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Palaeoenvironmental analysis of bivalve-dominated concentrations from the lower-middle Miocene succession, Gebel Gharra, Cairo-Suez District, Egypt

HEBA MANSOUR, MONA MANDOR, AHMED EL-SABBAGH, MAGDY EL HEDENY, OLEV VINN, ABDULLAH ALKAHTANE, SALEH AL FARRAJ, ÁRPÁD DÁVID, AHMED EL-REFAIY AND MOHAMED RASHWAN

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The most conspicuous feature of the lower-middle Miocene deposits of Gebel Gharra, Cairo-Suez District of Egypt, is the presence of three pectinid- and two oyster shell concentrations. They are paucispecific to polyspecific macrobenthic biotopes. Their shells were significantly colonized by abundant endobionts and common epibionts, characterising the *Entobia* ichnofacies, and representing successive phases of colonization and bioerosion on stable substrates with a low sedimentation rate in high energy, shallow marine environments. Four types of shell concentrations have been distinguished. Pectinid-shell concentration of bed 2 is interpreted as a simple transgressive lag concentration that formed by reworking of previous deposited sediments in a shoal environment. Pectinid-shell concentration of bed 13 represents a coquina of high and moderately convex, sub-horizontally oriented to chaotic, and highly disarticulated and fragmented pectinid valves. It is interpreted as a remnant of previously deposited sediments that have been reworked by a single storm event without major transport of shells, and deposition in a lagoon environment. Pectinid-shell concentration of bed 14b is characterized by completely disarticulated, highly fragmented, moderately to densely packed, and re-oriented pectinid shells. It represents a composite concentration that was originated in a lagoon environment by sporadic high-energy events. Oyster-dominated concentrations of beds 9 and 22 represent 'within-habitat' environmentally condensed assemblages, and formed by densely fossiliferous deposits with highly disarticulated, convex-up oysters along with articulated specimens preserved in life position, and with a moderate to high grades of bioerosion and encrustation. They were deposited by several high-energy events in supratidal and lagoonal environments, respectively. □ *Shell concentrations, taphonomy, palaeoecology, palaeoenvironment, Miocene, Egypt.*

Heba Mansour ✉ [heba.mansour@alexu.edu.eg], Mohamed Rashwan [Rashwan.m.a@gmail.com], Department of Biological and Geological Sciences, Faculty of Education, Alexandria University, Alexandria 14037, Egypt; Mona Mandor [monasalah9070@yahoo.com], Ahmed El-Sabbagh [ah.elsabbagh@alexu.edu.eg], Magdy El Hedeny ✉ [magdy.elhedeny@alexu.edu.eg], Ahmed El-Refaiy [ahmedshams_pg@alexu.edu.eg], Department of Geology, Faculty of Science, Alexandria University, Alexandria 21568, Egypt; Olev Vinn [olev.vinn@ut.ee], University of Tartu, Department of Geology, Ravila 14A, 50411 Tartu, Estonia; Abdullah Alkahtane [aalkahtane@ksu.edu.sa], Saleh Al Farraj [salfarraj@ksu.edu.sa], College of Sciences, King Saud University, Riyadh 11451, Saudi Arabia; Árpád Dávid [coralga@yahoo.com], University of Debrecen, Department of Mineralogy and Geology, H-4032 Egyetemtér 1., Debrecen, Hungary; manuscript received on 23/08/2023; manuscript accepted on 05/03/2024; manuscript published on 02/07/2024 in Lethaia 57(2).

Shell concentrations are characteristic features in most shelf and coastal areas (e.g. Kidwell *et al.* 1986; Fürsich 1995; Bressan & Palma 2010; El-Sabbagh *et al.* 2016; Kassab *et al.* 2021; Rashwan *et al.* 2022). They can provide significant palaeoecological information in addition to detailed data on the palaeoenvironment of their desposition (e.g. Brett 2003; Brett *et al.* 2011, 2012; Smrecak & Brett 2014; El-Sabbagh *et al.* 2015; El-Sabbagh & El Hedeny 2016; Rashwan *et al.* 2022). Most of these shell concentrations host endo- and epibiont faunal communities on their skeletal substrate. Thus, study of such shell concentrations contributes to the understanding of several aspects of the palaeo-ecosystem, including sclerobiont community, life position, distribution, and spatial orientation on the substrate. They also provide evidence of biological interactions between sclerobionts such as competition (e.g. Liddell & Brett 1982; El Hedeny *et al.* 2021a, b; Mandor *et al.* 2022). In addition, ecological succession can be studied in sclerobiont communities (e.g. Taylor & Wilson 2003; Liow *et al.* 2016; Taylor 2016; Salahi *et al.* 2018; El Hedeny *et al.* 2021b).

In Egypt, the lower-middle Miocene succession of Gebel Gharra is mainly represented by shallow-marine, mixed siliciclastic-carbonate sediments (Mandor *et al.* 2022, 2023). Throughout this succession, five beds containing relatively thick and highly concentrated pectinid and oyster shells hosting abundant sclerobiont assemblages and occurring as paucispecific to polyspecific macrobenthic biotopes. In general, the numerous occurrences of sclerobionts (both endo- and epibionts) on macrofauna have been described from Cenozoic of Egypt (e.g. El-Shazly *et al.* 2016; El Hedeny *et al.* 2021a; Kassab *et al.* 2021). However, only few studies have previously been devoted to Miocene sclerobiont communities (e.g. El Hedeny 2005, 2007; El-Sabbagh & El Hedeny 2016; El-Sabbagh *et al.* 2016; El Hedeny *et al.* 2021a). Thus, further studies are needed to understand palaeoecology and evolution of hard substrate communities in the Miocene of Egypt. The aims of this study are: 1) to describe the five shell concentrations of the lower-middle Miocene sediments of the Gebel Gharra succession; 2) to identify the ichno-assemblages of macro-bioeroding organisms and encrusting sclerobiont assemblages recorded on the studied shells; and 3) to use these shell concentrations and the associated sclerobiont assemblages as a tool to interpret and discuss the paleoenvironmental conditions prevailed during the formation of these concentrations.

Geological and stratigraphical framework

Along the Cairo-Suez District at the northern part of the Eastern Desert of Egypt, Miocene sediments are exposed in several hills (Said 1962). Tectonics combined with eustatic sea-level fluctuations and high terrigenous influx are considered to have been the main factors that controlled sedimentation (Said 1990; Patton *et al.* 1994; Issawi *et al.* 1999; Mandic & Piller 2001; Mandor *et al.* 2023). Sediments mainly occurred in two tectonic basins: the Geniefa (= Geneffe/Gineifa)-Gharra Basin to the north of Suez City and the Hagul-Sukhna Basin to the south of the city (Hermina *et al.* 1989; Said 1990). These basins are filled with mixed siliciclastic-carbonate sediments deposited on a shallow shelf (e.g. Mandor *et al.* 2023). In general, these Miocene rocks overlie either shallow-marine Eocene carbonates or non-marine Oligocene siliciclastics (Said 1962, 1990; Hermina *et al.* 1989).

The study is based on a succession cropping out at the Gebel Gharra area (30°11′13.80″N, 32°18′9.00″E), about 30 km NW of Suez City (Fig. 1). The c.140 m thick Miocene succession studied lies on the eastern flanks of the Gebel Gharra hill. It is subdivided

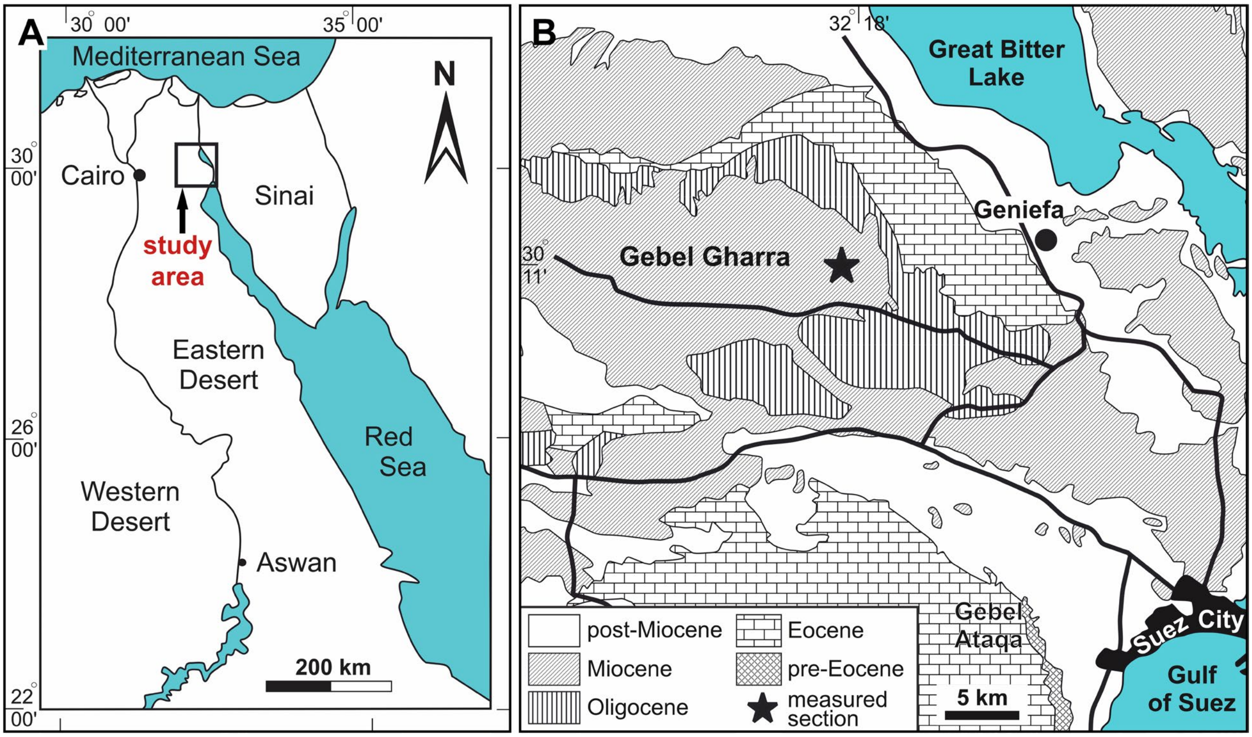


Fig. 1. Geographical and geological framework of the study area. A, geographical overview. B, simplified geological map of the study area (modified after Mandic & Piller 2001) with the location of the measured section at Gebel Gharra.

into siliciclastic-dominated and carbonate-dominated intervals, belonging to the lower Miocene Gharra and the middle Miocene Geniefa formations, respectively (Fig. 2). The Gharra Formation attains a thickness of about 65 m. The Geniefa Formation rests unconformably on the Gharra Formation and attains a thickness of about 75 m. Sediments of the two formations are characterized by highly abundant macrobenthic faunas (for more details, see Mandor *et al.* 2022, 2023). In addition, they contain three pectinid and two oyster shell concentrations (Fig. 2). Pectinid-shell concentrations exclusively are recorded in three marl beds in the lower Miocene Gharra Formation, between 20 and 21 m, 41.5 and 45 m, and between 59.5 and 61 m. In contrast, oyster shell concentrations were recorded in a sandstone interval between 35.5 and 40.5 m in the Gharra Formation and in a thin marl bed (118–119.5 m) in the Geniefa Formation (Fig. 2).

Material and methods

In the field, stratigraphical, sedimentological, and palaeontological data were gathered through detailed description of each bed. For each shell concentration, several features were also recorded, including stratigraphical (thickness, lateral extent, geometry, and stratigraphic contacts), sedimentological (close packing and size sorting of the bioclasts, type of matrix, physical sedimentary structures, microfacies, and depositional setting), palaeoecological (species richness, taxonomic composition, ontogenetic age, original mineralogy, life habits, and feeding modes), and taphonomic (disarticulation, fragmentation, orientation, bioerosion, encrustation, and preserved mineralogy) features. In addition, this study is based on laboratory examination of bioerosion traces and encrustation in 264 pectinid and 136 oyster specimens from the five recorded shell concentrations in the studied section. Pectinid specimens were collected from beds 2, 9, 13, and 14b (97, 13, 47, and 107 specimens, respectively), while oyster specimens were collected from bed 9 (43 specimens), bed 14b (5 specimens), and bed 22 (88 specimens). Whenever possible, way-up arrows were marked on shells at the time of collection. Their mode of fossilization ranges from exceptionally well-preserved shells including microscopic surface characters to slightly abraded material.

In the laboratory, the macrofossil specimens were treated with a diluted hydrogen peroxide solution and scrubbed with a soft toothbrush in order to remove adhering matrix. After these, both external and internal surfaces of the sampled pectinid and oyster left and right valves were systematically screened, using both a hand lens and a binocular microscope, in order to determine the type and number of bioerosion traces and encrusters. The number of borings is counted as the number of apertures visible on the surface of the examined shells omitting the partially eroded ones. The number of encrusters is counted as the number of oyster or pectinid shells with at least one encruster. Measurements of bioerosion structures (width and depth) were made using digital callipers (accurate to 0.1 mm). Determination of bioerosion structures was mainly based on criteria given by Voigt (1965), Bromley (1981), Bromley & D'Alessandro (1984), Mayoral (1987), Kelly & Bromley (1984), Bromley & Asgaard (1993a) and Verde *et al.* (2022).

All macrofossil specimens are housed in the collections of the Department of Geology, Faculty of Science, Alexandria University. Numbers of fossil specimens are prefixed by (Gh) for the Gebel Gharra section followed by bed number and (O) for oysters and (P) for pectinids. This work also benefited from data and the collection studied by Mandor *et al.* (2022, 2023).

Results

Characteristics of shell concentrations

Pectinid-shell concentration (bed 2).– This represents a remarkable thin pectinid concentration (0.4–0.7 m thick; Fig. 2). It is composed of marl (a tightly packed grainstone facies type; Mandor *et al.* 2023), with mud clasts at its base (Fig. 3A), and with a lateral extension of at least 100 m. It is characterized by loosely to moderately packed, moderately to poorly sorted shells (Fig. 3B), and rests on a sharp to erosive, intensively bioturbated lower boundary and a sharp upper contact (Table 1; Fig. 3A). This shell concentration consists mainly of pectinids (88.7% of the total macrobenthic assemblage), including *Flabellipecten schweinfurthi* (Blanckenhorn, 1901), *Macrochlamis ziziniae* (Blanckenhorn, 1901), *Oppenheimopecten josslingi* (Sowerby in Smith, 1847), *Pecten fraasi* Fuchs, 1883, and *P. kochi* Locard, 1877. In addition, rare echinoids (4.1%), solitary corals (3.1%), other bivalves, and gastropods (2.1% each) occur. Furthermore, bryozoans and balanoid barnacles are also recorded (Fig. 3B). Most of these bioclasts are fragmented. In general, shells of adult individuals are common. Upward, this concentration grades into less fossiliferous sediments (Fig. 3B). Finally, this macrobenthic assemblage is dominated by epifaunal and suspension-feeding taxa (93.8 and 91.8% of the total macrobenthic assemblage, respectively; Table 1).

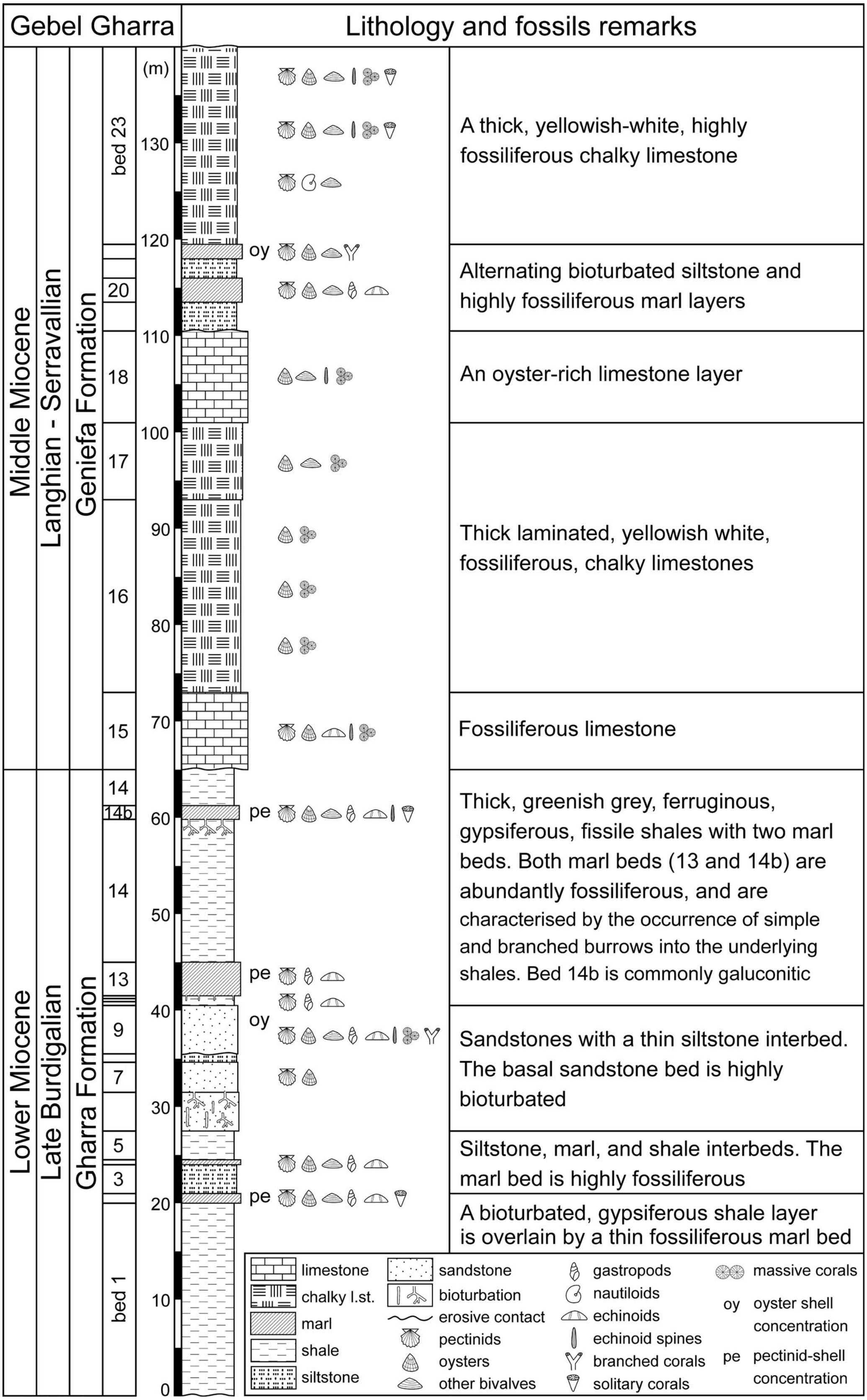


Fig. 2. Lithological descriptions of the Gebel Gharra section with occurrences of macrofossils and the five studied shell concentrations (modified after Mandor *et al.* 2023).

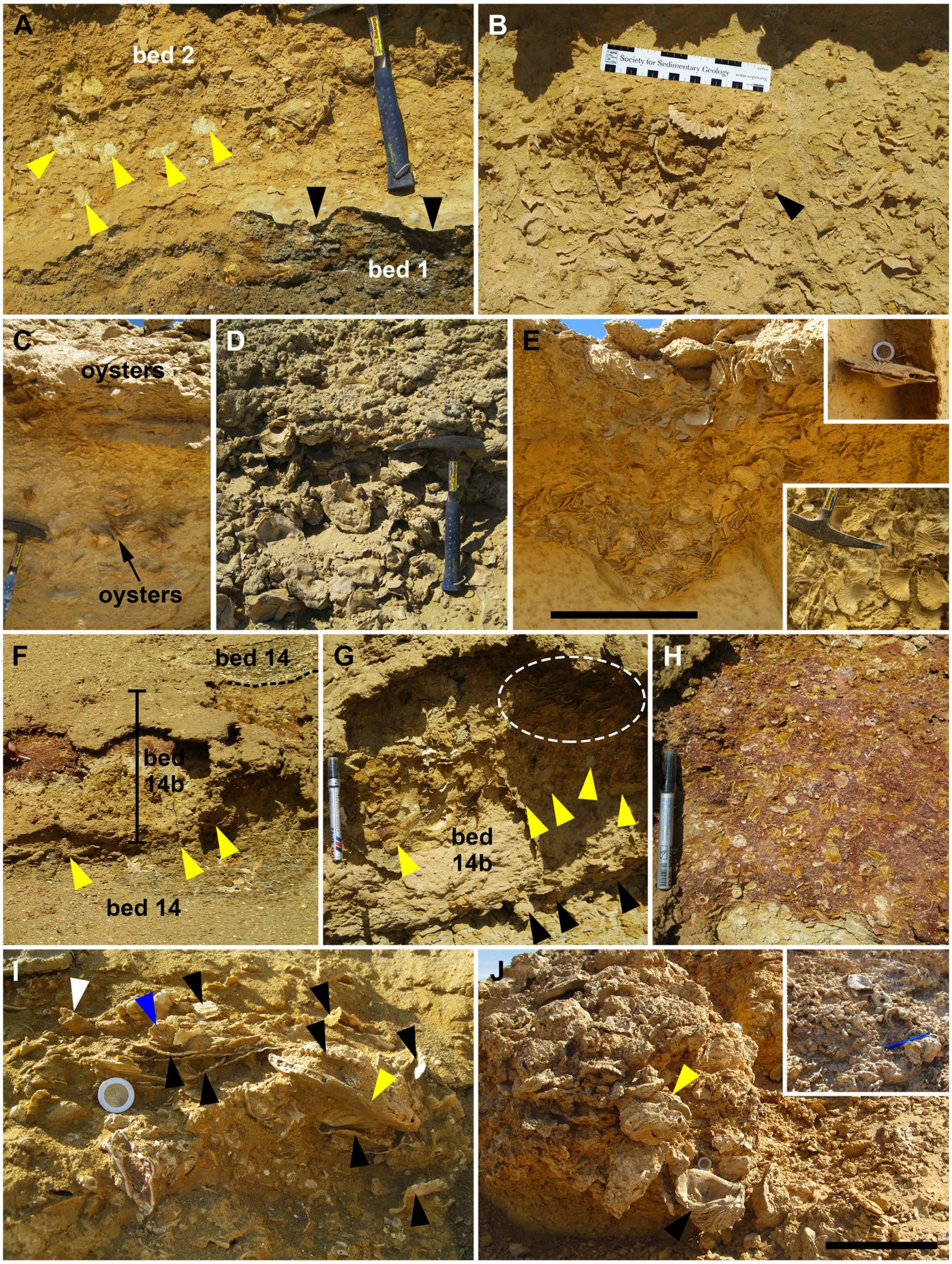


Fig. 3. Some field aspects of the five shell concentrations studied. A, bed 2 with mud clasts (yellow arrows) in the basal part and overlies, with a sharp to erosive contact (black arrows), a thick gypsiferous shale (bed 1). B, shell concentration of bed 2 with loosely to moderately packed, disarticulated, re-oriented, and fragmented pectinid valves. Note the occurrence of balanoid barnacle (arrow) in life position on the internal surface of a pectinid valve. C, oyster shell concentration of bed 9 at 37 m in the Gharra Formation showing two intervals of moderately to densely packed, and mostly concordant specimens of *Lopha virleti* (Deshayes, 1833). Note the upward increase in shell packing density and the occurrence of abundant fragmented *Acropora* branches between these two oyster intervals. D, the upper part of shell concentration of bed 9 showing densely packed, mostly concordant, convex-up, and adult large, disarticulated specimens of *L. virleti*. E, concentration of large, disarticulated, densely packed, and re-oriented *Flabellipecten schweinfurthi* (Blanckenhorn, 1901) valves (lower inset) of bed 13 at 43 m, the Gharra Formation. Note the uneven lower contact with a relief up to 40 cm. The upper inset represents articulated and well-preserved *F. schweinfurthi* specimen preserved in life position. F, bed 14b with an erosive, bioturbated lower contact (yellow arrows) and a sharp upper contact (dash line). Note the two parts of this concentration, including the lower greyish-greenish interval and the upper dark red part. G, the lower part of concentration of bed 14b with disarticulated pectinid valves (ellipse) at 60 m, the Gharra Formation. Note the occurrence of mud clasts (yellow arrows) in the basal part and the bioturbated lower contact (black arrows). H, the upper part of concentration of bed 14b with dark red glauconitic calcareous siltstone with coarse, yellowish to greenish mud-pebbles. I, concentration of bed 14b (the Gharra Formation) with disarticulated and fragmented pectinid valves (black arrows), solitary coral (blue arrow), irregular echinoid (yellow arrow), and cidarid echinoid spine (white arrow) in a glauconitic and calcareous sandstone matrix. Note that the echinoid test occurs with oral side up. J, the upper part of shell concentration of bed 22 at 118 m in the Geniefa Formation showing adult large, densely packed, mostly concordant, articulated and disarticulated specimens of *L. virleti* (yellow and black arrows, respectively) in life position. Inset showing abundant fragmented *Acropora* branches with disarticulated chaotic left and right oyster shells. Scale bars equal 30 cm for E, and 20 cm for J.

Table 1. Stratigraphical, sedimentological, palaeoecological, and taphonomic features of the five shell concentrations in the Gebel Gharra succession.

	Shell concentrations				
Features	**Pectinid (bed 2)**	**Oyster (bed 9)**	**Pectinid (bed 13)**	**Pectinid (bed 14b)**	**Oyster (bed 22)**
Stratigraphical					
Thickness (m)	0.4–0.7	0.5–1.0	1–1.5	1–1.5	0.5–1.0
Lateral extent (m)	at least 100	at least 200	at least 200	at least 200	at least 200
Geometry	tabular	tabular	tabular	tabular	tabular
Lower contact	sharp to erosive	sharp to erosive	uneven	erosive, bioturbated	sharp to erosive
Upper contact	erosive	erosive	sharp	sharp	erosive
Sedimentological					
Close packing	loosely/moderately packed	moderately/densely packed	densely packed	moderately/densely packed	densely packed
Size sorting	moderate-non	moderate-non	moderate-non	moderate-non	moderate-non
Type of matrix	marl	calcareous sandstone	calcareous sandstone	glauconitic, calcareous sandstone/siltstone	sandy marl
Physical sedimentary structures	within bed with intraclasts	within bed, laminated	within bed	within bed with intraclasts	within bed, laminated
Microfacies	tightly packed grainstone	dolomite cemented sandstone	sandy high porosity packstone	sandy high porosity packstone	sandy high porosity packstone
Depositional setting	shoal	supratidal	lagoon	shallow lagoon	lagoon
Palaeoecological					
Species richness	polyspecific (12 macrobenthic spp.)	polyspecific (15 macrobenthic spp.)	paucispecific (9 macrobenthic spp.)	polyspecific (19 macrobenthic spp.)	paucispecific (6 macrobenthic spp.)
Taxonomic composition	– pectinids-dominated, echinoids, corals, other bivalves, gastropods	– oyster-dominated, pectinids, other bivalves, gastropods, echinoids, corals	– pectinids-dominated, gastropods, echinoids	– pectinids-dominated, gastropods, echinoids, oysters, corals, other bivalves	– oyster-dominated, pectinids, other bivalves, corals
	– ichnological evidence of clionid sponges (*Entobia*), polychaete annelids (*Maeandropolydora*)	– ichnological evidence of clionid sponges (*Entobia*), polychaete annelids (*Maeandropolydora* and *Caulostrepsis*), endolithic bivalves (*Gastrochaenolites*), vermetid gastropods (*Santichnus*)	– ichnological evidence of polychaetes (*Maeandropolydora* and *Caulostrepsis*), clionid sponges (*Entobia*), ctenostome bryozoans (*Iramena*), vermetid gastropods (*Renichnus*), predatory gastropods (*Oichnus*)	– ichnological evidence of clionid sponges (*Entobia*), polychaetes (*Maeandropolydora*), endolithic bivalves (*Gastrochaenolites*), predatory gastropods (*Oichnus*)	– ichnological evidence of clionid sponges (*Entobia*), polychaete annelids (*Maeandropolydora* and *Caulostrepsis*), endolithic bivalves (*Gastrochaenolites*), sipunculid annelids (*Trypanites*), phoronid worms (*Talpina*), predatory gastropods (*Oichnus*), vermetid gastropods (*Santichnus*)
	– episkeletobionts: serpulids, bryozoans, balanoid barnacles	– episkeletobionts: bryozoans, serpulids, oysters, balanoid barnacles	– episkeletobionts: bryozoans, serpulids, oysters	– episkeletobionts: bryozoans, serpulids, oysters	– episkeletobionts: bryozoans, serpulids, oysters, balanoid barnacles, corals
Ontogenetic age	adults and juveniles	adults and juveniles	adults and juveniles	adults and juveniles	adults and juveniles
Original mineralogy	calcite	calcite	calcite	calcite	calcite
Life habits	E, EC, EM, IM, SI, SIM	E, EC, EM, I, IM, SI	E, EM	E, EC, EM, SIM, SI	E, EC, EM
Feeding modes	S, D, C, MC	S, D, C, G, MC	S, D, C, G	S, D, C, G, MC, OM	S
Taphonomic					
Specimens examined	97 pectinid shells	43 oyster shells	47 pectinid shells	107 pectinid shells	88 oyster shells
Disarticulation	high (97.9%)	high (88.4%)	high (91.5%)	complete (100%)	high (97.7%)

	Shell concentrations				
Features	**Pectinid (bed 2)**	**Oyster (bed 9)**	**Pectinid (bed 13)**	**Pectinid (bed 14b)**	**Oyster (bed 22)**
Fragmentation	high (61.9%)	low/moderate (18.6%)	high (51.1%)	high (44.9%)	low (12.5%)
Orientation	re-oriented	concordant/mostly convex-up	sub-horizontal/ re-oriented	re-oriented	concordant/rarely convex-up
Bioerosion	low (9.3%)	moderate (30.2%)	low (8.5%)	low (9.3%)	high (79.5%)
Encrustation	low (8.2%)	moderate (27.9%)	low/moderate (21.3%)	moderate/high (38.3%)	high (54.5%)
Preserved mineralogy	original	original	original	original	original

Life habits: E = epifaunal; EC = epifaunal cemented; EM = epifaunal mobile; I = infaunal; IM = infaunal mobile; SI = semi-infaunal; SIM = semi-infaunal mobile.

Feeding modes: S = suspension-feeder; D = deposit-feeder; C = carnivore; MC = microcarnivore, G = grazer; Om = omnivore.

Pectinid shells are highly disarticulated (97.9% of the total examined pectinid shells) and re-oriented (Fig. 3B). The average occurrence of left and right valves is distinctly unequal (30.9 and 69.1%, respectively). Pectinid specimens are highly fragmented (61.9% of the total examined pectinid shells), and rarely bioeroded (9.3%) and encrusted (8.2%; Table 1). Boring traces, referred to clionid sponges and polychaetes. Skeletal remains of encrusting organisms contain bryozoans, serpulids, and balanoid barnacles (Table 1).

Oyster shell concentration (bed 9).– This concentration attains a thickness of 0.5 to 1.0 m (Fig. 2), with a lateral extent of at least 200 m, sharp to erosional lower surface, and an erosive upper contact (Table 1). It is composed of fossiliferous, calcareous sandstone (a dolomite cemented sandstone facies type; Mandor *et al.* 2023) with moderately to densely packed and moderately to poorly sorted shells (Fig. 3C, D). This shell concentration is dominated by oysters (50.6% of the total macrobenthic assemblage), mainly *Lopha virleti* (Deshayes, 1833) and *Ostrea frondosa* (de Serres, 1829) (41.2 and 9.4%, respectively), associated with pectinids (36.5%), other bivalves (5.9%), gastropods, echinoids, and massive and fragmented branched corals (2.4% each). This macrobenthic assemblage is dominated by epifaunal and suspension-feeding taxa (92.9 and 94.1% of the total macrobenthic assemblage, respectively; Table 1).

Oyster shells are mainly disarticulated (88.4% of the total examined oyster shells), commonly concordant valves with low to moderate fragmentation (18.6%) and abrasion (Fig. 3C, D). The proportion of left (lower) valves is higher than the right one (60.5% and 39.5%, respectively). Most shells occur in a current-stable convex-up orientation (Fig. 3C, D). A few shells show a vertical position with the commissural plane nearly perpendicular to the bottom and the ligamental area pointing downwards. Right valves are thinner and more fragile than left ones, which probably led to abundant fragmented remains and fewer identifiable valves. Adult shells dominated, although shells of juvenile individuals are common. Borings are moderately recorded (30.2% of the total examined oyster shells; Table 1), and referred to clionid sponges, polychaete annelids, endolithic bivalves, and vermetid gastropods. Skeletal remains of encrusting organisms are likewise moderate (27.9% of the total examined oyster shells), including bryozoans, serpulids, oysters (adults and juveniles), and balanoid barnacles.

Pectinid-shell concentration (bed 13).– This concentration occurs in the upper part of the bioturbated marl of bed 13 (a sandy high porosity packstone facies type; Mandor *et al.* 2023). It is composed of pectinid shells in a calcareous sandstone matrix, attaining a thickness of 1.0 to 1.5 m (Fig. 2) with a lateral extension of at least 200 m. It is characterized by densely packed, moderately to poorly sorted shells, an uneven lower surface with a relief up to 0.4 m, and a sharp upper contact parallel to the bedding planes (Table 1; Fig. 3E). In this shell concentration, pectinids are the most common faunal element (96.6% of the total macrobenthic assemblage), including *Oppenheimopecten josslingi*, *Flabellipecten schweinfurthi*, *Macrochlamis ziziniae*, *Aequipecten submalvinae* (Blanckenhorn, 1901), *A. radians* (Nyst & Westendorp, 1839), *Pecten benedictus* Lamarck, 1819, and *P. subarcuatus* Tournouër, 1873. The remainders are represented by rare gastropods and echinoids (1.7% each). Up-section, this concentration grades into less fossiliferous sediments (Fig. 3E). Most of these bioclasts are fragmented. This macrobenthic assemblage is dominated by epifaunal and suspension-feeding taxa (100 and 96.6% of the total macrobenthic assemblage, respectively; Table 1).

Most of pectinid shells are adults and highly disarticulated (91.5% of the total examined pectinid shells; Table 1), showing high fragmentation (51.1%) and abrasion and sub-horizontal to chaotic orientations (Fig. 3E). However, shells of juvenile individuals are also present. In the disarticulated pectinid specimens, the average occurrence of left and right valves is unequal (67.4 and 32.6%, respectively). Borings are low (8.5% of the total examined pectinid shells), and referred to polychaete worms, clionid sponges, ctenostome bryozoans, and vermetid and predatory gastropods. Skeletal remains of encrusting organisms are low to moderate (21.3% of the total examined pectinid shells), comprising bryozoans, serpulids, and oysters (adults and juveniles) (Table 1).

Pectinid-shell concentration (bed 14b).– This thin pectinid concentration (1.0–1.5 m thick; Fig. 2) occurs in bed 14b (a sandy high porosity packstone facies type; Mandor *et al.* 2023), with a lateral extension of at least 200 m. It is characterized by an erosive bioturbated lower contact and a sharp upper contact (Table 1; Fig. 3F, G). This concentration can be subdivided into two parts. The lower greyish-greenish glauconitic sandstone interval with mud clasts in the basal part (Fig. 3G). The upper dark red, glauconitic, calcareous siltstone with coarse, yellowish to greenish mud-pebbles (Fig. 3F, H). This concentration composed of moderately to densely packed, moderately to poorly sorted pectinid shells (Table 1; Figs 2, 3G, I). Towards the top, pectinids dominate. This pectinid assemblage represents 84.2% of the total macrobenthic assemblage, and includes *Pecten fraasi*, *Oppenheimopecten josslingi*, *P. kochi*, *P. cristatocostatus* Sacco, 1897, *Aequipecten submalvinae*, and *Macrochlamis ziziniae*. In addition, gastropods (5.5%), echinoids (4.2%), oysters (3%), solitary and fragmented branched corals (2.4%), and other bivalves (0.6%) occur throughout the bed. Furthermore, celleporid bryozoans are also recorded, covering skeletal and non-skeletal elements. Most of these bioclasts are fragmented. This diverse macrobenthic assemblage is dominated by epifaunal and suspension-feeding taxa (95.2 and 90.9% of the total macrobenthic assemblage, respectively; Table 1).

Pectinid shells are totally disarticulated and reoriented (Fig. 3G, I). Shells of adult individuals are common. They mostly display a preferred convex-upward orientation. The average occurrence of left and right valves is unequal (42.1 and 57.9%, respectively). Pectinid specimens are highly fragmented (44.9% of the total examined pectinid shells), moderately to highly encrusted (38.3%), and rarely bioeroded (9.3%, Table 1). Skeletal remains of encrusting organisms include bryozoans, serpulids, and oysters (adults and juveniles). Boring traces include those of clionid sponges, polychaetes, endolithic bivalves, and predatory gastropods (Table 1).

Oyster shell concentration (bed 22).– This concentration is composed of a 0.5–1.0 m thick sandy marl (a sandy high porosity packstone facies type; Mandor *et al.* 2023), with a lateral extension of at least 200 m (Table 1; Fig. 2). It is characterized by densely packed oyster shells (Fig. 3J) and rests on a sharp to erosive lower contact and displays an erosive upper contact (Table 1). Oysters are the dominant group, accounting for 84.6% of the total macrobenthic assemblage, and including *Lopha virleti* (71.1%) and *Ostrea frondosa* (13.5%). The remainders are represented by rare pectinids (13.5%), other bivalves, and fragmented branched corals (1.0% each) (see inset in Fig. 3J). This macrobenthic assemblage is exclusively dominated by epifaunal and suspension-feeding taxa (Table 1).

Adult shells dominate, although shells of juvenile individuals are present. Oyster shells are highly disarticulated (97.7% of the total examined oyster shells), moderately to poorly sorted, and rarely fragmented (12.5%; Table 1; Fig. 3J). Shells commonly concordant, mostly in life position. However, a few valves show a chaotic orientation (Fig. 3J). In the disarticulated specimens, the average occurrence of left and right valves is distinctly unequal (67.4 and 32.6%, respectively). Boring traces are remarkably widespread (79.5% of the total examined oyster shells), and are attributed to clionid sponges, polychaete worms, endolithic bivalves, phoronid worms, and vermetid and predatory gastropods. Skeletal remains of encrusting organisms are likewise high (54.5% of the total examined oyster shells), including bryozoans, serpulids, oysters (adults and juveniles), balanoid barnacles, and corals (Table 1).

Sclerobiont assemblages

In the five examined Miocene pectinid and oyster shell concentrations, the external and internal surfaces of the left and right valves of both groups served as habitats for macroborers, microborers, and encrusting organisms, resulting in the occurrence of a characteristic endobiont and/or epibiont assemblages (Tables 1–3). The former dominate these sclerobiont faunas.

Bioerosion traces are represented by chambers and/or tunnels, which are the product of varied endolithic organisms, including clionid sponges, polychaete and sipunculid annelids, endolithic bivalves, phoronid worms, and ctenostome bryozoans. In addition, traces of gastropod activities also occurred (Table 2). In general, the abundance of bioerosion structures on the oyster valves are moderate to high (varies from 30.2 to 79.5% of shells affected), while in the pectinid shells, in contrast, the occurrence of these traces is remarkably low (<10%; Table 1). At least 15 endobiont ichnotaxa, belonging to 10 ichnogenera, have been identified (Table 2). Among this endobiont assemblage, *Entobia* and *Maeandropolydora* ichnospecies dominate, while traces of *Caulostrepsis*, *Gastrochaenolites*, *Oichnus*, *Renichnus*, *Santichnus*, *Talpina*, *Trypanites*, and *Iramena* represent subordinate components. Moreover, an unnamed trace of crab predation also occurs. It is worth mentioning that the ichnogenus *Entobia* dominates this endobiont assemblage by the rock volume removed and by the number of affected substrates (see below).

On oyster valves, abundant borings are found, particularly on the external and internal surfaces of the left valves (Table 3). Borings also occur, to a lesser extent, on both surfaces of the right valves. Dealing with pectinid shells, uncommon occurrences on the external and internal surfaces of the left valves, as well as a relatively rare occurrences on both surfaces of the right valves, have also been observed (Table 3). Collectively, all these traces belong to three ethological categories, including domichnia (80% of the total identified ichnotaxa), fixichnia (13.3%), and praedichnia (6.7%) (Table 2).

In the five studied shell concentrations, the occurrence of traces of encrustation on oyster and/or pectinid valves is moderate to high, varying between 27.9 and 54.5%, and between 8.2 and 38.3% of the total examined valves, respectively (Table 1). However, shells without any encrustation are numerous. At least six skeletobionts are recorded, including serpulids, bryozoans, oysters (adults and/or juveniles), balanoid barnacles, and corals (Table 3). On the encrusted pectinid and oyster valves, common occurrences of these epibionts on the external and internal surfaces of the left valves, as well as on both surfaces of the right valves, have been observed (Table 3). It is worthy of mention that serpulids represent the most abundant encrusters in terms of number of specimens and bryozoans in terms of area occupied and skeletal biovolume. Among this skeletobionts assemblage, suspension feeders (e.g. serpulids, bryozoans, oysters,

Table 2. The recorded ichnotaxa, their ethological categories, life habits and feeding modes of their producers.

Ichnotaxa	Ethological category	Producers	Producer life habit/feeding mode
Entobia cateniformis Bromley & D'Alessandro, 1984	domichnia	*Cliona vermifera* Hancock, 1867	stationary boring/suspension feeder
E. laquea Bromley & D'Alessandro, 1984	domichnia	*C. viridis* (Schmidt, 1862), *Pione vastifica* (Hancock, 1849)	stationary boring/suspension feeders
E. megastoma (Fischer, 1868)	domichnia	*C. celata* Grant, 1826	stationary boring/suspension feeder
Entobia isp.	domichnia	clionaid sponges	stationary boring/suspension feeders
Caulostrepsis taeniola Clarke, 1908	domichnia	*Polydora ciliate* (Johnston, 1838), *Lysidice ninetta* Audouin & Milne Edwards, 1833	stationary low-level epifaunal/mixed deposit-suspension feeders
Gastrochaenolites torpedo Kelly & Bromley, 1984	domichnia	*Lithophaga lithophaga* (Linné, 1758)	stationary boring/suspension feeder
Gastrochaenolites isp.	domichnia	*Lithophaga* sp.	stationary boring/suspension feeder
Maeandropolydora sulcans Voigt, 1965	domichnia	spionid polychaetes	stationary low-level epifaunal/mixed deposit-suspension feeders
Maeandropolydora isp.	domichnia	spionid polychaetes	stationary low-level epifaunal/mixed deposit-suspension feeders
Oichnus simplex Bromley, 1981	praedichnia	predatory gastropods	epifaunal/carnivores
Renichnus arcuatus Mayoral, 1987	fixichnia	vermited gastropods	stationary epifaunal/suspension feeders
Santichnus mayorali Verde et al., 2022	fixichnia	vermited gastropods	stationary epifaunal/suspension feeders
Talpina ramosa von Hagenow, 1840	domichnia	Phoronida	stationary boring/suspension feeders
Trypanites isp.	domichnia	polychaetes, sipunculoids acrothoracican barnacles	epifaunal/mixed deposit-suspension feeders stationary epifaunal/suspension feeders
Iramena danica Boekschoten, 1970	domichnia	Ctenostomata (*Penetrantia, Immergentia*)	stationary epifaunal/suspension feeders

Palaeoautecology based on the Getaway to the Paleobiology Database (http://www.fossilworks.org).

Table 3. Distribution of the recorded endobionts and epibionts on the affected external (ext.) and internal (int.) surfaces of the left and right valves (LV and RV, respectively) of the examined oyster and pectinid shells in the studied shell concentrations.

Endobionts/Epibionts	**Oyster valves**				**Pectinid valves**			
	LV		**RV**		**LV**		**RV**	
	ext.	**int.**	**ext.**	**int.**	**ext.**	**int.**	**ext.**	**int.**
Endobionts								
Entobia cateniformis Bromley & D'Alessandro, 1984	•	•		•				
E. laquea Bromley & D'Alessandro, 1984	•	•	•					
E. megastoma (Fischer, 1868)			•					
Entobia isp.	•	•	•	•		•	•	•
Caulostrepsis taeniola Clarke, 1908	•	•	•	•		•		
Gastrochaenolites torpedo Kelly & Bromley, 1984	•	•	•					
Gastrochaenolites isp.	•	•	•	•				
Maeandropolydora sulcans Voigt, 1965	•	•	•	•	•	•		•
Maeandropolydora isp.	•	•		•	•		•	
Oichnus simplex Bromley, 1981	•		•		•			
Renichnus arcuatus Mayoral, 1987	•		•		•	•		
Santichnus mayorali Verde et al., 2022	•							
Talpina ramosa von Hagenow, 1840		•						
Trypanites isp.	•	•				•		
Iramena danica Boekschoten, 1970					•			
Decapod predation					•			
Total endobionts recorded	12	10	9	6	6	5	2	2
Epibionts								
Serpulids	•	•	•	•	•	•	•	•
Bryozoans	•	•	•	•	•	•	•	•
Adult oysters	•		•	•		•	•	•
Juvenile oysters	•		•	•	•	•	•	•
Balanoid barnacles	•	•		•				•
Corals				•				
Total epibionts recorded	5	3	4	6	3	4	4	5

balanoid barnacles) are the most common faunal elements. Microcarnivores (i.e. corals), in contrast, rarely occur.

Shell concentration of bed 2.– Pectinid shells in this concentration are rarely affected by bioerosion (9.3%; Table 1). The following ichnospecies have been recorded: *Entobia* isp. (66.7% of the total affected pectinid valves) and *Maeandropolydora* isp. (44.4%) (Fig. 4).

Encrusting organisms on pectinid shells in this concentration are also rarely abundant (8.2%; Table 1). Three encrusting organisms have been recorded. Bryozoans and serpulids dominate this epibionts assemblage (62.5 and 50%, respectively), followed by balanoid barnacles (25%) (Fig. 4).

Shell concentration of bed 9.– As was mentioned, oyster shells in this concentration are moderately affected by bioerosion (30.2%; Table 1). The recorded endobionts assemblage is represented by 10 ichnospecies (Fig. 4). The ichnogenus *Entobia* dominates this assemblage, accounting for 77% of the total affected oyster valves, and including *Entobia* isp. (46.2%), *E. cateniformis*, and *E. laquea* (15.4% each) (Fig. 4). In addition, *Maeandropolydora sulcans* (30.8%), *Gastrochaenolites torpedo* (15.4%), and *Caulostrepsis taeniola* (15.4%) occur. Moreover, rare occurrences of *Maeandropolydora* isp., *Gastrochaenolites* isp., *Renichnus arcuatus*, and *Santichnus mayorali* (7.7% each) are also observed (Fig. 4).

Encrusting organisms on the examined oyster shells in this concentration are moderately abundant

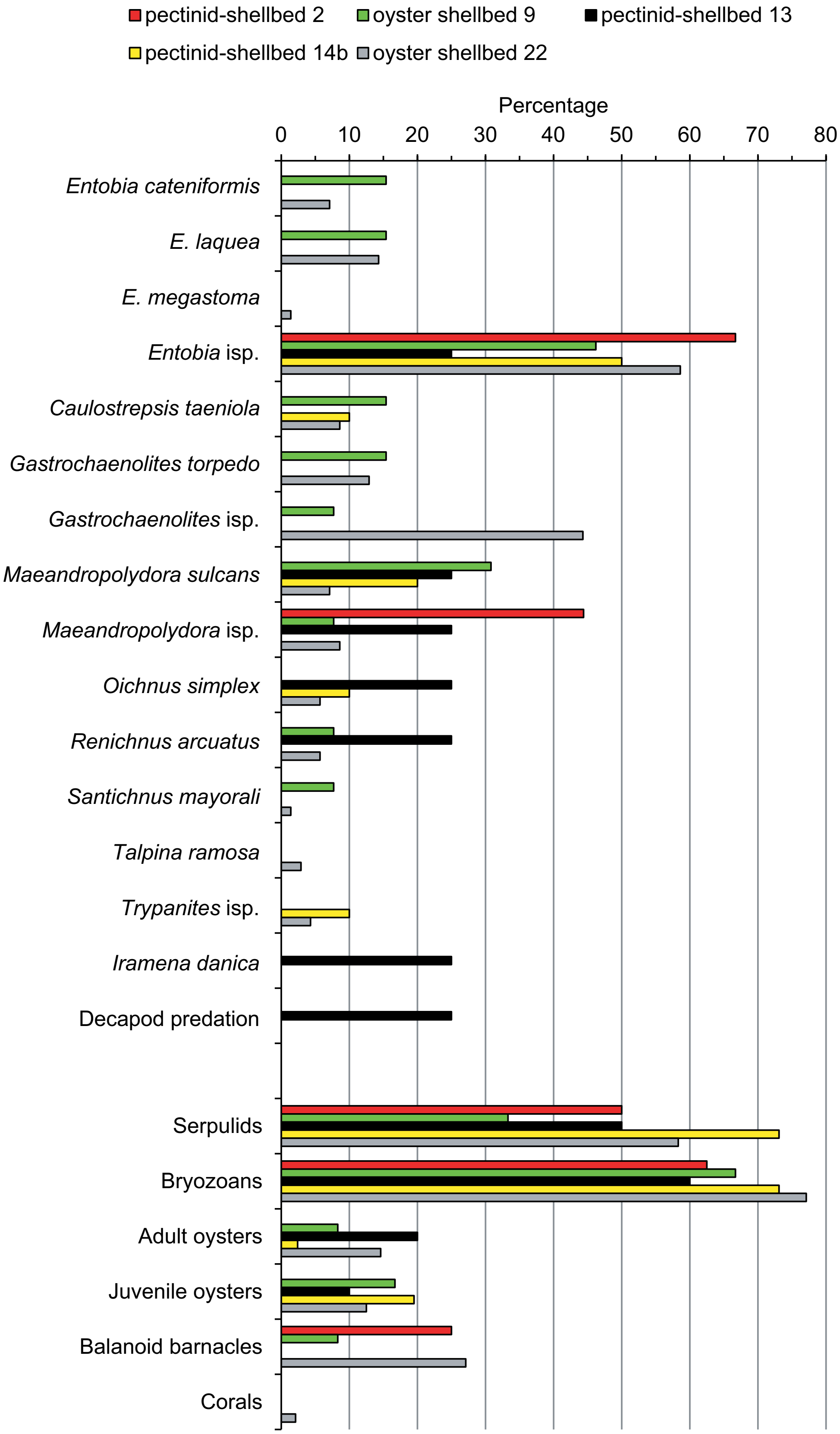


Fig. 4. Distribution and occurrences (percentage) of the observed bioerosion structures and encrusting organisms in the five shell concentrations of the Miocene succession in the study area.

(27.9%; Table 1). The recorded epibionts assemblage comprises five encrusters (Fig. 4). Bryozoans dominate this assemblage with 66.7% of the total affected oyster valves. Serpulids (33.3%) and juvenile oysters (16.7%) also occur (Fig. 4). Furthermore, rare occurrences of adult oysters and balanoid barnacles (8.3% each) are also recorded (Fig. 4).

Shell concentration of bed 13.– In this concentration, pectinid shells are rarely affected by bioerosion (8.5%; Table 1). The recorded endobionts assemblage is represented by seven ichnospecies (Fig. 4). The ichnogenus *Maeandropolydora* accounts for 50% of the total affected pectinid valves, including *Maeandropolydora sulcans* and *Maeandropolydora* isp. (25% each). In addition, traces of *Entobia* isp., *Oichnus simplex*, *Renichnus arcuatus*, *Iramena danica*, and a trace of decapod predation are observed (25% each) (Fig. 4). Noteworthy is the occurrence of all these bioerosion structures on the external surfaces of the left and right valves, particularly at the lower halves of the valves.

Epibionts on the total examined pectinid shells in this concentration are low to moderately abundant (21.3%; Table 1), including four encrusting organisms. Bryozoans and serpulids dominate this assemblage, accounting for 60 and 50% of the total affected pectinid valves, respectively (Fig. 4). The remainders are represented by adult (20%) and juvenile (10%) oysters.

Shell concentration of bed 14b.– Pectinid shells in this concentration are likewise rarely affected by bioerosion (9.3%; Table 1). The following ichnospecies have been recorded: *Entobia* isp. (50% of the total affected pectinid valves), *Maeandropolydora sulcans* (20%), *Caulostrepsis taeniola*, *Oichnus simplex*, and *Trypanites* isp. (10% each) (Fig. 4).

Encrusting organisms on pectinid shells in this concentration are moderately to highly abundant (38.3%; Table 1). Four encrusting organisms have been recorded. Serpulids and bryozoans dominate this epibionts assemblage (73.1% each), followed by juvenile and adult oysters (19.5 and 2.4%, respectively) (Fig. 4).

Shell concentration of bed 22.– Oyster shells in this concentration are highly affected by bioerosion (79.5%; Table 1). In comparison with those occurring in the first oyster shell concentration in bed 9, this concentration is characterized by a further increase in the richness of ichnospecies. The recorded endobionts assemblage is represented by 14 ichnospecies (Fig. 4). The ichnogenera *Entobia* and *Gastrochaenolites* remarkably dominate this assemblage, accounting for 81.4% and 57.2% of the total affected oyster valves, respectively. The ichnogenus *Entobia* includes the following ichnospecies: *Entobia* isp. (58.6%), *E. laquea* (14.3%), *E. cateniformis* (7.1%), and *E. megastoma* (1.4%) (Fig. 4). The ichnogenus *Gastrochaenolites* is represented by *Gastrochaenolites* isp. (44.3%) and *G. torpedo* (12.9%). Other endobiont faunal elements, in contrast, are relatively rare and comprise *Caulostrepsis taeniola*, *Maeandropolydora* isp. (8.6% each), *M. sulcans* (7.1%), *Oichnus simplex*, *Renichnus arcuatus* (5.7% each), *Trypanites* isp. (4.3%), *Talpina ramosa* (2.9%), and *Santichnus mayorali* (1.4%) (Fig. 4).

Encrusting organisms on the examined oyster shells are highly abundant (54.5%; Table 1). The recorded epibionts assemblage includes six encrusters (Fig. 4). Bryozoans and serpulids dominate this assemblage with 77.1 and 58.3% of the total affected oyster valves, respectively (Fig. 4). Balanoid barnacles (27.1%), adult oysters (14.6%), and juvenile oysters (12.5%) also occur (Fig. 4). Furthermore, a single occurrence of coral, accounting for 2.1% of the total affected oyster valves, has also been observed (Fig. 4).

Boring ichnotaxa

In the five studied shell concentrations, varieties of bioerosion traces produced by different bioeroding organisms were recorded in the examined oyster and pectinid shells. Fifteen endobiont ichnotaxa, belonging to 10 ichnogenera, have been identified (Table 2; Figs 5–8). Among them, dwelling borings (domichnia) are abundant and are represented by *Entobia cateniformis*, *E. laquea*, *E. megastoma*, *Entobia* isp., *Caulostrepsis taeniola*, *Gastrochaenolites torpedo*, *Gastrochaenolites* isp., *Maeandropolydora sulcans*, *Maeandropolydora* isp., *Talpina ramosa*, *Trypanites* isp., and *Iramena danica* (Table 2; Fig. 4). Other traces are less frequent, including fixichnia (attachment structures; *Renichnus arcuatus* and *Santichnus mayorali*), and praedichnia (predation structures; *Oichnus simplex*). In addition, an unnamed trace of a decapod predation also occurs (Fig. 4).

Entobia cateniformis *Bromley & D'Alessandro, 1984.–* The boring comprises long rows of cylindrical chambers that form an irregular maze through branching and anastomosis (Fig. 5A–C). Numerous chambers are elongated, T- and L- (Fig. 5B, C). The apertures are small with well-developed canals. They are irregularly distributed on the shell surface. The growth phases 'A' and 'B' occur, representing exploratory tubules and underdeveloped chambers, respectively (*sensu* Bromley & D'Alessandro 1984) (Fig. 5A–C). A natural mould is also recorded in the left valve of an oyster shell (Fig. 5B).

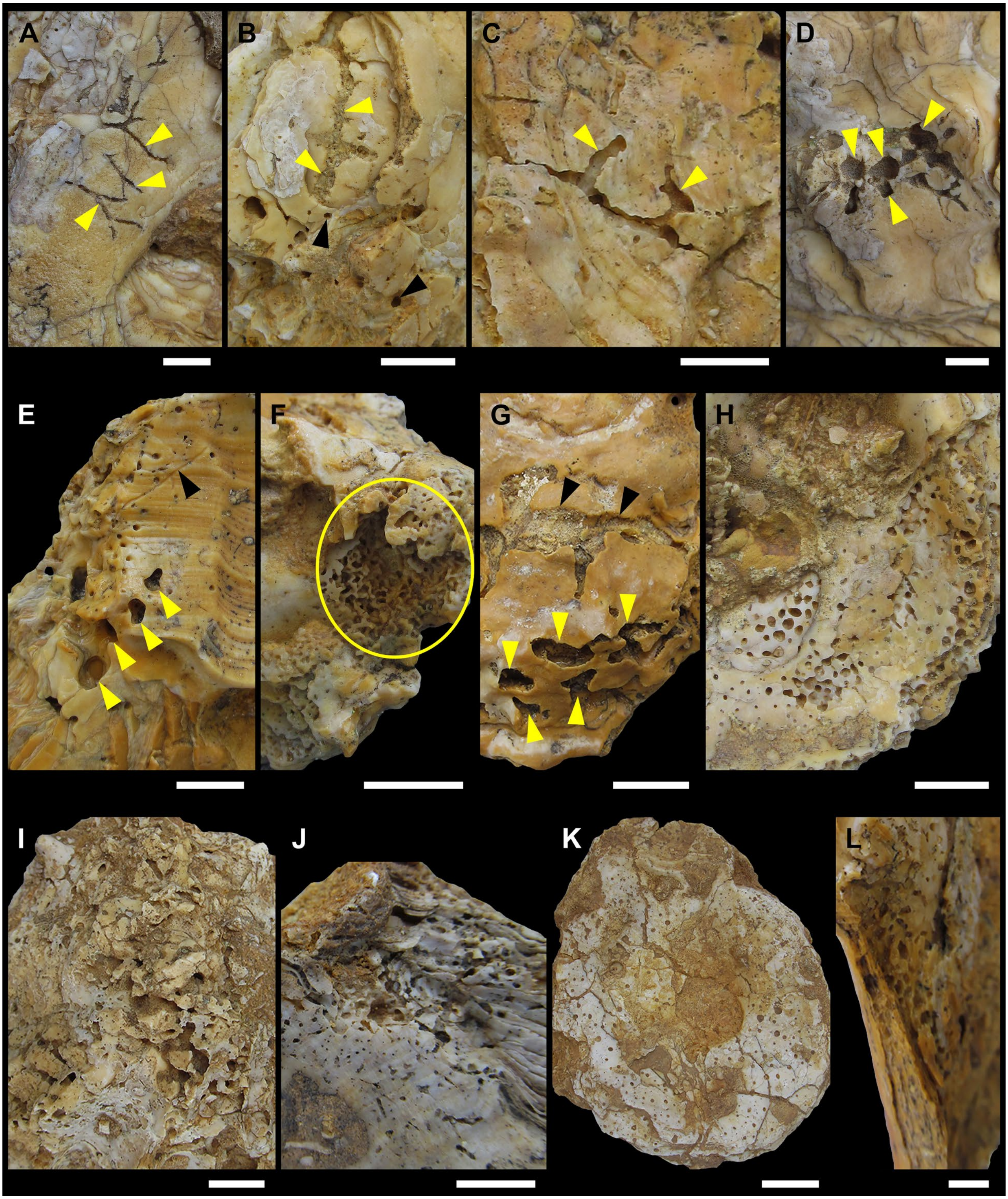


Fig. 5. Endobionts on oyster shells. A–C, *Entobia cateniformis*. A, represents the growth phase 'A' (arrows) (Gh9O18). B, natural mould, and apertures (yellow and black arrows, respectively) of *E. cateniformis* (Gh9O33). C, an irregular maze of *E. cateniformis* (arrows) with T- and L- elongated chambers (Gh22O200). D–F, *Entobia laquea*. D, tunnel systems and chambers (arrows) (Gh9O1). E, *E. laquea* (yellow arrows) associated with curved tunnels of *Talpina ramose* (black arrow) (Gh22O201). F, *E. laquea* (circle) showing growth phase 'B' and 'C', stenomorphic (Gh22O212). G, subcylindrical gallery of *E. megastoma* growth phase 'C-D' showing branching via bifurcation and swollen at nodal points (yellow arrows) with merging of several galleries (black arrows) (Gh22O243). H–L, circular to subcircular apertures of *Entobia* isp on surface of some oyster shells (Gh22O213, Gh9O4, Gh9O3, Gh9O27, and Gh22O237, respectively). Scale bars equal 1 cm, except for D and K, which are 2 cm.

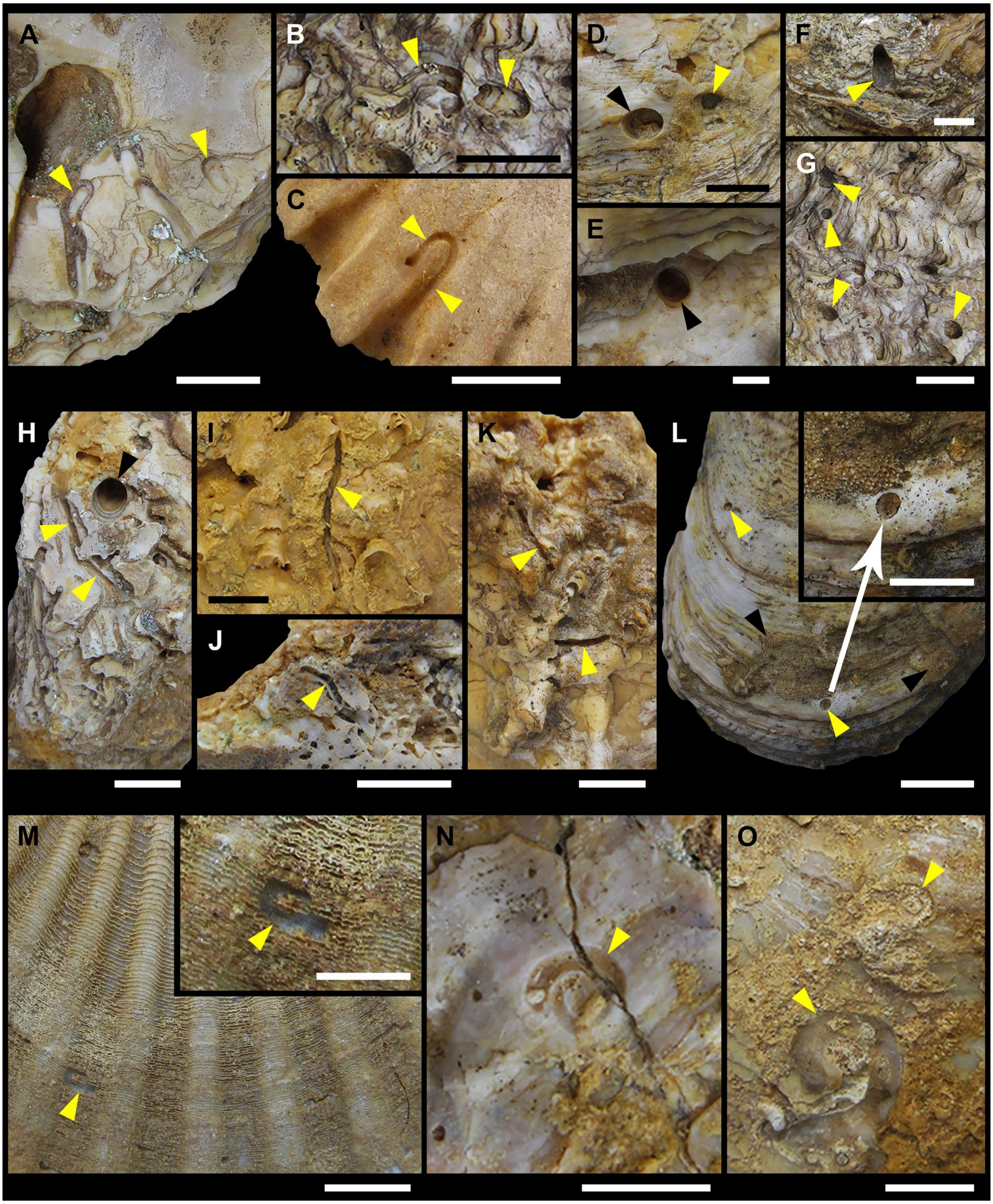


Fig. 6. Endobiont assemblage on oyster and pectinid shells. A–C, narrow U-shaped borings of *Caulostrepsis taeniola* (arrows). A, *C. taeniola* on the internal surface of oyster valve (Gh9O22). B, *C. taeniola* on the external surface of oyster valve (Gh22O253). C, *C. taeniola* on the internal surface of pectinid valve (Gh14bP99). D, E, clavate- to flask-shaped borings of *Gastrochaenolites torpedo*. D, *G. torpedo* on the external surface of an oyster shell (black arrow) with a single *Gastrochaenolites* isp. (yellow arrow) (Gh22O257). E, an ellipsoidal cross-section of *G. torpedo* (arrow) on the external surface of an oyster shell (Gh9O2). F, G, *Gastrochaenolites* isp. (arrows) in external surface of an oyster shell (Gh22O182 and Gh22O253, respectively). H, boring of *Gastrochaenolites* isp., showing the internal surface with concentric lines sculpture (black arrow). Note the cylindrical gallery of *Maeandropolydora sulcans*, running parallel and in contact with each other in pairs (yellow arrows) (Gh9O15). I, J, sinuous excavations of *Maeandropolydora sulcans* (arrows) on the surfaces of oyster shells (Gh22O241 and Gh9O3, respectively). K, *Maeandropolydora* isp. (arrows) on the external surface of an oyster shell (Gh9O1). L, short cylindrical to subcylindrical borings of *Oichnus simplex* (yellow arrows) in the external surface of the oyster shell. Note the occurrence of bryozoan sheet (black arrows) (Gh22O260). M, a small single crescentic depression of the ichnospecies *Renichnus arcuatus* (arrows) on the external surface of pectinid shell (Gh13P86). N, O, spiral shallow structure of *Santichnus mayorali* (arrows) in the external surfaces of oyster shells (Gh9O2 and Gh22O262, respectively). Scale bars equal 1 cm, except for A, F, H and K, which are 2 cm, and for C and insets in L and M, which are 0.5 cm.

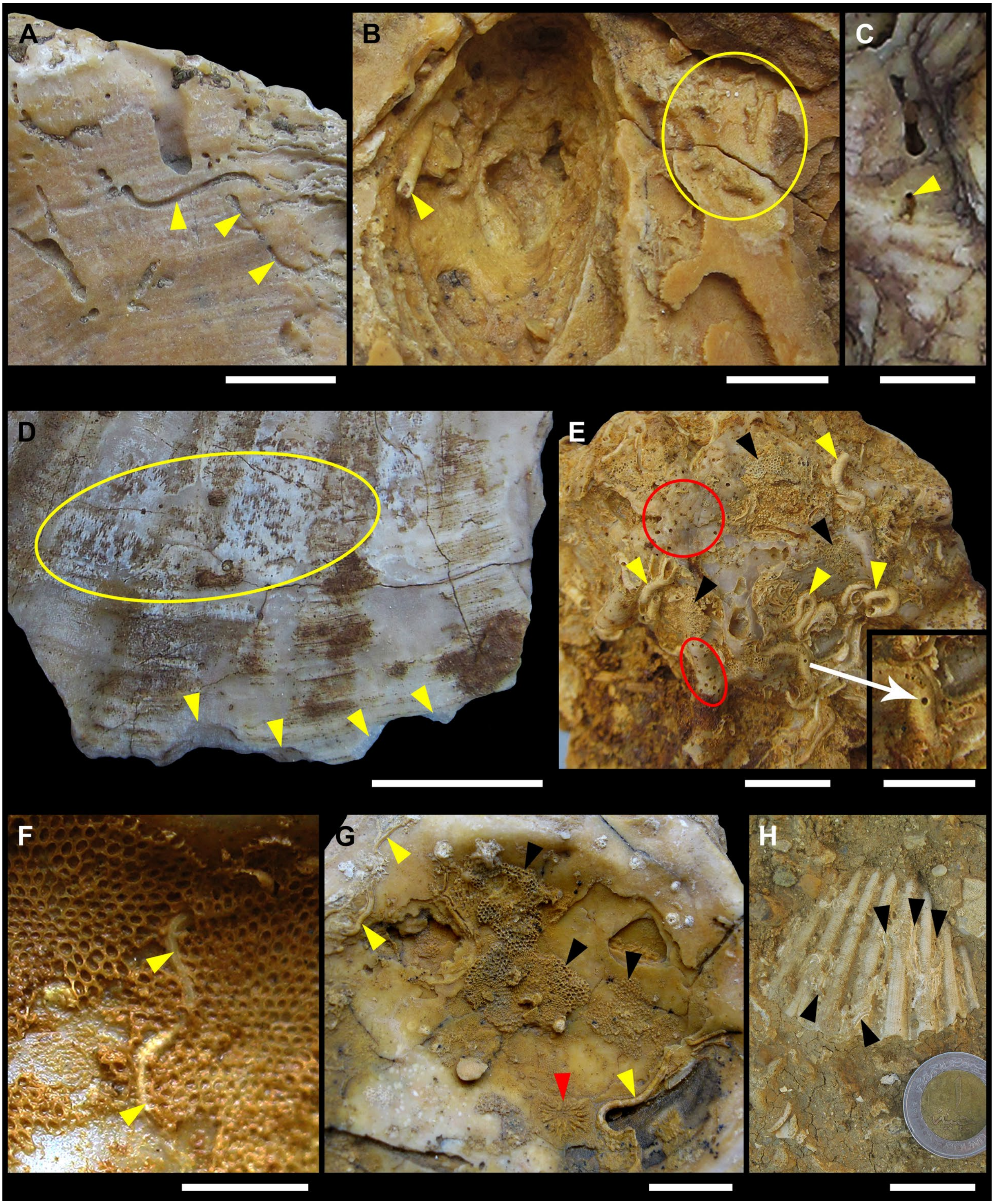


Fig. 7. Epi- and endobiont faunal communities on oyster and pectinid shells. A, straight to slightly curved tunnels of *Talpina ramosa* (arrows) slightly parallel to an oyster shell surface (Gh22O192). B, C, single entrance cylindrical boring of *Trypanites* isp. (arrows) perpendicular to the surface of shell (Gh22O221 and Gh22O253, respectively). Note the natural mould of *?Entobia laquea* (circle). D, irregular bifurcated long primary tunnels of *Iramena danica* (ellipse). Note the decapod predation on the ventral margin of the pectinid shell (yellow arrows) (Gh13P51). E, cluster of sepulid worms (*Hydroides*) (yellow arrows) on the external surface of oyster shell and together with bryozoan sheets (black arrows) and *Entobia* isp. (red ellipse). Note the occurrence of *Oichnus simplex* (inset), penetrating a *Serpula* tube (Gh14bO44). F, sheet-like cheilostome bryozoan overgrows the serpulid worm (arrows) on the internal surface of an oyster valve (Gh14bO44). G, epibiont assemblage, including bryozoans (black arrows), serpulids (yellow arrows) and a single eroded solitary coral (red arrow) on the internal surface of an oyster shell (Gh22O237). H, a swarm of serpulid worms (arrows) in inter-ribs of the external surface of a pectinid shell (bed 14b). Scale bars equal 1 cm, except for H, which is 2 cm, the inset in E, which is 0.5 cm, C, which is 0.25 cm, and for F, which is 0.3 cm.

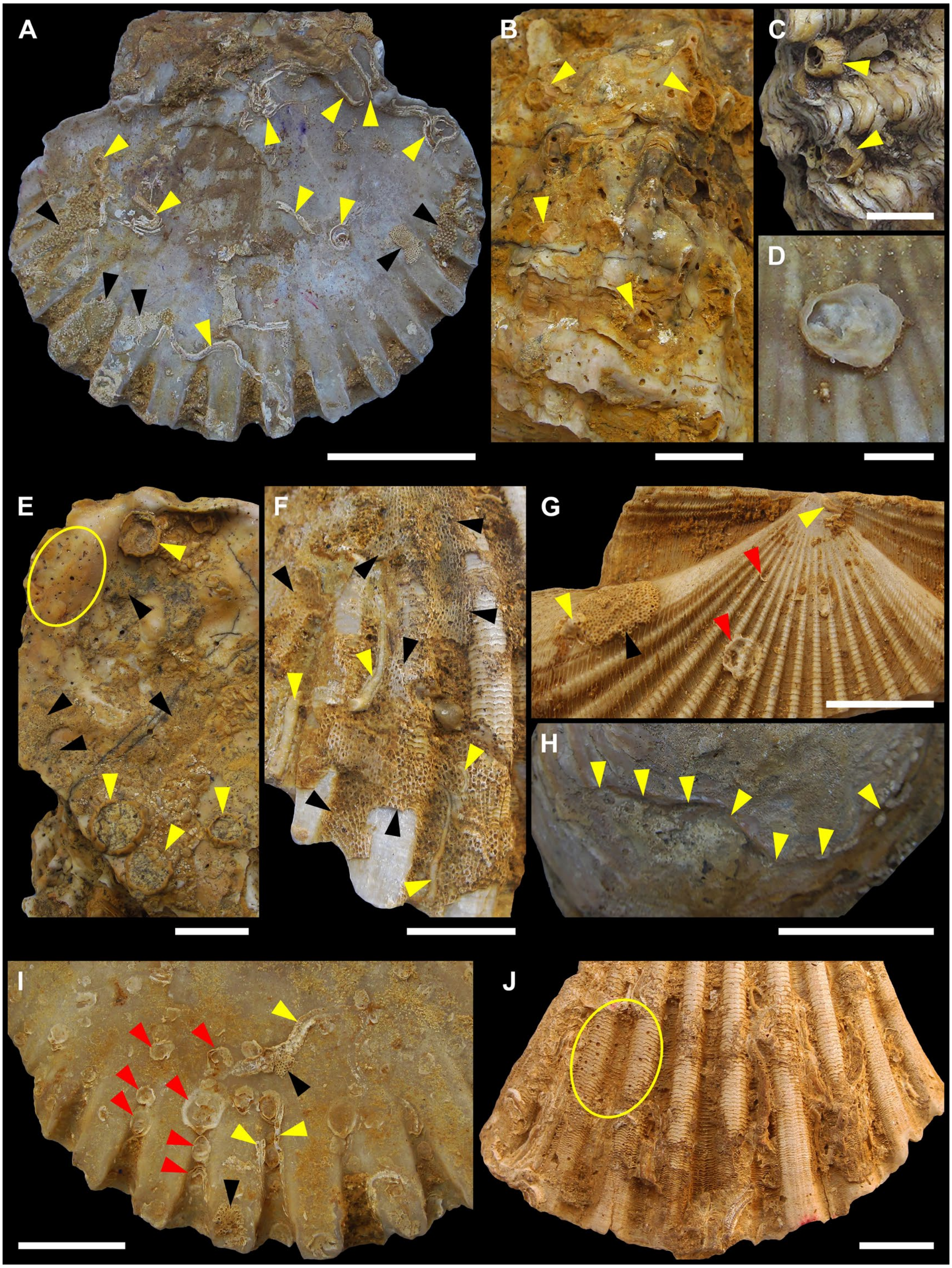


Fig. 8. Epibionts on oyster and pectinid shells. A, epibiont assemblage, including bryozoans (black arrows) and serpulids (yellow arrows) on the internal surface of a pectinid valve (Gh13P318). B, C, balanoid barnacles (arrows) on the external surface of an oyster valve (Gh22O193 and Gh22O253, respectively). D, small juvenile oyster valve encrusted the internal surface a pectinid shell (Gh13P89). E, balanoid barnacles (yellow arrows) and bryozoans (black arrows) on the internal surface of an oyster valve. Note the occurrence of *Entobia* isp. (ellipse) (Gh22O248). F, epibiont assemblage, including bryozoans (black arrows) and serpulids (yellow arrows) on the external surface of a pectinid shell (Gh14bP130). G, epibiont assemblage, including bryozoans (black arrow), serpulids (yellow arrows) and juvenile oyster (red arrows) on the external surface of a pectinid shell (Gh14bP95). H, pathological phenomena; shell repair structure (arrows) on the external surface of an oyster shell (Gh22O256). I, epibiont assemblage, including bryozoans (black arrows), serpulids (yellow arrows) and several juvenile oyster shells (red arrows) on the internal surface of a pectinid shell (Gh14bP94). J, cluster of serpulid worms in inter-ribs of the external surface of a pectinid interribs (Gh14bP129). Note the occurrence of *Entobia* isp. (ellipse). Scale bars equal 2 cm, except for F, G, I and J, which are 1 cm, C, which is 0.5 cm, and for D, which is 0.25 cm.

The described specimens resemble *E. cateniformis* type specimens described by Bromley & D'Alessandro (1984, pl. 16, figs 1, 3, 4, 5, pl. 17, fig. 3, pl. 27, fig. 3, text-fig. 3). In beds 9 and 22, this ichnospecies co-occurs with *Entobia* isp. and *Caulostrepsis taeniola*. This structure was produced by the boring sponge *Cliona vermifera* Hancock, 1867 (Table 2) (Bromley & D'Alessandro 1984).

Entobia laquea *Bromley & D'Alessandro, 1984.*– Borings appear as tunnel systems and chambers in well-developed growth phases 'A' and 'C' (Fig. 5D, E). In the growth phase 'A', the network is composed of thin, almost straight tunnels, about 0.5 mm in diameter. Growth phase 'C' is represented by irregular, oval, and elongate to subangular chambers (underdeveloped chambers of Bromley & D'Alessandro 1984), 1.5–2.5 mm in diameter (Fig. 5D, E). Besides borings, natural moulds are also recorded (Fig. 7B). Apophyses are rare, probably due to the state of preservation.

Entobia laquea shows a great morphological variety of chambers, including subtriangular, irregularly oval, or sub-globose form that are filled with calcite or fine-grained sand (Fig. 5D, E). However, eroded, half-cut, empty chambers also occur in some specimens. The described specimens resemble *E. laquea* type specimens described by Bromley & D'Alessandro (1984, pl. 17, fig. 2, pl. 19, fig. 2, pl. 23, fig. 1, text-figs 5–6). In beds 9 and 22, it co-occurs with *Talpina ramosa*, *Gastrochaenolites torpedo*, *Maeandropolydora sulcans*, *Trypanites* isp. and *Entobia* isp. *Entobia laquea* was produced by clionid sponges (Table 2), e.g. *Cliona viridis* (Schmidt, 1862) and/or *Pione vastifica* (Hancock, 1849) or its close relatives (Bromley & Asgaard 1993a; Perry 1996).

Entobia megastoma *(Fisher, 1868).*– The galleries are subcylindrical, branching via bifurcation and swollen at nodal points where several galleries merge (Fig. 5G). The apertures of borings are numerous and large, circular to oval. The growth phases 'C' and 'D' occur, representing underdeveloped and adult chambers, respectively (*sensu* Bromley & D'Alessandro 1984).

The described specimens resemble *E. megastoma* specimens described and illustrated by Bromley & D'Alessandro (1984, pl. 23, fig. 3, pl. 24, fig. 2, 3, pl. 26, fig. 1, pl. 27, fig. 2, text-fig. 8). In bed 22, it co-occurs with *Gastrochaenolites* isp. This structure was produced by clionid sponges of the species *Cliona celata* Grant, 1826 (Table 2; Bromley & D'Alessandro 1984).

Entobia *isp.*– The circular to subcircular apertures on the shell surface. The diameter of apertures is variable (0.4 to 2.0 mm); they are irregularly distributed on the shell surface (Figs 5H–L, 7E, 8E, J). In bed 22, these borings co-occur with *Balanus* sp. and *Maeandropolydora sulcans*. A remarkable example is given by an oyster valve where natural mould of ?*Entobia laquea* can be seen in the wall of a *Gastrochaenolites* boring. This structure is recorded on most of the studied oyster and pectinid shells. *Entobia* isp. is a product of boring sponges (Table 2).

Caulostrepsis taeniola *Clarke, 1908.*– Smooth, elongate, and narrow U-shaped boring with a single aperture and distinct limbs that are interconnected by a vane (Fig. 6A–C). Borings vary in size from 8.0 to 25.0 mm in length and 1.0 to 1.5 mm in width. This trace occurs on the external and internal surfaces of oyster shells (Fig. 6A, B), and on the internal surface of pectinid left valves (Fig. 6C). In bed 9, *Caulostrepsis taeniola* co-occurs with *Entobia* isp. In bed 22, it also associated with *Gastrochaenolites* isp., *Trypanites* isp. and serpulid tubes. *Caulostrepsis* is mainly considered to be produced by the polychaetes of the genus *Polydora* (Table 2; Radwański 1969).

Gastrochaenolites torpedo *Kelly & Bromley, 1984.*– Smooth elongate chamber, clavate-shaped to flask-shaped, with ellipsoidal cross-section, and pointed distal end (Fig. 6D, E). The neck has a constriction near the aperture. The internal surfaces of borings are either smooth or display a sculpture of concentric lines (Fig. 6H). Majority of borings maintain their siphonal apertures towards the shell edges. The chamber is 14–22 mm long and 9–13 mm in diameter.

The studied specimens resemble the ichnospecies type material of Kelly & Bromley (1984, p. 802, fig. text-figs 3F, 8A–B). *Gastrochaenolites torpedo* was recorded on external and internal surfaces of left and right oyster valves. In bed 9, it co-occurs with *Maeandropolydora sulcans*, and in bed 22 with *Entobia* isp., *Trypanites* isp., and *Caulostrepsis taeniola*. The specimens from bed 22 are only tentatively assigned to the ichnospecies. *Gastrochaenolites torpedo* is produced by the rock-boring bivalve *Lithophaga lithophaga* (Linné, 1758) (Table 2).

Gastrochaenolites *isp.*– *Gastrochaenolites*-like structures commonly occur in the oyster shells (Fig. 6D, F, G). They occur as unlined, deep depressions, with rounded to oval apertures in cross-section, 4–6 mm in depth. The poor preservation of these traces prevents their assignment to an ichnospecies. *Gastrochaenolites* is generally produced by rock-boring bivalves, comprising mostly *Lithophaga*, or less commonly *Jouannetia* and *Gastrochaena* (e.g. Kelly & Bromley 1984; Radwański *et al.* 2011).

Maeandropolydora sulcans *Voigt, 1965.*– Cylindrical galleries, usually with two apertures, running parallel, and in contact with each other in pairs, with or without fusion (Fig. 6H–J). Borings are sinuous excavations on the surfaces of oyster shells. Loose or tight loops may occur. The size of borings is somewhat variable, length ranges from 11 to 32 mm and the width from 0.9 to 2.0 mm. Vanes and pouches are absent. The described borings are in the form of cylindrical galleries with a winding course as in *M. sulcans* according to the definition of the ichnospecies (see Knaust 2008, p. 364).

In bed 9, *M. sulcans* co-occurs with *Gastrochaenolites torpedo* and *Entobia* isp. In bed 22, it co-occurs with *Entobia* isp., *Santichnus mayorali*, *Balanus* sp., serpulids, and bryozoans. This boring is interpreted as a dwelling structure of one of several polychaete families, especially spionidae (Table 2) (Bromley & D'Alessandro 1983; Bromley 1994).

Maeandropolydora *isp.*– Traces are common in both oyster and pectinid shells. They occur as a long, shallow, and sinuous cylindrical gallery with at least two apertures (Fig. 6K). The borings run through the substrate in irregular contorted tunnels. Vanes and pouches are absent. The length varies between 8 and 14 mm. The diameter ranges from 0.7 to 1.3 mm. As mentioned above, *Maeandropolydora* is usually attributed to polychaete annelid worms (Bromley & D'Alessandro 1983; Bromley 1994).

Oichnus simplex *Bromley, 1981.*– Short cylindrical to subcylindrical boring; axis nearly perpendicular to the substrate surface (Figs 6L, 7E). All borings (about eight) do not penetrate the shell wall, i.e. incomplete borings. The described examples resemble the ichnospecies type material described and illustrated by Bromley (1981, p. 60, figs 2, 4, 5). This ichnospecies is recorded in oysters and pectinids of beds 13, 14b, and 22. It co-occurs with *Renichnus arcuatus*, *Entobia* isp., and *Maeandropolydora* isp. *Oichnus simplex* is interpreted as praedichnia of certain gastropod families, particularly naticids (Table 2) (Bromley 1981; Pickerill & Donovan 1998).

Renichnus arcuatus *Mayoral, 1987.*– A crescentic depression in the surface of shell (Fig. 6M). The edges of the depression are not elevated. The length of the depression is about 0.1 mm. The depression closely resembles shape of crescentic depressions of *Renichnus arcuatus* described and illustrated by Verde *et al.* (2022, p. 8, fig. 5G). In the studied samples, this ichnospecies is recorded only on the external surfaces of oyster and pectinid shells. It co-occurs with *Oichnus simplex* (incomplete) and *Maeandropolydora* isp. This ichnospecies is generated by vermetid gastropods (Table 2) when a high trochospiral shell attaches to the substrate with the coiling axis parallel or tangential to the attachment surface (Mayoral 1987; Verde *et al.* 2022; Khalili & Vinn 2023).

Santichnus mayorali *Verde et al., 2022.*– Spiral shallow structure appeared as a canal; semi-circular in cross-section following a spiral path of up to three whorls (Fig. 6N, O); the width of the canal increases in a gradual manner following the development of spiral. The spiral lies with its coiling axis perpendicular to the shell surface.

The described specimens resemble the ichnospecies type material figured by Verde *et al.* (2022, p. 8, fig. 5). In bed 22, *Santichnus mayorali* co-occurs with *Maeandropolydora sulcans* on the external surfaces of oyster shells. This ichnotaxon is interpreted as an etched trace (fixichnia) produced by vermetid gastropods (Table 2; Verde *et al.* 2022). They scratch the surface of hard substrates to eliminate material and then cement themselves directly to it (Savazzi 1996; Bromley & Heinberg 2006).

Talpina ramosa *von Hagenow, 1840.*– Burrow systems formed of straight to slightly curved tunnels nearly parallel to the shell surface (Figs 5E, 7A). Tunnels are usually preserved as variably open canals on the surface of shells. The burrow system shows a more or less constant diameter of tunnels (0.2 to 0.3 mm). The described branching tunnels are similar to *Talpina ramosa* and can be assigned to this ichnospecies with confidence.

This ichnospecies is recorded only on the internal surfaces of oyster left valves of bed 22. It co-occurs with *Gastrochaenolites* isp. and *Entobia* isp. Although *T. ramosa* is considered as a dwelling trace (domichnion) produced by suspension-feeding worms (Fatka *et al.* 2011), Bertling (1992) interpreted it as a feeding structure, produced by opportunistic, infaunal and detritus- or deposit-feeding polychaetes. Furthermore, others suggested that *Talpina* was formed by phoronids (Table 2; Taylor & Wilson 2003).

Trypanites *isp.*– Cylindrical boring with a single entrance perpendicular to the surface of shell (Fig. 7B, C). These borings are assigned to *Trypanites* Mägdefrau, 1932 (p. 151–153, fig. 5:1–2) because their characters match definition of the ichnogenus (Blissett & Pickerill 2007). In bed 22, *Trypanites* co-occurs with *Entobia laquea* and *Entobia* isp. This trace fossil is produced mainly by polychaetes, sipunculoids, and/or acrothoracican barnacles (Table 2; Ekdale *et al.* 1984).

Iramena danica *Boekschoten, 1970.*– The boring system consists of irregular bifurcated long primary tunnels (Fig. 7D). The apertures are rounded to kidney-shaped, opened into a main cavity (along the tunnels). The described specimen resembles the ichnospecies type material described and illustrated by Boekschoten (1970, p. 45, fig. 1). In bed 13, it co-occurs with traces of possible decapod predation (see below). This boring is produced by ctenostome bryozoans (Table 2) (Boekschoten 1970; Barrier & D'Alessandro 1985).

Predation

On the studied shells, boring predation is rare. Durophagous predation may also have been rare as estimated from a single shell repair structure. The undulated edge of a pectinid valve indicates crab predation (Fig. 7D). However, there is a possibility that durophagous predation may have been more common if the predators were extremely efficient and destroyed the shells of their prey (Fig. 7D).

Encrusting taxa

As has been mentioned, the recorded skeletobionts assemblage includes serpulids, bryozoans, oysters (adults and/or juveniles), balanoid barnacles, and corals (Table 3; Figs 4, 7E–H, 8). Serpulid worms and bryozoans are among the most widely distributed organisms, while oysters, balanoid barnacles, and corals are recorded on a relatively few specimens (Fig. 4). Several reciprocal overgrowths were also observed between different encrusters (Fig. 7E–G, 8A, F, I).

Serpulids.– Abundant polychaete specimens have been found attached to pectinid shells with lesser numbers on oyster shells (Fig. 4). They encrusted on external and internal surfaces of the affected left and right valves of both oysters and pectinids (Table 3). The tubeworm association is dominated by *Hydroides*, *Filograna*, and *Spirobranchus* among others (for more details, see Mandor *et al.* 2022). They mostly grew as solitary individuals (Figs 7F, G, 8F, I), but in other cases, they form a rather dense cluster (Figs 7E, H, 8J).

Bryozoans.– In the skeletobionts community recorded in the five shell concentrations studied, bryozoans represent the most abundant encrusters in terms of abundance and area covered (Table 3; Fig. 4). As with serpulids, bryozoans encrusted on both external and internal surfaces of the affected oyster and pectinid left and right valves (Table 3). They include at least three species of multiserial, unilaminar cheilostome bryozoans showing moderate to poor preservation (Figs 7E–G, 8A, F, G, I). The present bryozoan species are comparable to the bryozoan species described from the middle Miocene Marmarica Formation of the Siwa Oasis (Ziko *et al.* 2000; El Hedeny *et al.* 2021a).

Oysters (adults and juveniles).– In the five studied shell concentrations, some oyster valves encrust the external and internal surfaces of the affected oyster and pectinid valves (Figs 4, 8D, G, I). The attached oysters are mainly represented by different ontogenetic stages of the left valves. Noteworthy is the absence of adult and juvenile oyster encrusters on the internal surface of the affected oyster left valves (Table 3). On the other hand, several juvenile oysters are clustered in the internal surfaces of the affected pectinid valves (Fig. 8I).

Balanoid barnacles.– Collectively, barnacles occur only on three of the five studied shell concentrations, including beds 2, 9, and 22 (Fig. 4). They are observed on the external and internal surfaces of the affected oyster left valves, and only on the internal surfaces of the affected oyster and pectinid right valves (Table 3). The balanoid barnacle' assemblage is characterized by different-sized individuals, ranging between 0.25 to 1.7 cm in basal diameter (Fig. 8B, C, E). These balanoid barnacles may represent forms of one or more species of the genus *Balanus*.

Corals.– Corals occur as a single small (0.7 cm diameter), solitary scleractinian specimen (probably *Ceratotrochus* sp.), being attached to the internal surface of an oyster right valve in the oyster concentration of bed 22 (Table 3; Figs 4, 7G). *Ceratotrochus* sp. was recorded in the topmost part of the middle Miocene succession in the Gebel Gharra area (see Mandor *et al.* 2023).

Discussion

Depositional palaeoenvironments

In Egypt, the Oligocene and the Oligocene/Miocene transition were times of rifting, uplift, regression, volcanicity, opening of the Red Sea, and continental sedimentation (Said 1962, 1990; Sestini 1984; Issawi *et al.* 1999; Guiraud *et al.* 2005). Following these remarkable tectonic events, the Miocene transgressive phase advanced toward the northern parts of the country. Consequently, Miocene sediments were recorded in several outcrops in the northern parts of the Western and Eastern Deserts, the Gulf of Suez, and the Red Sea areas (Said 1962, 1990; Gindy & El Askary 1969; Abdel-Fattah & Assal 2016; El-Sabbagh *et al.* 2016; Mandor *et al.* 2023). These successions are characterized by great facies variations and include a large number of unconformity surfaces (Gindy & El Askary 1969; Said 1990; Issawi *et al.* 1999; Abdel-Fattah *et al.* 2013; Hewaidy *et al.* 2018; Mandor *et al.* 2023).

In the Cairo-Suez District, the lower–middle Miocene succession was deposited under shallow-marine conditions on a mixed siliciclastic and carbonate inner ramp setting (Abou Khadrah *et al.* 1993; Piller *et al.* 1998; Mandic & Piller 2001; Nebelsick & Kroh 2002; Kroh & Nebelsick 2003; Tawfik *et al.* 2015; El-Sorogy *et al.* 2017; Mandor *et al.* 2023). Based on detailed litho- and biofacies analyses of the Gebel Gharra Miocene section, Mandor *et al.* (2023, Fig. 11) concluded that the lower Miocene Gharra and the middle Miocene Geniefa formations were deposited in a relatively wide spectrum of shallow-marine environments, ranging from supratidal, lagoonal to shoal settings. These facies record early–middle Miocene transgressive-regressive cycles, and document potential environmental fluctuations under different energy conditions (Fig. 9). These environmental fluctuations may indicate the effect of local tectonics associated with the beginning of the Red Sea and Gulf of Suez rifting (e.g. Said 1990; Purser & Bosence 1998). The noticeable variations in the abundance and distribution of macrofaunal content within the studied Gharra and Geniefa formations likewise confirm these controlling factors (Fig. 2; Mandor *et al.* 2022, 2023; present study).

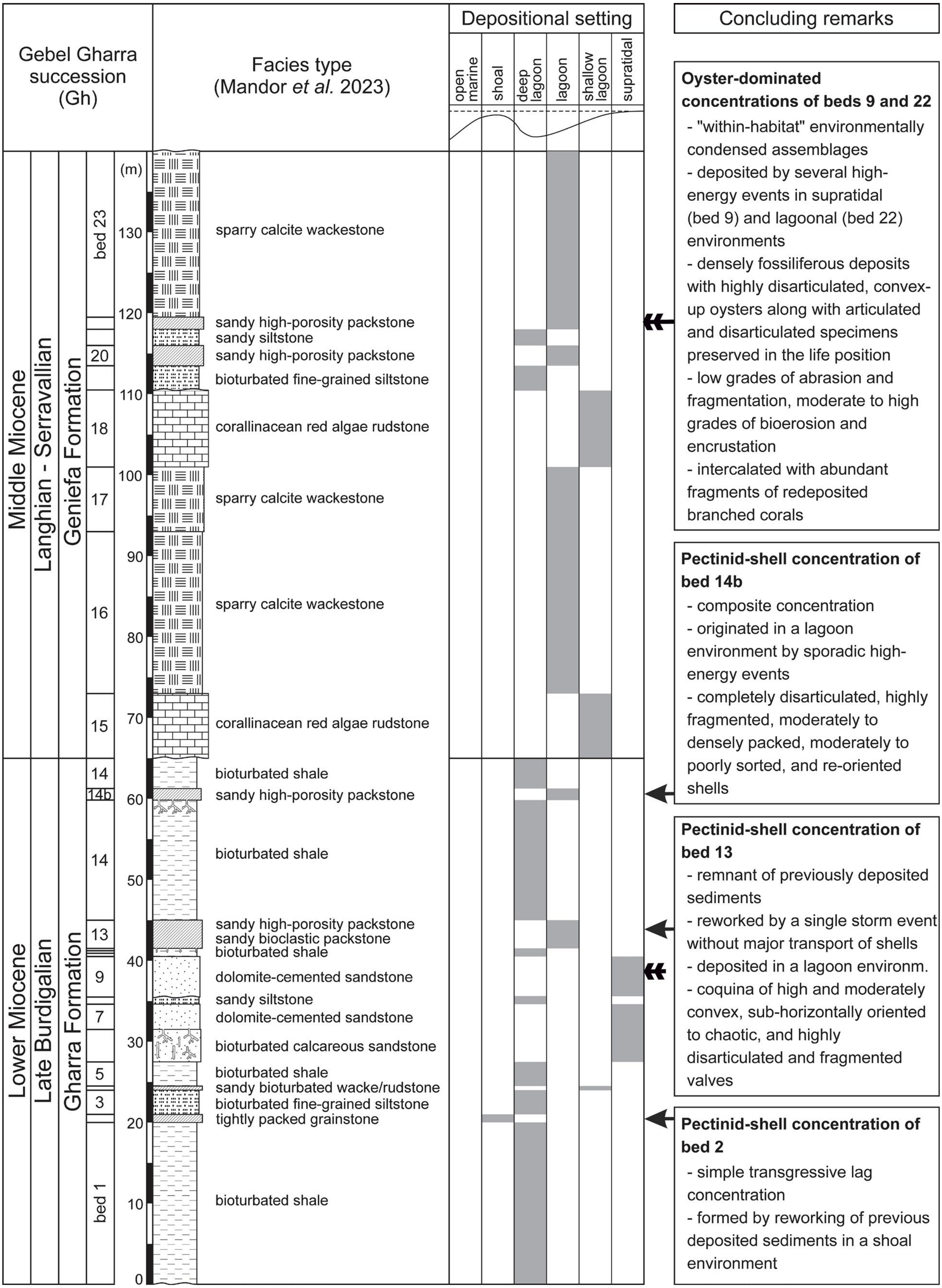
Macrobenthic palaeocommunities and interpretations

The potential utility of macrofaunal benthic shells as qualitative indicators of physical environmental parameters was previously reported in several studies (e.g. Fürsich 1977, 1984; Bottjer 1981; Brett & Baird 1986; Kidwell 1986, 1991; Kidwell *et al.* 1986). In the present work, the most conspicuous feature of the lower–middle Miocene succession of Gebel Gharra is the presence of three pectinid- (beds 2, 13 and 14b) and two oyster- (beds 9 and 22) shell concentrations (Figs 2, 9). As mentioned above, these five studied shell concentrations are characterized by varying conditions of preservation, packing, articulation, sorting, fragmentation, and orientation (Table 1). These results indicate that we are dealing with slightly transported skeletons deposited in the original life habitat, i.e. parautochthonous community relicts (e.g. Boucot *et al.* 1958; Fürsich 1977, 1984; Kidwell *et al.* 1986). Thus, several aspects of the preserved fossil and sedimentological record can be utilized to draw a good palaeoenvironmental and palaeoecological picture for each shell concentration.

In the studied bivalve-dominated concentrations, the presence of corals and/or echinoids indicates euhaline conditions and a position probably within the photic zone (Smith *et al.* 1988, 1995; Ayoub-Hannaa & Fürsich 2012). Pectinids mostly occur in high-energy, shallow-marine environments (20–50 m water depths; Fuchs 1900; Dakin 1909; Cox 1952; Fleming 1957; Waller 1969). Among the recorded pectinid assemblage, *Macrochlamis* species typically occur in high-energy, shallow-marine environments (e.g. Ctyroky 1969). Other identified pectinid species, including *Pecten fraasi*, *P. kochi*, and *Oppenheimopecten josslingi*, are characterized by highly convex, sculptured, and inequivalve pectinid shells, i.e. morphological features that can resist these higher energy levels (Pérès 1961; Kauffman 1969; Waller 1969, 1991). This highly sculptured ornamentation, in addition, may represent an adaptation to ward off predators (e.g. Waller 1969). Oysters lived in very shallow-water environments (<20 m depth; Stenzel 1971; Bottjer 1981). They can also occur in high-energy, nutrient-rich, and low-salinity waters, i.e. in faunally restricted conditions (e.g. Pufahl & James 2006). The recorded oyster species, including *Lopha virleti* and *Ostrea frondosa*, are characterized by a radially ribbed ornamentation, i.e. a character helps in the adhesion of the organisms to the substrate, particularly, in high-energy depositional settings (e.g. Seilacher 1984).

Furthermore, the recorded sand dollars (*Clypeaster marginatus* Lamarck, 1816 and *Clypeaster* sp.; see Mandor *et al.* 2023, Table 2) (Fig. 3I) characterize shallow-water, higher-energy environments (e.g. Ebert & Dexter 1975; Mooi & Telford 1982). The presence of reworked and resedimented branches of *Acropora* sp. likewise confirms episodic elevated water-energy events in a shallow marine environment (McCall *et al.* 1994; Schuster 2000; Mandor *et al.* 2023). The occurrence of cidaroid spines (Fig. 3I) and the near absence of the much thinner cidaroid skeletal elements may reflect selective destruction of more fragile skeletons in high-energy conditions (Greenstein 1992; Moffat & Bottjer 1999; Nebelsick & Kroh 2002).

In the five studied shell concentrations, the dominance of epifauna (>92%) and the rare occurrence of infaunal and semi-infaunal taxa indicate a firm fine- to medium-grained substrate (grainstone, packstone, and sandstone; Table 1) and a relatively low sedimentation rate (Ayoub-Hannaa & Fürsich 2012; El-Sabbagh *et al.* 2021; Mandor *et al.* 2023). On the other hand, the



Oyster-dominated concentrations of beds 9 and 22
- "within-habitat" environmentally condensed assemblages
- deposited by several high-energy events in supratidal (bed 9) and lagoonal (bed 22) environments
- densely fossiliferous deposits with highly disarticulated, convex-up oysters along with articulated and disarticulated specimens preserved in the life position
- low grades of abrasion and fragmentation, moderate to high grades of bioerosion and encrustation
- intercalated with abundant fragments of redeposited branched corals

Pectinid-shell concentration of bed 14b
- composite concentration
- originated in a lagoon environment by sporadic high-energy events
- completely disarticulated, highly fragmented, moderately to densely packed, moderately to poorly sorted, and re-oriented shells

Pectinid-shell concentration of bed 13
- remnant of previously deposited sediments
- reworked by a single storm event without major transport of shells
- deposited in a lagoon environm.
- coquina of high and moderately convex, sub-horizontally oriented to chaotic, and highly disarticulated and fragmented valves

Pectinid-shell concentration of bed 2
- simple transgressive lag concentration
- formed by reworking of previous deposited sediments in a shoal environment

Fig. 9. Lithostratigraphy, facies types, interpreted depositional environments, and concluding remarks of the five studied shell concentrations in the lower–middle Miocene succession in the study area.

high percentage of suspension-feeders (>90%) points to high surface water productivity (e.g. Vermeij 1990) as well as to high-energy conditions. The increase of water energy keeps food particles suspended in the water column, i.e. reduced sedimentation rates (e.g. Ayoub-Hannaa & Fürsich 2012; Abdelhady & Fürsich 2014). Consequently, the remarkable decrease in the percentage of deposit-feeding taxa may be explained by the by-passing of particulate organic matter under the effect of these elevated water-energy conditions (e.g. Abdelhady & Fürsich 2014).

Sclerobionts and their palaeoenvironmental significance

In the studied shell concentrations, the presence of abundant and diverse endobionts and epibionts assemblages (Tables 1–3; Figs 4–8) supports colonization in shallow water depths during periods of reduced sedimentation rates, i.e. conditions offering the required time to affect shells prior to final burial (e.g. Ekdale *et al.* 1984; Bromley & Asgaard 1993b; Bromley 1994; Perry 1996; Wilson & Taylor 2001; Taylor & Wilson 2003; El Hedeny & El-Sabbagh 2018). In general, the ichnogenus *Entobia* is widespread in shallow-sea high-energy environments (e.g. Bromley & Asgaard 1993b; Calcinai *et al.* 2005; El Hedeny & El-Sabbagh 2018). However, some of its ichnospecies are also occurred in both deep and shallow water (Bromley 1994; Wilson 2007; Brett et al. 2011). The occurrence of mytilid bivalve *Lithophaga*, the main producer of *Gastrochaenolites* ichnospecies, also points to shallow euphotic settings (<10 m water depth; Kleemann 1973; Bromley 1992, 1994; Bromley & Asgaard 1993b; Wilson & Taylor 2001; El Hedeny & El-Sabbagh 2018). The polychaete worms that produce *Caulostrepsis* and *Maeandropolydora* ichnogenera are common in the lower intertidal and upper subtidal environments (<25 m water depth; Wilson & Taylor 2001; El Hedeny & El-Sabbagh 2007; Kassab *et al.* 2021). Epibionts, including serpulids, bryozoans, oysters, and balanoid barnacles, also typically occur in intertidal to shallow, euphotic marine environments (e.g. Taylor & Wilson 2003; Mandor *et al.* 2022). These observations are in accordance with the present results.

Many endobionts and epibionts affect the host organisms directly after their death (i.e. post-mortem). However, there are some others may start their action during the lifetime of the host animal (i.e. pre-mortem) (e.g. Lescinsky 1995; El Hedeny *et al.* 2021b). Several clionid sponges (producers of the ichnogenus *Entobia*) were observed on living oyster shells (Carver *et al.* 2010; Dunn *et al.* 2014). In addition, El Hedeny & El-Sabbagh (2005) have regarded that activities of bioeroders may extend from a pre-death to the pre-final burial stage. In the present study, the abundant domichnial structures (Table 2; Fig. 4) may be produced on either live or dead hosts (cf. Pickerill *et al.* 2002), but their abundance increases mostly after the death of the animal (Bromley 1994; El Hedeny & El-Sabbagh 2007; Wilson 2007). On the other hand, the common occurrence of traces of bioerosion and encrustation on the internal surface of the affected pectinid and oyster valves definitely confirms a post-mortem process.

Noteworthy is the lower percentage of sclerobionts on pectinid shells in comparison with those on oyster shells (Table 1). Colonization by both epilithic and endolithic communities are mainly dependent on continuous intervals of nondeposition in shallow marine environments (Wilson & Taylor 2001; Taylor & Wilson 2003; El Hedeny & El-Sabbagh 2007). Both the rate and diversity of bioerosion traces increase with decreasing water depth (Bromley & Allouc 1992; Bromley 1994). The greater overall diversity of epibionts on oyster shells relative to pectinids may be partially related to surface area available for these epibionts (Lescinsky *et al.* 2002; El Hedeny & El-Sabbagh 2007). Pectinid shells are strongly ornamented with sharp and high radial costae, while oyster shells are characterized by less prominent ribs (Fig. 8). Shell wall microstructure significantly affected the occurrence and distribution of endobionts. The foliated calcitic shell microstructure characterizes oyster shells is relatively weak (e.g. Currey & Taylor 1974). In contrast, pectinids are known to have cross-lamellar structures that play a significant role in improving the mechanical strength of the shell (e.g. Meyers *et al.* 2008).

Within the obtained results, several aspects document a long period of exposure of the studied pectinid and oyster shells before final burial, representing successive phases of colonization and bioerosion on stable substrates with a low sedimentation rate. These aspects include: (1) the occurrence of abundant *in situ* epibionts; (2) several reciprocal overgrowths between different encrusters; (3) the dominance and diversity of deep-tier domichnial bioerosion structures; (4) overgrowth of bryozoans and serpulids over borings (i.e. a later larval settlement phase); and (5) borings in these encrusting organisms indicating further time averaging (Table 2; Figs 4–8). Thus, the recorded bioerosion assemblage in the studied shell concentrations can be assigned to the *Entobia* ichnofacies, characterising long-term bioerosion in high energy, shallow marine environments (Bromley & Asgaard 1993b; Gibert *et al.* 1998, 2007; Farinati & Zavala 2002; Parras

& Casadío 2006). At Siwa Oasis in the northern part of the Western Desert of Egypt, El Hedeny & El-Sabbagh (2018) described an assemblage of borings in a middle Miocene hard, fully lithified carbonate substrate with well-developed patch reefs. They assigned this assemblage to the *Entobia* ichnofacies in a shallow marine lagoonal setting.

The recognition of the *Entobia* ichnofacies in the studied lower–middle Miocene succession may indicate the effect of eustatic sea-level fall in the study area during the late Middle Miocene (i.e. a Serravallian regressive cycle; Haq *et al.* 1987). The upper Miocene deposits, in contrast, have not been reported throughout the Cairo-Suez District, including the study area, as well as in most of the northern parts of the Western Desert of Egypt (Said 1962, 1990; Gindy & El-Askary 1969; Issawi *et al.* 1999; Abdel-Fattah *et al.* 2013; Mandor *et al.* 2022, 2023; present study), confirming a remarkable phase of tectonic instability. The Late Miocene (Tortonian and Messinian) was marked by folding and uplift of the northern Unstable Shelf areas of Egypt accompanied with a regional marine regression (Said 1962, 1990; Guiraud *et al.* 2005).

Palaeoenvironments of shell concentrations

Based on the above-mentioned results, the specific features of each of the bivalve-dominated concentrations of the studied lower–middle Miocene section could be attributed to differences in basin characteristics, palaeoproductivity level, and the preservation potential of the host pectinid and oyster shells and their sclerobionts (e.g. Kidwell 1986, 1991; Fürsich 1995; Lescinsky & Vermeij 1995; Parras & Casadío 2005).

Pectinid-shell concentrations.– The pectinid-shell concentration of bed 2 (between 20 and 21 m, the Gharra Formation; Figs 2, 9) is interpreted as a simple transgressive lag concentration that formed by reworking of previous deposited sediments in a shoal environment (Kidwell 1986, 1991; Fürsich 1995; Cattaneo & Steel 2003; Parras & Casadío 2005; Catuneanu 2006). This interpretation is supported by a distinct erosional lower contact, the occurrence of coarse-grained intraclasts of mudstone, and highly disarticulated, fragmented, loosely to moderately packed, poorly sorted, and re-oriented pectinid shells (Table 1; Fig. 3A, B). The apparent dominance of right valves points to transport and a moderate level of sorting. This relatively rapid accumulation of shells is also documented by the rarity of traces of bioerosion and encrustation (Table 1) (e.g. Kidwell 1986, 1991; Fürsich 1995). This concentration can be correlated with the Type IV shell bed of Kidwell (1986, Fig. 2), reflecting an increase in the net sedimentation rate from negative (erosion) through zero (omission) to positive (deposition) values (i.e. a general fining- and deepening-upward trend; Fig. 9). Additionally, this shell concentration can be correlated with the base-of-parasequence (BOP) shell beds as described by Banerjee & Kidwell (1991), representing a single-event storm concentration composed of comminuted, exotic shell debris. In this concentration, the basal erosional surface may be considered as a transgressive or flooding surface at the base of parasequences, particularly in the distal regions of the transgressive systems tract (Banerjee & Kidwell 1991; Holz & Simões 2005).

The pectinid-shell concentration of bed 13 (between 41.5 and 45 m, the Gharra Formation; Figs 2, 9) represents a coquina of high and moderately convex, sub-horizontally oriented to chaotic, and highly disarticulated and fragmented pectinid valves (Table 1; Figs 2, 3E). It occurs above a bioturbated surface. The majority of shells are adult left valves, which indicates transport with a moderate level of sorting. The distinct relief may point to high water energy (cf. Mandic & Piller 2001, p. 187). This concentration is interpreted as a remnant of previously deposited sediments that have been reworked by a single storm event without major transport of shells (Kidwell 1986, 1991; Fürsich & Oschmann 1993). The presence of sub-horizontally oriented pectinid valves clearly indicates transport by currents. However, the occurrence of chaotically-oriented valves may display the effect of different hydrodynamic behaviour of these valves depending on their morphology (e.g. Mandic & Piller 2001). Skeletal remains of biogenic borings and encrusting organisms are rarely abundant (Table 1), suggesting a relatively rapid accumulation of shells. This pectinid-shell concentration is comparable to the Type III shell bed (*sensu* Kidwell 1986, Fig. 2), reflecting an increase in the net sedimentation rate from zero (omission) to positive (deposition) values. In addition, it can be correlated with the reworked event-concentration of Kidwell (1991). Furthermore, this shell concentration is comparable to the top-of-parasequence (TOP) shell beds as described by Banerjee & Kidwell (1991), representing thick, complex, and local reworking or indigenous concentrations. The TOP shell-beds are capped by flooding surfaces and are particularly useful in the shallower parts of the transgressive systems tract (Banerjee & Kidwell 1991; Holz & Simões 2005). Above this concentration, the occurrence of some adult pectinid specimens preserved in life position (see the upper inset in Fig. 3E) may confirm this interpretation (Fürsich 1995; Mandic & Piller 2001; Parras & Casadío 2005). Additionally, this upper part of bed 13 contains planktic foraminifera (see Mandor *et al.* 2023, Table 1, Fig. 4J, K), confirming the influence of a more marine transgression, i.e. coincides with a maximum flooding surface that defines the top of a parasequence (Fig. 9).

The pectinid-shell concentration of bed 14b (between 59.5 and 61 m, the Gharra Formation; Figs 2, 9) is characterized by completely disarticulated, highly fragmented, moderately to densely packed, moderately to poorly sorted, and re-oriented pectinid shells (Table 1; Fig. 3F, G), confirming high water energy as does the occurrence of mud pebbles above the lower bioturbated boundary (Fig. 3G). Up-section, the presence of coarse mud-pebbles indicates that the depositional environment became slightly higher energy (Fig. 3H), i.e. documents deposition in coarsening upward cycles of highstand systems tract (Banerjee & Kidwell 1991; Holz & Simões 2005). This concentration is interpreted as a composite concentration (*sensu* Kidwell 1991), representing accretion or amalgamation of multiple events. Furthermore, it is comparable to the Type I shell bed (*sensu* Kidwell 1986, Fig. 2), reflecting a decrease in sedimentation rate from positive (net deposition) to zero (omission) values, and exhibiting an up-section increase in shell density. The presence of mud pebbles throughout this concentration (Fig. 3G, H) supports the reworking of the underlying bed by storm turbulence. The common occurrence of glauconite and encrusting organisms, including bryozoans, polychaetes, and oysters (Table 1; Fig. 4), reflects reduced sedimentation rates and time-averaging (e.g. Kidwell 1986).

Oyster shell concentrations.– Oyster-dominated concentrations of bed 9 (between 35.5 and 40.5 m, the Gharra Formation) and bed 22 (between 118–119.5 m, the Geniefa Formation; Figs 2, 9), forming oyster biostromes, indicate very shallow-water environments (Stenzel 1971; Bottjer 1981; Pufahl & James 2006). They were deposited in supratidal (bed 9) and lagoonal (bed 22) environments in an inner ramp setting (Fig. 9; for more details, see Mandor *et al.* 2023). The noticeable high percentage of disarticulated oyster specimens (Table 1) points to high-energy conditions with a low rate of sedimentation. Low sedimentation is also indicated by the dominance of epifauna, particularly cemented oyster species (Seilacher 1984), along with the abundant traces of epibionts and endobionts over both surfaces of the disarticulated left and right valves (Tables 1–3; Figs 4–8) (Kidwell 1986, 1991; Bromley & Asgaard 1993b; Fürsich 1995; Wilson & Taylor 2001). On the other hand, the low level of shell fragmentation (Table 1) and the occurrence of articulated and disarticulated specimens preserved in life position (Fig. 3J) suggest a limited reworking, confirming autochthonous to parautochthonous relicts of oysters' palaeocommunities (Boucot *et al.* 1958; Fürsich 1977; Kidwell *et al.* 1986; Fürsich *et al.* 2004, 2009). Consequently, these oyster concentrations are interpreted as a 'within-habitat time-averaged' oyster assemblages (Walker & Bambach 1971; Fürsich & Aberhan 1990; Kidwell & Bosence 1991). Because of the occurrence of abundant fragments of redeposited branches of *Acropora* sp. in both oyster concentrations (Figs 2, 3C, J), they can be interpreted as a 'within-habitat' environmentally condensed assemblage (e.g. Fürsich 1975; Fürsich & Kauffman 1984; Kidwell & Bosence 1991). They can be also correlated with the Type II shell beds (*sensu* Kidwell 1986, Fig. 2), reflecting an up-section increase in shell packing density and terminate in an erosional surface. Additionally, they can be correlated with oyster-dominated concentrations formed in the early phase of the transgressive systems tract as described by Parras & Casadío (2005).

Conclusions

Deposits of the Gebel Gharra succession consists of a lower Miocene siliciclastic interval (the Gharra Formation) and a middle Miocene carbonate-dominated upper part (the Geniefa Formation). Throughout the section, there are no sharp compositional differences in the macrobenthic assemblages; all are dominated by pectinids, oysters, other bivalves, gastropods, echinoids, and corals. However, three pectinid- and two oyster shell concentrations can be distinguished, differing from one another in several stratigraphical, sedimentological, palaeoecological, and taphonomic features.

These shell concentrations are paucispecific to polyspecific macrobenthic biotopes. Their shells were significantly colonized by abundant endobionts and common epibionts. The *Entobia* ichnogenus is represented by *E. laquea*, *E. cateniformis*, *E. megastoma*, and *Entobia* isp. The next most abundant boring traces are *Maeandropolydora sulcans* and *Gastrochaenolites torpedo*. The other recorded borings include *Caulostrepsis taeniola*, *Talpina ramosa*, *Renichnus arcuatus*, *Santichnus mayorali*, *Oichnus simplex*, *Iramena danica*, and *Trypanites* isp. Epibionts include bryozoans, serpulids, adult and juvenile oysters, balanoid barnacles, and corals. These bioerosion structures and encrusters characterize the *Entobia* ichnofacies, representing successive phases of colonisation and bioerosion on stable substrates with a low rate of sedimentation in high energy, shallow marine environments.

Environmental parameters controlling the distribution and the formation of the studied shell concentrations include bathymetry, water-energy, productivity level, and rate of sedimentation. Four types of shell concentrations have been distinguished. The pectinid-shell concentration of bed 2 is interpreted as a simple transgressive lag concentration that formed by reworking of previously deposited sediments in a shoal environment. The pectinid-shell concentration of bed 13 represents a coquina of high and moderately convex, sub-horizontally oriented to chaotic, and highly disarticulated and fragmented pectinid valves. It is interpreted as a remnant of previously deposited sediments that have been reworked by a single storm event without major transport of shells, and deposition in a lagoon environment. Pectinid-shell concentration of bed 14b is characterized by completely disarticulated, highly fragmented, moderately to densely packed, moderately to poorly sorted, and re-oriented pectinid shells. It is interpreted as a composite concentration that was developed in a lagoonal environment by sporadic high-energy events. Oyster-dominated concentrations of beds 9 and 22 represent 'within-habitat' environmentally condensed assemblages, formed of densely fossiliferous deposits with highly disarticulated, convex-up oysters along with articulated and disarticulated specimens preserved in life position, with low grades of abrasion and fragmentation, moderate to high grades of bioerosion and encrustation, and intercalated with abundant fragments of redeposited branched corals. They were deposited by several high-energy events in supratidal and lagoonal environments, respectively.

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