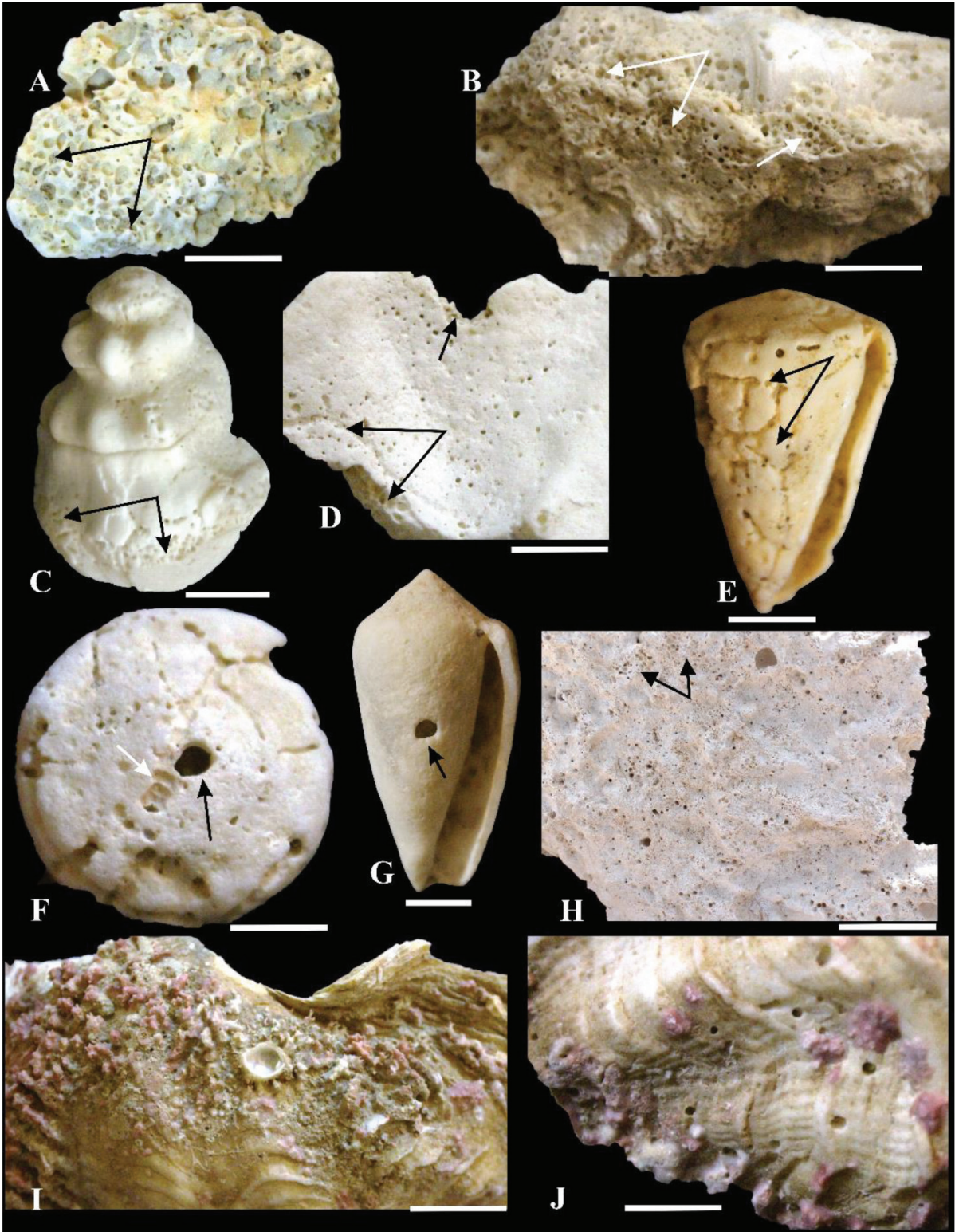
**Figure 4.** Field pictures. A.1) *Gastrochaenolites* isp. B. 2–3) *Gastrochaenolites* isp., cf. *Maeandropolydora* isp. at site 10. C. 4–5) *Gastrochaenolites torpedo* with faviid coral site 10. D. 6) *Gastrochaenolites* isp. with its producer inside. 7) *Gastrochaenolites* isp. and site 4 (scale bars: 10 mm).

Chambers are not spherical but are irregularly nodular and tend to occur in closely adjacent rows. A few chambers fuse in pairs at a mature growth stage (phase C) to produce 2 types of chambers, fused and unfused. Further fusion is not seen. Apertures are of several sizes, the largest produced by fusion, reaching several millimeters in width.

Remarks: *E. goniodes* is produced today by *Cliona viridis* and rarely *C. schmidtii* in the photic zone of the Mediterranean Sea (Demircan, 2012). *C. viridis* was found at a water depth of 20 m (Bromley and Asgaard, 1993a).

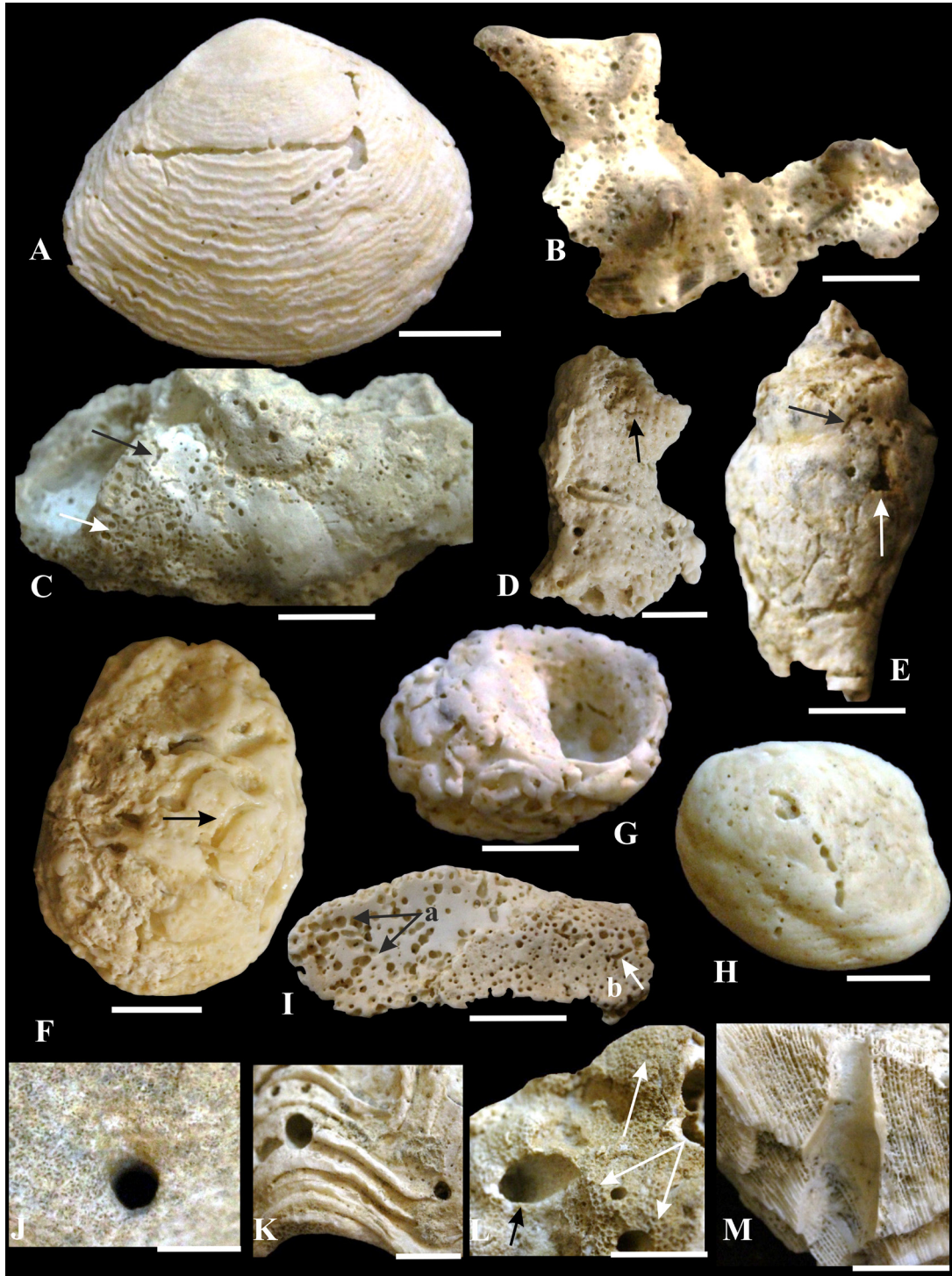
Occurrences: *Entobia* cf. *goniodes* represented 2.69% of the entobian trace fossils.



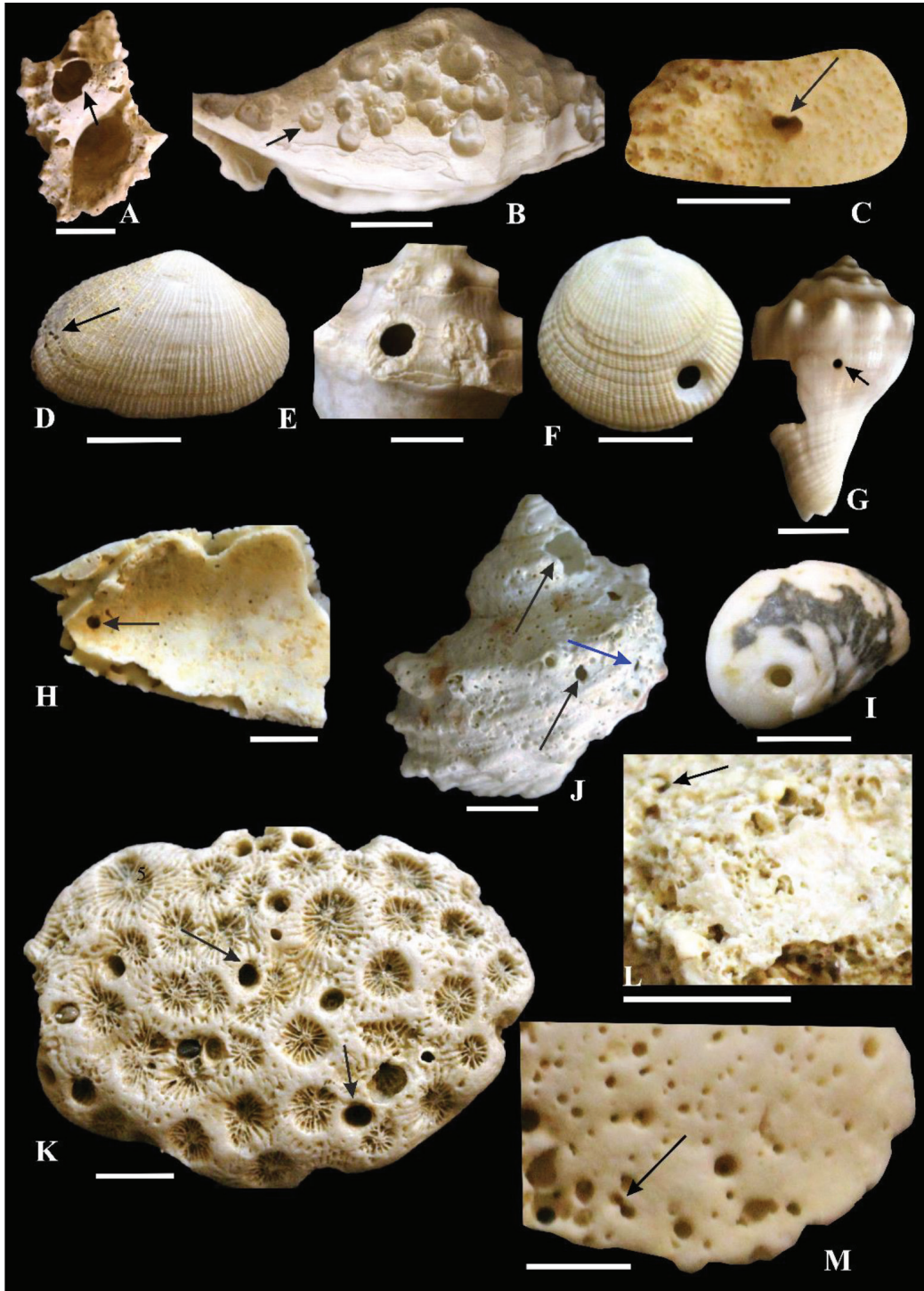


**Figure 5.** A–D) *Entobia geometrica* on the hard substrate of *Ch. aspersa* (site 10), *M. antiquus* (site 3), *C. aquatile* (site 7), and *T. maxima* (site 3), respectively. E) *Entobia ovula* on the hard substrate of *C. virgo*. F) *Gastrochaenolites* isp., (black arrow), *Renichnus* isp., (white arrow) *Entobia* isp. (site 9). G) *Gastrochaenolites* isp., (black arrow) (site 4). H) *Entobia* cf. *goniodes* (black arrow), with *Entobia* isp., on coral *Acropora* sp., (site 10). I–J) *Entobia* cf. *retiformis* with fixed *Chama* (arrow) on the bivalve *T. maxima* (site 4) (scale bars: 10 mm).





**Figure 6.** A) *Entobia cretacea* on the external surface of the bivalve *Q. palatam* (site 1). B) *Entobia* isp. on the external surface of *H. kuesterianus* (site 6). C) *Maeandropolydora* cf. *sulcans* (black arrow), *Entobia geometrica* (white arrow) on the gastropods *M. antiquus*, site 10. D) *Maeandropolydora* cf. *sulcans* site 10. E) cf. *Maeandropolydora* isp., (black arrow), *Gastrochaenolites* isp., (white arrow) on the gastropod *S. erythrinus*, site 7. F) *Caulostrepsis taeniola* (black arrow), *Entobia* isp., on the bivalve *T. maxima*, site 8. G) *Caulostrepsis taeniola*, *Entobia geometrica* on the gastropod *N. albicilla*, site 10. H) *Entobia cretacea* on *Ch. aspersa*, site 2. I) *Entobia geometrica* (a), *Maeandropolydora* cf. *sulcans* (b), on *T. maxima*, site 8. J) *Gastrochaenolites lapidicus*, in *P. lutea* (site 5), *T. maxima* (site 9), *P. solida* (site 5), and *P. daedalea* (site 6). K–M) Borings of *Gastrochaenolites torpedo* in *P. lutea* (site 5), *T. maxima* (site 9) with *Entobia* cf. *goniodes* (white arrow), *P. solida* (site 5), and *P. daedalea* (site 6), respectively (scale bars: 10 mm).



**Figure 7.** A) *Gastrochaenolites lapidicus* (black arrow) with *Entobia* isp., on the gastropod *H. kuesterianus*, site 1. B) *Centrichnus* isp., on the external surface of the bivalve *T. maxima*, site 4. C) *Gastrochaenolites* cf. *dijugus* (black arrow) on the coral *Favia stelligera*, site 8. D) *Entobia* isp., on the external surface of the bivalve *Asaphis violascens*, site 9. E) *Oichnus simplex* on the external surface of *H. kuesterianus*, site 10. F–G) Borings of *Oichnus paraboloides* on the bivalve *C. divergens* (site 2) and the gastropod *S. persicus* (site 4), respectively. H) *Oichnus* isp., (black arrow), *Entobia* isp., in the internal surface of the gastropod *Conus virgo*, site 10, I) *Oichnus paraboloides* on the gastropod *Nerita albicilla*, site 10. J) *Gastrochaenolites* isp., (black arrows), *Rogerella* isp., (blue arrow), *Entobia* isp., on the gastropod *Turbo radiatus*, site 10. K) *Gastrochaenolites* isp., on the upper surface of *Favia pallida*, site 10. L–M) *Caulostrepsis* isp., (black arrow), *Entobia* isp., on the bivalve *T. maxima*, site 8 (scale bars: 10 mm).



*Entobia* cf. *retiformis* (Stephenson, 1952)

(Figures 5I and 5J)

1987 *Entobia retiformis* (Stephenson), Bromley & D'Alessandro, 391, pl. 42, Figures 1 and 3; pl. 46, Figures 2 and 3; pl. 49, Figures 1–3.

Substrate: The bivalve *T. maxima*.

Description: Structures in phase A are composed of long, much branched exploratory threads, and in phase B, small irregularly round chambers emerge from the expanding much branched intercameral canals. Phase C is characterized by pustulose, small, rounded chambers evaginating from relatively thick, cylindrical intercameral canals. The chambers cover the canals entirely or, more usually, are scattered along them in rings or groups, owing to cameral fusion. In some samples, phase D occurs, showing crowding of the camerate branches in interspaces.

Remarks: *Entobia retiformis* was produced by *Cliona retiformis* and this entobian-type resembled *E. volzi* Bromley and D'Alessandro, 1987 in the shape and development of chambers, as well as in having wide intercameral canals. However, the overall form of the 2 borings was entirely different (Bromley and D'Alessandro, 1987).

Occurrence: *Entobia* cf. *retiformis* represents 3.54% of the entobian trace fossils made by clinoid sponges.

*Entobia cretacea* Portlock, 1843

(Figures 6A and 6H)

Substrate: The bivalve *Q. palatam*.

Description: The boring pattern is frequently branching and resembles a well-developed camerate or string-of-beads form.

Remarks: It was produced by clionid sponges. *E. cretacea* differed from *E. geometrica* in several respects (Bromley and D'Alessandro, 1984). The apertures of *E. geometrica* were larger and the chambers, to a greater extent, resulted in thinner dividing walls than in *E. cretacea*, in which the chambers were normally connected by single intercameral canals.

Occurrences: *Entobia cretacea* accounted for 1.85% of the entobian trace fossils.

*Entobia* isp.

(Figures 5F, 6B, 7A, 7D, 7H, and 7J)

Substrate: Bivalves (*T. maxima*, *A. lacunose*, *A. antiquata*, *Q. palatam*, *A. ventricosa*, *Ch. aspersa*), gastropods (*C. virgo*, *H. kuesterianus*, *C. grayana*, *M. antiquus*, *C. aquatile*, *T. radiatus*, *C. flavidus*, *N. albicilla*), and corals (*P. lutea*, *P. solida*, *G. pectinata*, *F. klunzingeri*, *M. platyphylla*, *S. pistillata*).

Description: This ichnospecies is represented by networks of linear chambers, with circular apertures (0.5–1.8 mm in diameter). It occurs in 14.5% of the total substrates. Clusters of irregular, small, and densely crowded openings.

Remarks: *Entobia* was produced by several species of sponges belonging to the family Clionidae (Radwański, 1969; Bromley and D'Alessandro, 1984).

Occurrences: *Entobia* isp. was the most common of the structures made by clionid sponges (65.25%), on bivalves (42.86%), gastropods (41.56%), and corals (15.58%).

Ichnofamily Osteichnidae Hopner and Bertling, 2017

Ichnogenus *Maeandropolydora* Voigt, 1965

*Maeandropolydora* cf. *sulcans* Voigt, 1965

(Figures 6C, 6D, and 6I)

1987 *Maeandropolydora sulcans* Voigt, Bromley & D'Alessandro, 400, pl. 41, Figure 3; pl. 42, Figure 3.

1993 *Maeandropolydora sulcans* Voigt, Bromley and Asgaard, 277, Figure 1/20.

2008 *Maeandropolydora sulcans* Voigt, Santos and Mayoral, 50, Figure 5J1–9, Figures 7/1–3, 9, and 11.

2011 *Maeandropolydora sulcans* Voigt, Santos et al., 537, pl. 1, Figure 3.

2012 *Maeandropolydora sulcans* Voigt, Demircan, 339, pl. 1, Figure G.

Substrate: The gastropods *M. antiquus*, and *C. aquatile*.

Description: Well-developed cylindrical galleries. The borings are either sinuous or irregular. The size is highly variable; the length ranges from 12 to 28 mm and the width between 0.4 and 2.3 mm.

Remarks: The well-developed cylindrical galleries and lack of pouches and vanes exhibited a strong similarity to *Maeandropolydora sulcans* Voigt, 1965. This trace fossil was produced by suspension-feeding spionid polychaetes (e.g., Bromley and D'Alessandro, 1983, 1987), like the recent *Polydora hoplura* Claparède, 1868 (Mikuláš and Pek, 1996).

Occurrences: It represented 9.10% of the polychaete annelid trace fossils on gastropod shells.

*Maeandropolydora* isp.

(Figures 4B and 6E)

Substrate: Bivalves (*A. antiquata*, *Q. palatam*), gastropod *S. erythrinus*, and coral *P. lutea*.

Description: *Maeandropolydora* isp. occurs as shallow, long, and sinuous borings, 0.2 mm in diameter, 2.0 mm wide and at least 16 mm long.

Remarks: This boring was produced by polychaetes of various families (Bromley and D'Alessandro, 1983).

Occurrences: *Maeandropolydora* isp. accounted for 36.36% of the polychaete annelid trace fossils (50% on bivalves, 50% on gastropods and corals).

Ichnogenus *Caulostrepsis* Clarke, 1908

*Caulostrepsis taeniola* Clarke, 1908

(Figures 6F and 6G)

1993 *Caulostrepsis taeniola* Clarke, Bromley and Asgaard, 277, Figure 1/11.

2007 *Caulostrepsis taeniola* Clarke, De Gibert et al., 791, Figure 7.

2004 *Caulostrepsis taeniola* Clarke, Lorenzo and Verde, 322, pl. 1, Figure 3C.

2008 *Caulostrepsis taeniola* Clarke, Santos and Mayoral, 50, Figures 5H1–3, Figures 7/1–3.

2011 *Caulostrepsis taeniola* Clarke, Santos et al., 537, pl. 1, Figure 4.

2012 *Caulostrepsis taeniola* Clarke, Demircan, 338, pl. 1, Figures C and D.

Substrate: Bivalve *T. maxima*, and gastropods *T. radiatus* and *N. albicilla*.

Description: *C. taeniola* is a pouch-shaped boring, that looks like a very tight U-gallery, with an aperture, 1 mm in diameter. The diameter of the limb is about 2 mm, while the aperture is nearly 4.5 mm wide. Maximum observed length reaches up to 36 mm.

Remarks: It has been mainly considered to be produced by polychaetes of the genus *Polydora* (Radwański, 1969). *Caulostrepsis* occurred in shallow water environments, at a water depth between 7 and 15 m (Wisshak et al., 2005).

Occurrences: *Caulostrepsis taeniola* represented 27.27% of the polychaete annelid trace fossils (75% on gastropods and 25% on bivalve shells).

*Caulostrepsis* isp.

(Figures 7L–7M)

Substrate: The bivalves *T. maxima*, and *Ch. aspersa*.

Description: Relatively long galleries with a figure-of-eight-shaped cross-section, and a pouch-shaped boring, typically found in most external part of shells and tests.

Remarks: Bromley and D'Alessandro (1983) revised the systematics of this ichnotaxon and recognized several ichnospecies. It was produced by polychaetes (Radwański, 1969).

Occurrences: *Caulostrepsis* isp. also represented 27.27% of the polychaete annelid trace fossils on bivalve shells.

Ichnofamily Renichnidae Knaust, 2012

Ichnogenus *Renichnus* Mayoral, 1987

*Renichnus* isp.

(Figure 5F)

Substrate: The gastropod *C. virgo*

Description: It is a half-moon or kidney-shaped depression, disposed in a crude row or coarsely coiled. There is a flat and gently curved succession of progressively wider, kidney-shaped depressions closely related to the smooth walls. There is a maximum of 3 depressions per specimen. The walls between the depressions are perpendicular to the surface or slightly oblique.

Remarks: *Renichnus* was formed as the etching trace of vermetid gastropods (Mayoral, 1987; Uchman et al., 2017).

Occurrences: *Renichnus* isp. represented 2.81% of the total borings.

Ichnofamily Gastrochaenolitidae Wisshak, Knaust and Bertling, 2019

Ichnogenus *Gastrochaenolites* Leymerie, 1842

*Gastrochaenolites torpedo* Kelly and Bromley, 1984 (Figures 4C and 6K–6M)

1993 *Gastrochaenolites torpedo* Kelly and Bromley, Bromley and Asgaard, 277, Figure 1/19.

2002 *Gastrochaenolites torpedo* Kelly and Bromley, Uchman et al., 265, Figures 4A and 5A.

2006 *Gastrochaenolites torpedo* Kelly and Bromley, Donovan and Hensley, 13, Figure 3.

2012 *Gastrochaenolites torpedo* Kelly and Bromley, Demircan, 341, pl. 3, Figures C and D.

2018 *Gastrochaenolites torpedo* Kelly and Bromley, El-Hedeny and El-Sabbagh, 8, Figures 6B, 6C, 9A, and 9B.

Substrate: Bivalves (*T. maxima*, *A. lacunose*), and corals (*P. lutea*, *P. solida*, *F. stelligera*, *F. pallida*, *P. daedalea*).

Description: This is a smooth, strongly elongated chamber, 49 mm long, up to 17 mm in depth and 8–16 mm in diameter. Elongate smooth boring, widest point close to mid-line with the base is acutely parabolic. The chamber ranges from 17–60 mm in length.

Remarks: *Gastrochaenolites torpedo* was produced by some bivalves of the genus *Lithophaga* and *Gastrochaena* (Kelly and Bromley, 1984), and in the Mediterranean Sea by *Lithophaga lithophaga* (Linnaeus). It has been reported from Miocene rocky shores of many regions in Europe and neighboring areas (Radwański, 1969).

Occurrences: *G. torpedo* occupied 25.38% of the endolithic bivalve borings (63.63% on corals and 36.37% on bivalves).

*Gastrochaenolites lapidicus* Kelly and Bromley, 1984

(Figures 6J and 7A)

1993 *Gastrochaenolites lapidicus* Kelly and Bromley, Bromley and Asgaard, 277, Figure 1/14.

2002 *Gastrochaenolites lapidicus* Kelly and Bromley, Uchman et al., 265, Figure 4B.

2012 *Gastrochaenolites lapidicus* Kelly and Bromley, Demircan, 341, pl. 3, Figure B.

2018 *Gastrochaenolites lapidicus* Kelly and Bromley, El-Hedeny and El-Sabbagh, 7, Figures 6B, 6C, 9C, 9E, and 9F.

2018 *Gastrochaenolites lapidicus* Kelly and Bromley, El-Sorogy et al., 268, Figures 5A–5C.

Substrate: Bivalve *T. maxima*, gastropod *H. kuesterianus*, and coral *F. pallida*.

Description: It is a smooth ovate chamber with an apertural neck and is circular throughout crosssection. The neck is also circular in crosssection or elliptical. The boring is 6–22 mm long and maximum 5–12 mm wide. The widest diameter is located slightly below the center of the chamber.

Remarks: This type of boring was produced by some bivalves of the genus *Lithophaga* (Kelly and Bromley, 1984).



Occurrences: *G. lapidicus* represented 10.32% of the total endolithic bivalve borings (62.5% on gastropods, 25% on corals, and 12.5% on bivalves).

*Gastrochaenolites* cf. *dijugus* Kelly and Bromley, 1984 (Figure 7C)

2008 *Gastrochaenolites dijugus* Kelly and Bromley, Santos and Mayoral, 50, Figures 5K1–6, Figures 7/3 and 5.

Substrate: Coral *Favia stelligera* and bivalve *Asaphis violascens*.

Description: The clavate or flask-shaped borings have a circular or oval cross section, and figure-8-shaped apertures, 2.5–4 mm in diameter.

Remarks: It was characterized by a clavate or flask-shaped chamber, with a circular to oval cross section, connected by a narrow neck region that exhibited a figure-8-shaped aperture (Zain et al., 2018). According to Kelly and Bromley (1984), *G. dijugus* exhibited a figure-8-shaped aperture in the cross section, a characteristic, which was observed clearly in the material studied.

Occurrences: *G. dijugus* represented 2.97% of the *Gastrochaenolites* borings in the corals and bivalves.

*Gastrochaenolites* isp.

(Figures 4A, 4B, 4D, 5F, 5G, 6E, 7J, and 7K)

Substrate: Bivalves (*T. maxima*, *Ch. aspersa*), gastropods (*H. kuesterianus*, *T. radiatus*, *C. flavidus*, *C. virgo*, *S. erythrinus*), and corals (*P. lutea*, *F. pentagona*, *P. solida*, *P. daedalea*, *G. pectinata*, *Favia* sp., *F. stelligera*, *F. pallida*, *S. pistillata*).

Description: This ichnospecies is strongly developed as small subcircular borings, 2–6 mm in diameter, up to 9 mm deep, without distinct neck. It is oriented perpendicular on the hard substrate.

Remarks: This ichnogenus was produced by boring bivalves (Kelly and Bromley, 1984), such as Pholadidae, Gastrochaenidae, and Mytilidae (Warme, 1975; Fisher, 1990).

Occurrences: *Gastrochaenolites* isp. was the most common endolithic bivalve boring, comprising 61.33% of the total borings (51% on corals, 35% on gastropods, and 15% on bivalves).

Ichnofamily Centrichnidae Wisshak, Knaust, and Bertling, 2019

Ichnogenus *Centrichnus* Bromley and Martinell, 1991

*Centrichnus* isp.

(Figure 7B)

Substrate: The bivalve *T. maxima*.

Description: Shallow biogenic etching traces in carbonate lithic or skeletal substrates with centrally arranged curved or annular grooves.

Remarks: It was produced by anomiid bivalves (Bromley and Martinell 1991; Bromley, 1999).

Occurrences: *Centrichnus* isp. was uncommon; it accounted for about 0.40% of the total borings.

Ichnofamily Oichnidae Wisshak, Knaust, and Bertling, 2019

Ichnogenus *Oichnus* Bromley, 1981

*Oichnus paraboloides* Bromley, 1981

(Figures 7F, 7G, and 7I)

2004 *Oichnus paraboloides* Bromley, Lorenzo and Verde, 324, Figures 3D–3I.

2018 *Oichnus paraboloides* Bromley, El-Sorogy et al., 267, Figure 4D.

Substrate: Bivalves (*C. divergens*, *Q. palatam*), and the gastropod *S. persicus*.

Description: It is found as spherical paraboloid holes, from 1.5–3 mm in size. In thick surfaces, some excavations terminate within the surface without penetration, which indicate a failed drilling attempt. External diameter is 3–4.1 mm and internal diameter is 1.8–2.2 mm.

Remarks: The circular to subcircular drill hole was originally assigned to the ichnogenus *Oichnus* (Bromley, 1981). Some ichnogenera with similar looking traces were also erected, including *Sedilichnus* (Müller, 1977) and *Tremichnus* (Brett, 1985). It is known that *O. paraboloides* was formed by naticid gastropods traces (Kowalewski, 1993; Reymont, 1999).

Occurrences: *Oichnus paraboloides* accounted for 57.14% of the boring gastropods (75% on bivalves and 25% on gastropods).

*Oichnus simplex* Bromley, 1981

(Figure 7E)

2007 *Oichnus simplex* Bromley, De Gibert et al., 791, Figure 9/D.

2018 *Oichnus simplex* Bromley, El-Sorogy et al., 267, Figures 4A–4C.

Substrate: The gastropod *Conus virgo*.

Description: Borings are cylindrical or sub-cylindrical, 1.8–2.2 mm in diameter, more or less perpendicular to the bivalve surface.

Remarks: They consisted of subcircular boreholes. The hemispherical shape allowed for the interpretation of it as the result of a carnivorous gastropod activity (Bromley, 1981).

Occurrences: *Oichnus simplex* represented 14.29% of the gastropod borings on *Conus virgo*.

*Oichnus* isp.

(Figure 7H)

Substrate: Gastropod *Nerita albicilla*.

Description: Cylindrical to subcylindrical borings, diameters range from 1.5–2 mm.

Remarks: *Oichnus* is has been generally interpreted as praedichnia of gastropod families Naticidae and Muricidae, respectively (Bromley, 1981; Pickerill and Donovan, 1998).

Occurrences: *Oichnus* isp. represented 28.58% of the gastropod borings.

Ichnofamily Echinoidea Wisshak, Knaust and Bertling, 2019

Ichnogenus *Rogerella* de Saint-Seine, 1951

cf. *Rogerella* isp.

(Figure 7J)

Substrate: Gastropod *Turbo radiatus*.

Description: Small, rounded to oval-like or comma-shaped depressions, with a slit-shaped aperture extend obliquely to the substrate, varying in length from 0.5 to 2.0 mm. The borings are 1.1 to 2.2 mm deep and 1.2 and 1.8 mm wide.

Remarks: *Rogerella*'s trace maker has been considered to be barnacles of the order Acrothoracica (Mikuláš, 1992; Donovan and Jagt, 2013).

Occurrences: *Rogerella* isp. was uncommon; it accounted for about 0.40% of the total borings observed.

## 5. Discussion

The abundance of the bioerosion structures among the investigated bivalves, gastropods, and corals showed some interesting differences (Figure 3). Most of the bivalves and gastropods were bioeroded by clionid sponges, while most of the corals were bioeroded by *Gastrochaenolites*, especially *G. torpedo*. Some parts of the molluscan shells (e.g., *Chama*, *Conus*, *Tridacna*, *Magilus*, *Canarium*), however, were intensively bored (Figures 5A, 5B, 6B, 6F, and 6I). The external surfaces were more intensively bored than the internal ones, implying that boring occurred during their life-time. Most of the specimens of *Gastrochaenolites*, *Maeandropolydora*, and *Caulostrepsis* occupied the surfaces of the larger and thicker skeletons (e.g., *T. maxima*, *Ch. aspersa*, *H. kuesterianus*, *F. klunzingeri*, *S. pistillata*, *Acropora* sp.). Such skeletons represented a favorable substrate for the settlement of larger endoskeletozoans of polychaetes, lithophages, naticids, and mytilids. Furthermore, they acted as a suitable substrate for many filter-feeding epifauna (e.g., encrusting bryozoans, serpulid worms fixed to chameids and ostreids, corals, barnacles, and epibiont *Spirorbis*). The larger and thicker corals, bivalve, and gastropod skeletons were characterized by the absence of the ichnogenus *Oichnus*, which has been mostly recorded in thinner bivalve and gastropod shells, such as *Ctena*, *Quidnipagus*, *Nerita*, and *Conus* (Figures 7F–7I).

The boring assemblage in the present study represented several communities that formed during the formation of Late Pleistocene reef unit. Increasing water depth during transgression and eustatic fluctuations changed the shallow, well-oxygenated coral rock, back-reef, and reef crest assemblages dominated by polychaete and bivalve borings into the deep lower-energy upper reef slope community

dominated by boring sponges (Bassant, 1999; Uchman et al. 2002, Kahal et al. 2020). The present assemblage of trace fossils was typical of the *Entobia* ichnofacies, as defined by Bromley and Asgaard (1993b). The presence of *G. torpedo* perpendicular to steep surfaces of corals and molluscs (Figures 6J–6M) may have been attributed to trace maker *Lithophaga lithophaga* avoiding sedimentary deposition (Bromley and Asgaard, 1993a; De Gibert et al. 1998; Uchman et al. 2002). In contrast, *G. lapidicus* was occupied locally and horizontal, and even on inclined surfaces, since the main trace maker, *Gastrochaena dubia*, had a greater tolerance than that of *L. lithophaga* (Bromley and Asgaard, 1993b).

## 6. Conclusion

The bivalves, gastropods, and corals collected from the coastal area and the Late Pleistocene reef unit along the Red Sea coast of northwest Saudi Arabia showed abundant bioerosional structures produced by clionid sponges, endolithic bivalves, drilling gastropods, polychaete annelids, and acrothoracican barnacles. A total of 20 ichnospecies belonging to 8 ichnogenera were identified and, in descending order of abundance, comprised the following: *Entobia* (*E. geometrica*, *E. ovula*, *Entobia* cf. *gonioides*, *E. cf. retiformis*, *E. cretacea*, *Entobia* isp.), *Renichnus* (*Renichnus* isp.), *Gastrochaenolites* (*G. torpedo*, *G. lapidicus*, *G. cf. dijugus*, *Gastrochaenolites* isp.), *Oichnus* (*O. paraboloides*, *O. simplex*, *Oichnus* isp.), *Caulostrepsis* (*C. taeniola*, *Caulostrepsis* isp.), *Maeandropolydora* (*M. cf. sulcans*, *Maeandropolydora* isp.), *Centrichnus* (*Centrichnus* isp.), and *Rogerella* (cf. *Rogerella* isp.). Most specimens of the *Gastrochaenolites*, *Maeandropolydora*, and *Caulostrepsis* trace fossils occupied the surfaces of the larger and thicker corals, bivalve, and gastropod skeletons, which offered a favorable substrate for the settlement of larger endoskeletozoans of polychaetes, lithophages, naticids, and mytilids. The diversity and abundance of the trace fossils indicated an *Entobia* ichnofacies that had formed during transgression. The change from shallow, high-energy waters to deep, low-energy waters was confirmed by the trace fossil assemblages, first dominated by polychaete and bivalve borings, and then by boring sponges. The waters were well-oxygenated.

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