

INTEGRATED MICROFACIES, MACROBENTHOS AND TRACE-FOSSIL ANALYSIS OF THE LOWER–MIDDLE MIOCENE SUCCESSION OF GEBEL GHARRA, CAIRO-SUEZ DISTRICT, EGYPT

Mona MANDOR¹, Magdy EL HEDENY^{1*}, Ahmed EL-SABBAGH¹, Emad NAGM^{2,3}, Abdelaal ABDELAAL¹, Mohamed RASHWAN⁴ & Heba MANSOUR⁴

¹ Department of Geology, Faculty of Science, Alexandria University, Alexandria 21568, Egypt; e-mail: magdy.elhedeny@alexu.edu.eg

² Department of Geology, Faculty of Science, Al-Azhar University, Assiut, 71524, Egypt

³ Department of Geology, College of Science, Taibah University, Madinah, 41477, Saudi Arabia

⁴ Department of Biological and Geological Sciences, Faculty of Education, Alexandria University, Alexandria 14037, Egypt

* Corresponding author

Mandor, M., El Hedeny, M., El-Sabbagh, A., Nagm, E., Abdelaal, A., Rashwan, M. & Mansour, H., 2023. Integrated microfacies, macrobenthos and trace-fossil analysis of the lower–middle Miocene succession of Gebel Gharra, Cairo-Suez District, Egypt. *Annales Societatis Geologorum Poloniae*, 93: 381–409.

Abstract: The palaeoecology and palaeoenvironments of the lower–middle Miocene succession in Gebel Gharra, NW of Suez, Egypt, are interpreted, on the basis of a detailed study of microfacies, trace fossils, and macrofaunal benthic assemblages. This succession consists of a lower siliciclastic part (the Gharra Formation) and a carbonate-dominated upper part (the Geniefa Formation), corresponding to a general transgression-regression cycle. Facies characteristics indicate depositional palaeoenvironments, ranging from supratidal, lagoonal, to shoal settings on an inner ramp that was influenced proximally by clastic input. At least seven ichnotaxa were recorded in the lower Miocene Gharra Formation, representing suites of the *Skolithos* ichnofacies. Among them, the ichnogenus *Polykladichnus* is recorded for the first time in Egypt. The macrobenthic taxa identified in 13 statistical samples are grouped into five assemblages (A–E) that are described and interpreted as the remains of communities. The faunal distribution and trophic structure of most of these assemblages confirm the existence of relatively stable and low-stress conditions. However, the trophic structure of the assemblages reflects the influence of particular environmental parameters, the dissolution of aragonitic shells and/or sample-size effects. Environmental parameters, controlling the distribution of trace and/or body fossils, include substrate consistency, bathymetry, water energy, productivity level, rate of sedimentation, salinity, and oxygen availability. The results of integrated litho- and biofacies analysis confirm that the succession studied was deposited in different environmental settings, providing perfect conditions for the occurrence and preservation of trace-fossil and macrobenthos assemblages.

Key words: Macrobenthos, taphonomy, trace fossils, palaeoecology, palaeoenvironment, lower–middle Miocene, Egypt.

Manuscript received 11 March 2023, accepted 30 June 2023

INTRODUCTION

Mixed siliciclastic-carbonate Miocene successions are common stratigraphic phenomena on shelves and slopes, and/or in ocean basins (e.g., Goldhammer, 1978; El Haddad *et al.*, 1984; Bashri *et al.*, 2017; Du *et al.*, 2022). They may appear as reciprocal mixed carbonate-siliciclastic deposits, in which carbonate and siliciclastic sediments alternate in a vertical sequence or are juxtaposed laterally (e.g., Van Siclen, 1958; Wilson, 1967; Handford and Loucks, 1993).

They also may occur as coeval mixed siliciclastic-carbonate deposits, in which both types of sediments coexist and are mixed in the strata (e.g., Mount, 1984; Spalletti *et al.*, 2000; Caracciolo *et al.*, 2013).

In Egypt, the lower–middle Miocene siliciclastic-carbonate deposits crop out in the Cairo-Suez District, in the northern part of the Eastern Desert (Fig. 1A). They represent characteristic marine sediments that were deposited in

response to the early Miocene transgression at the southern margin of the Mediterranean Sea (e.g., Scotese, 2013). Stratigraphical and sedimentological studies of these Miocene deposits have been carried out for over a hundred years (Depéret and Fourtau, 1900; Sadek, 1959; Said, 1962, 1990; Abou Khadrah *et al.*, 1993; Issawi *et al.*, 1999; Tawfik *et al.*, 2015; El-Sorogy *et al.*, 2017). In general, siliciclastics

predominate in the lower part of these successions, whereas carbonates mark the upper part (Said, 1962, 1990; Abou Khadrah *et al.*, 1993; Tawfik *et al.*, 2015; El-Sorogy *et al.*, 2017). Eustatic sea-level fluctuations, combined with tectonics and high terrigenous influx, are considered to have been the main factors that controlled sedimentation (e.g., Said, 1990; Issawi *et al.*, 1999; Tawfik *et al.*, 2015).

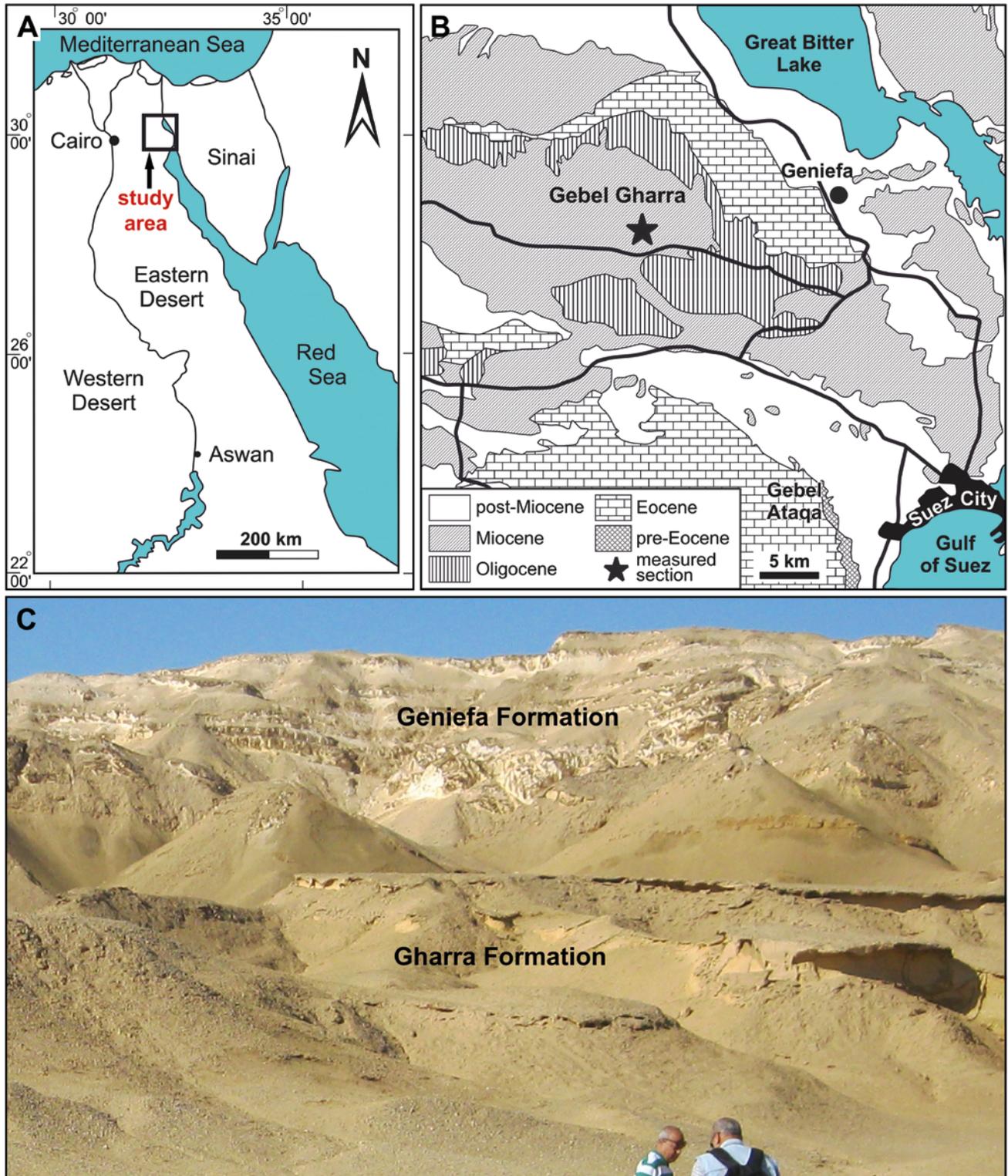


Fig. 1. Geographical and geological framework of the study area. **A.** Geographical overview. **B.** Simplified geological map of the study area (modified after Mandic and Piller, 2001) with the location of the measured section at Gebel Gharra. **C.** Field photo of the outcrop showing the Gharra and Geniefa formations.

The lower–middle Miocene deposits of the Cairo-Suez District contain diversified and abundant macro-invertebrate assemblages, including molluscs, echinoids, and corals. Since the second half of the nineteenth century, these varied macrofauna have been studied mostly from a taxonomic point of view (e.g., Fraas, 1867; Fuchs, 1883; Blanckenhorn, 1901, 1903; Fourtau, 1920; Said and Yallouze, 1955). Subsequently, rare studies for the biostratigraphic use of this rich macrofauna were made by Hamza (1992) and El-Sorogy *et al.* (2017). From a taphonomical and palaeoecological perspective, more studies were carried out by Piller *et al.* (1998), Mandic and Piller (2001), Nebelsick and Kroh (2002), Kroh and Nebelsick (2003) and Mandor *et al.* (2022). Furthermore, the Miocene sediments of the Cairo-Suez District are sporadically and moderately burrowed (e.g., Piller *et al.*, 1998), representing an ichno-assemblage with low diversity.

Undoubtedly, the abundance and environmental distribution of the Miocene macrobenthos and/or trace fossils were controlled by several factors that greatly affected the diversity and dominance of species. However, no study has yet focused on the analysis of the lower–middle Miocene palaeoenvironment of the Cairo-Suez District within the framework of sedimentological and palaeoecological relationships. Therefore, the present study aims to (1) interpret the environmental conditions that predominated during deposition of the lower–middle Miocene succession, exposed along the Cairo-Suez District on the basis of the description of its microfacies, trace fossils, and macrofaunal benthic assemblages, and (2) discuss different factors, controlling the occurrence and distribution of the identified macrobenthic palaeocommunities.

The present work is based on the Miocene succession, exposed at Gebel Gharra, which lies about 30 km NW of Suez City. It extends from longitude 32.1635 to 32.1809, and from latitude 30.1024 to 30.1113 (Fig. 1B).

GEOLOGICAL SETTING

The Miocene rocks, exposed in the Cairo-Suez District at the northern part of the Eastern Desert of Egypt, form remarkable hills. Sedimentation in this region was greatly controlled by tectonics (Said, 1962, 1990; Patton *et al.*, 1994). Two main shallow tectonic basins occurred (Fig. 1B), including the Geniefa (= Geneffe/Gineifa)-Gharra Basin to the north of Suez City and the Hagul-Sukhna Basin to the south (Hermina *et al.*, 1989; Said, 1990). These basins are filled with shallow-marine, mixed siliciclastic-carbonate sediments. In general, the Miocene succession of this area increases in thickness from west (i.e., east of Cairo) to east (i.e., the Suez Canal; Said, 1962, 1990), overlying shallow-marine Eocene carbonates and non-marine Oligocene siliciclastics (Said, 1962, 1990; Hermina *et al.*, 1989).

The Miocene succession studied (about 140 m thick) lies on the eastern flanks of the Gebel Gharra Hill, spanning from the lower to the middle Miocene. It is subdivided into lower, siliciclastic-dominated and upper, carbonate-dominated intervals, representing the Gharra (Said, 1962) and Geniefa (Said, 1990) formations, respectively (Figs 1C, 2).

Noteworthy is the occurrence of Oligocene red sands and gravels in the foothill of Gebel Gharra. However, direct contact between the Oligocene and the Miocene sediments studied was not recorded.

MATERIALS AND METHODS

In the measured lower–middle Miocene succession, stratigraphical, sedimentological and palaeontological data were gathered through detailed field description of each bed. Sedimentary textures and structures, the nature of bedding and bedding contacts, macro- and/or trace fossil content, and the lateral variability for each bed were documented. Ichnological observations were focussed on the identification of ichnogenera and the documentation of their distribution in the exposed succession. The size of the trace fossils and their physical interrelationships (e.g., interpenetrating, intercalated, and isolated occurrences) were also noted. A total of 20 rock samples were collected from each characteristic facies. Furthermore, macrofossils were recovered at specific horizons. Quantitative samples of macrofossils were collected at intervals of 0.5 and 20 m. From each horizon, 20 or more specimens were taken from the surface to obtain a statistically useable sample. Shells were marked with arrows to indicate an *in situ* orientation within the rock. In the case of dense occurrences in hard beds, specimens were counted and photographed and only representative specimens were collected for further study. Some intervals lack a fauna (< 10 specimens per sample) and thus could not be used for statistical purposes.

In the laboratory, standard petrographic thin-section techniques were used for petrographic studies. Dunham's (1962) nomenclature for the textural classification of carbonates was used, with modifications by Embry and Klovan (1971). The macrofossil specimens collected were treated with a diluted hydrogen peroxide solution and scrubbed with a soft toothbrush in order to remove adhering matrix. After identification, specimens in each sample were counted for quantitative analysis. The number of bivalve individuals was obtained by adding the number of right or left valves to the number of articulated valves (Minimum Number of Individuals, 'MNI' method; Gilinsky and Bennington, 1994).

A total of 1,579 (out of 1,600) macrobenthic specimens in 13 samples from the study area were selected for a quantitative palaeoecological analysis. A list of relative abundances was constructed for each quantitative sample. The Q-mode cluster analysis of the species' relative abundance data set was chosen to categorise the benthic assemblages. A dendrogram was constructed on the basis of Ward's method (Euclidean distance) and applied using the PAST software package, v. 3 (Hammer *et al.*, 2001). To normalise the sample size, evenness values for each macrobenthic assemblage ($E = e^H/S$), where H is the Shannon index and S is the species richness, were calculated, using the same software package. Species evenness values range from zero to one, with zero signifying the strong predominance of a particular species and one, complete evenness. In general, diversity values, based on evenness, allow reliable interpretations,

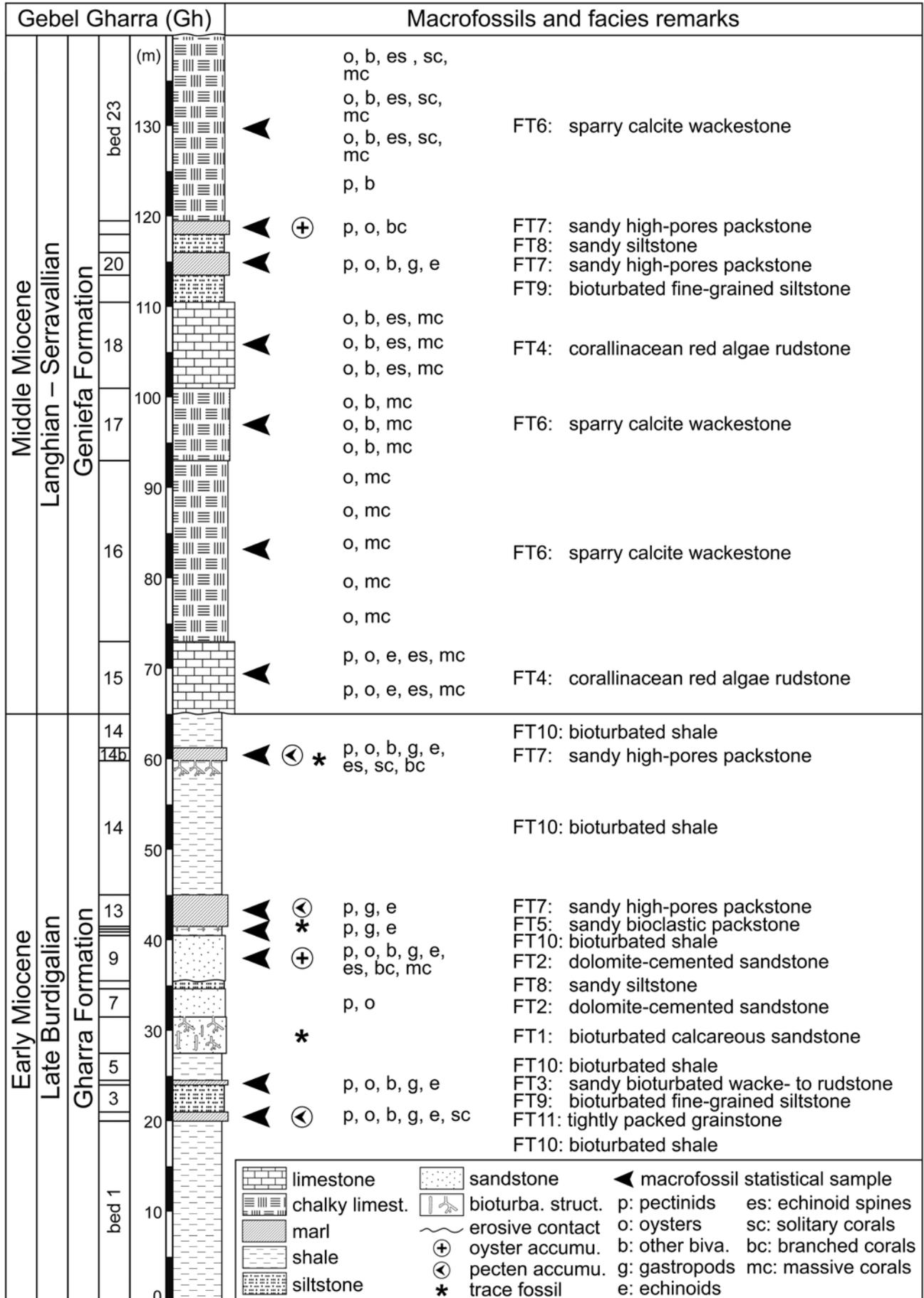


Fig. 2. Stratigraphic log of the Gebel Gharra section with occurrences of macrofossils and facies distribution.

because it is not affected by sample size, in contrast to values of species richness (Whittaker, 1972; Tuomisto, 2010).

For taphonomic analysis, the acceptable terminologies applied by Fernández-López (1991, 2011) and Fernández-López *et al.* (2002) have been used. The term “accumulated assemblage” represents shells remaining at the place of their biological production. “Resedimented assemblage” refers to shells that were displaced across the sea floor after accumulation and prior to their final burial. For synecological analysis, the trophic nucleus of an assemblage is defined as the most abundant faunal elements, accounting for approximately 80% (Neyman, 1967).

All macrofossil specimens were collected during field work for a PhD study by one of us (Mona Mandor) at the Gebel Gharra section, Cairo-Suez District, Egypt, and 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, (p) for pectinids, (b) for other bivalves, (g) for gastropods, (e) for echinoids and (c) for corals.

RESULTS

Lithostratigraphy

The Gharra Formation

This unit attains a thickness of about 65 m. It is composed of shale, sandstone, siltstone and sandy marl interbeds, moderately bioturbated and yielding a rich and diversified macrofaunal assemblage (Fig. 2). The basal 20 m consists of a non-fossiliferous bioturbated shale layer with gypsum veins and veinlets (Fig. 3A). Above it, there is a thin marl bed (1.0 m thick) with mud clasts at its base (Fig. 3A) and it is fossiliferous with abundant pectinids, oysters, other bivalves, gastropods, echinoids, solitary corals, and balanoid barnacles (Fig. 3B, C). The interval between 21–27.5 m consists of a lower bioturbated siltstone layer (3 m thick), a thin fossiliferous marl bed at 24 m, and a 3-m-thick ferruginous, gypsiferous and bioturbated shale layer at the top. The marl bed is highly fossiliferous with pectinids, rare oysters, other bivalves, gastropods and echinoids (Fig. 3D). A clastic interval between 27.5 and 40.5 m consists of sandstones with a thin siltstone bed at 34.5 m that is topped by an erosional unconformity (Fig. 2). This interval is characterised by a unique 4-m-thick calcareous laminated egg-yellow sandstone bed at the base. This layer is highly bioturbated with vertical burrows and horizontal to three-dimensional burrowing networks (Fig. 3E). In addition, this clastic interval is commonly fossiliferous with oysters, pectinids, other bivalves, gastropods, echinoids, and coral colonies (Fig. 3F). The top part of the Gharra Formation consists of thick, greenish grey, ferruginous, gypsiferous, and fissile shales (40.5–65 m) with marl beds, 3.5 and 1.5 m thick, in the lower and upper parts, respectively. Both marl beds are commonly glauconitic and fossiliferous with pectinids, oysters, other bivalves, gastropods, echinoid tests and spines, solitary corals and bryozoans (Fig. 3G). In addition, the marls (beds 13 and 14b) are characterised by the occurrence of simple and branched burrows into the underlying shales

(Fig. 3H, I). Moreover, the marl of bed 14b contains mud clasts at its base (Fig. 3I).

Diverse assemblages of bivalves, gastropods, echinoids, corals, as well as planktic and benthic foraminifera support a late Burdigalian age for the Gharra Formation (Souaya, 1963; Abdelghany and Piller, 1999; Mandic and Piller, 2001; Abdelghany, 2002; Kroh and Nebelsick, 2003; El-Sorogy *et al.*, 2017; Mandor *et al.*, 2022; present study). In general, no Aquitanian sediments are recognised in the Cairo-Suez District (e.g., Said, 1990).

The Geniefa Formation

At the Gebel Gharra section, shale deposition ends at 65 m, which may represent the Gharra/Geniefa boundary. The Geniefa Formation unconformably rests on the Gharra Formation (Fig. 3J), attaining a thickness of about 75 m. In comparison to the Gharra Formation, the Geniefa Formation consists mainly of highly fossiliferous chalky and reefal limestones with few siltstone and marl intercalations (Fig. 2). The basal 8 m of the Geniefa Formation consists of fossiliferous limestone, with oysters, pectinids, echinoid tests and spines, and coral colonies (Fig. 3K). Between 73 and 101 m, the sediments consist of thick laminated yellowish white chalky limestones fossiliferous with small and large oyster shells, bivalve moulds, and coral colonies (Fig. 2). An oyster-rich limestone layer (101–110.5 m) overlies this interval and, in addition, contains bivalve moulds, echinoid spines and coral colonies. Above is an interval of alternating poorly fossiliferous partly bioturbated siltstone and fossiliferous marl layers (110.5–119.5 m). These marls are fossiliferous with oysters, pectinids, other bivalves, gastropods, echinoids, and coral colonies, bryozoans and large balanoid barnacles (Fig. 3L). The top of the section (119.5–140 m) consists of a thick yellowish-white chalky limestone with pectinids and oyster shells, other bivalve and rare nautiloid cephalopod moulds, echinoid spines, and corals. The termination of the succession is erosional (Fig. 2).

In the Geniefa Formation, the recorded molluscs, echinoids, corals, bryozoans, large balanoid barnacles, and benthic foraminifera indicate a Langhian–Serravallian age (Souaya, 1963; Hassan and Hany, 2012; El-Sorogy *et al.*, 2017; Mandor *et al.*, 2022; present study).

Microfacies analysis

The microfacies analysis of the lower–middle Miocene Gharra and Geniefa formations is based on an investigation of rock thin-sections, supplemented by field observations of some features, such as lithology, bedding, sedimentary structures, and trace- and body-fossil content. Detailed petrographic analysis of the lower–middle Miocene succession studied has revealed the occurrence of mixed siliciclastic and carbonate facies (Tab. 1). In the siliciclastic facies, bioclasts are rare or nearly absent. In the carbonate facies, in contrast, skeletal grains are represented by benthic and planktic foraminifera (mainly textulariids and globigerinids, respectively), bivalves, rare echinoids, and algae. In addition, the carbonate facies show a high-porosity texture within and between the skeletal grains (Tab. 1; Fig. 4).

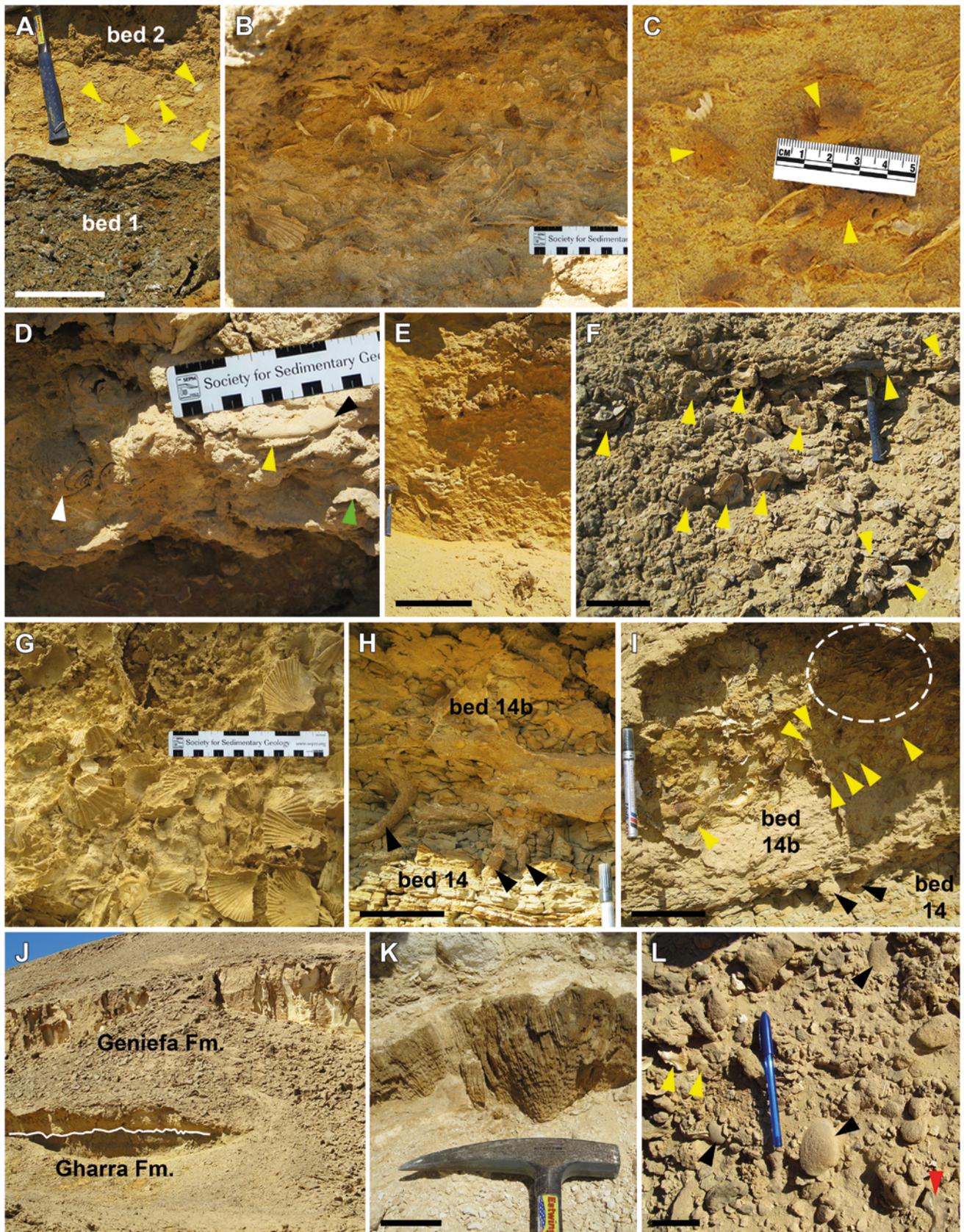


Fig. 3. Some field aspects of the section studied. **A.** Gypsiferous shale (bed 1) underlies a thin marl layer (bed 2). Note the occurrence of mud clasts (arrows) in the basal part of bed 2. **B, C.** Marl of bed 2 with (B) pectenid valves and (C) solitary coral *Desmophyllum* sp. (arrows). **D.** Bed 4 fossiliferous with pectenid (yellow arrow), oyster (green arrow), gastropod (white arrow), and echinoid (black arrow) specimens. **E.** Thick, calcareous, egg-yellow and highly bioturbated sandstone (bed 6). **F.** Thick dolomitic sandstone (bed 9) containing abundant re-oriented valves of *Lopha virleti* (arrows) and fragmented *Acropora* sp. branches. **G.** Marl of bed 13 with abundant pectenid valves. **H, I.** Shale of bed 14 underlies a thin marl layer (bed 14b) that is characterised by the occurrence of burrows (black arrows in

Table 1

Facies association (FA) and characteristic features of facies types (FT) in the lower–middle Miocene succession and their depositional setting.

Facies association (FA)	Facies type (FT)	Occurrence (bed no.)	Description	Depositional setting
FA1: Sandstone	FT1: Bioturbated calcareous sandstone (Fig. 4A)	Gharra Formation (Gh6)	Medium- to fine-grained, angular- to subrounded quartz grains in a calcareous matrix (both micrite and sparite). Bioturbation is a common character with dolomitisation	Supratidal (Kleesmenta <i>et al.</i> , 2012; Ali <i>et al.</i> , 2021)
	FT2: Dolomite-cemented sandstone (Fig. 4B, C)	Gharra Formation (Gh7, Gh9)	Poorly sorted sand grains cemented by intense dolomite grains. Cement represents about 25% of fine-crystalline euhedral dolomite	
FA2: Bioclastic rudstone	FT3: Sandy bioturbated wacke- to rudstone (Fig. 4D)	Gharra Formation (Gh4)	Large-sized bivalves with intensive boring in sparite matrix. Dolomitisation is a well-observed as a bioturbation feature. Medium-sized quartz grains are also noted. Some open pores within the bivalves occur	Shallow lagoon (Wilson, 1975; Wray, 1977; Flügel, 2010)
	FT4: Coralline red algae rudstone (Fig. 4E, F)	Geniefa Formation (Gh15)	Large-sized coralline red algae showing internal structures are floated in sparite matrix. It shows a high-porosity within its grains	
FA3: High-porosity, bioclastic wacke- to packstone	FT5: S Sandy bioclastic packstone (Fig. 4G, H)	Gharra Formation (Gh12)	Benthic foraminifera are a common component, with few large bivalves. Sand and glauconite grains are noted. Dolomitisation is also observed	Lagoon (Flügel, 2010; Wilmsen and Nagm, 2012; Roozpeykar <i>et al.</i> , 2019)
	FT6: Sparry calcite wackestone (Fig. 4I)	Geniefa Formation (Gh16, Gh23)	Recrystallised medium-sized bivalve fragments are common in sparry calcite matrix. Many of these bioclasts were dissolved represents a high-porosity texture. Rare echinoids are noted	
	FT7: Sandy high-porosity packstone (Fig. 4J, K)	Gharra Formation (Gh13)	Abundant benthic (<i>Textularia</i> sp.) and planktic (<i>Globigerinoides</i> spp.) foraminifera, dolomitic matrix and sand grains are the main constituents. Open pores between and within grains is a dominated feature	
FA4: Fine-grained mudrocks	FT8: Sandy siltstone (Fig. 4L)	Gharra and Geniefa formations (Gh8 and Gh21, respectively)	Some medium-sized sand grains embedded in siltstone. Few benthic foraminifera (<i>Textularia</i> sp.) occur	Open lagoon (Burchette and Wright, 1992; Wilmsen and Nagm, 2012)
	FT9: Bioturbated fine-grained siltstone (Fig. 4M)	Gharra and Geniefa formations (Gh3 and Gh19, respectively)	Bioturbated, inhomogeneous fine-grained siltstone. Dolomitisation is a common feature, with rare fine-grained bioclast fragments	
	FT10: Bioturbated shale (Fig. 4N)	Gharra Formation (Gh1, Gh5, Gh10, Gh14)	Bioturbated, thick, fissile shales. Dolomitisation is a well-noted character	
FA5: Tightly packed grainstone	FT11: Tightly-packed grainstone (Fig. 4O)	Gharra Formation (Gh2)	Rounded to subangular lime clasts and aggregate grains are the main components. Large, recrystallised bivalve fragments occur. Bioturbation is common and indicated by selective dolomitisation	Shoal (Flügel, 2010; Nagm <i>et al.</i> , 2018)

H and I) into the underlying shales. The basal part of bed 14b, characterised by the occurrence of mud clasts (yellow arrows in I) and pectinid valves (circle in I). **J.** The middle Miocene Geniefa Formation is unconformably underlain by the lower Miocene Gharra Formation. **K.** Limestone of bed 15, containing middle Miocene coral *Favites* sp. **L.** Marl of bed 20 fossiliferous with bivalve moulds (black arrows), and pectinid and oyster valves (yellow and red arrows, respectively). Scale bars equal 20 cm for A and F, 50 cm for E, 10 cm for H and I, and equal 5 cm for K and L.

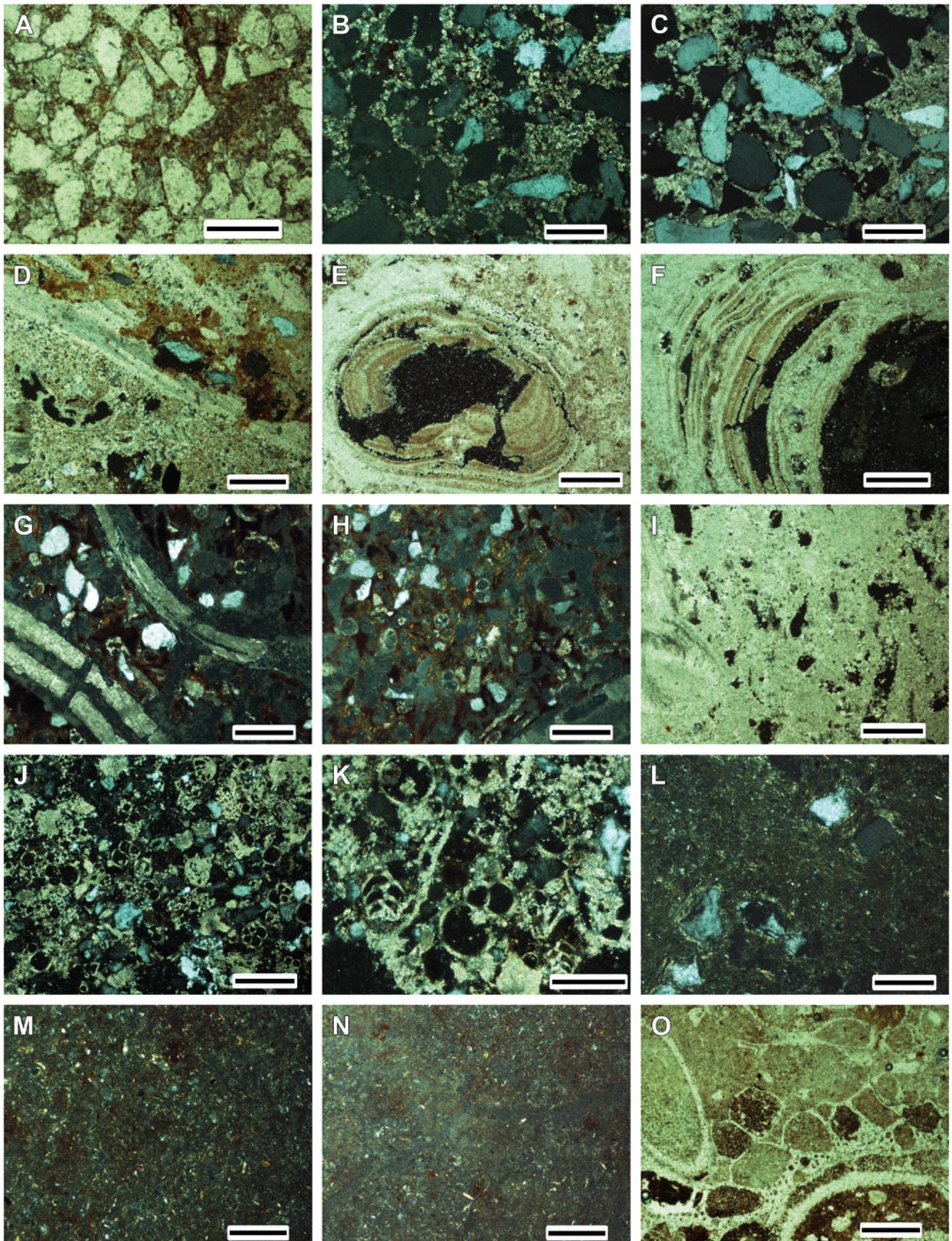


Fig. 4. Facies types (FT1–11) of the studied lower–middle Miocene succession. **A.** FT1, bioturbated calcareous sandstone, Gh6. **B, C.** FT2, dolomite-cemented sandstone, Gh7 and Gh9, respectively. **D.** FT3, sandy bioturbated wacke- to rudstone, Gh4. **E, F.** FT4, corallinacean red algae rudstone, Gh15. **G, H.** FT5, sandy bioclastic packstone, Gh12. **I.** FT6, sparry calcite wackestone, Gh16. **J, K.** FT7, sandy high-porosity packstone, Gh13. **L.** FT8, sandy siltstone, Gh8. **M.** FT9, bioturbated fine-grained siltstone, Gh3. **N.** FT10, bioturbated shale, Gh1. **O.** FT11, tightly-packed grainstone, Gh2. All photographs were taken under cross-polarised light, except for A and O, which were under plane polarised light. Scale bars equal 0.4 mm.

Facies analysis allows differentiation of the succession studied into 11 microfacies types (FT1–FT11). All these facies types (five siliciclastics and six carbonates) are described and interpreted (Tab. 1). On the basis of similar attributes, the recorded facies types are grouped into five different facies associations (FA1–FA5), representing deposition of the studied facies on an inner ramp setting, with dominance of a lagoonal environment (Tab. 1; Fig. 4).

Trace fossils

Trace fossils exclusively occur in the siliciclastic sediments of three horizons (beds 6, 13 and 14b) in the lower Miocene succession of the Gharra Formation. The recorded ichnofossil assemblages are composed of horizontal, branched, and/or vertical traces, attributable to the activity of a variety of organisms (see below). At least seven ichnotaxa, belonging to six ichnogenera, have been identified (Fig. 5). Layer 6 (calcareous laminated egg-yellow sandstone) is moderately bioturbated with *Arenicolites carbonarius* (Binney, 1852), *Ophiomorpha* isp., *Skolithos linearis* Haldeman, 1840, *Thalassinoides paradoxicus*? Kennedy, 1967, and *T. suevicus*? (Rieth, 1932). The basal part of bed 13 (fossiliferous marl) is characterised by the occurrence of a monospecific population of *Ophiomorpha* isp. extending into the underlying shales. Similarly, the basal part of the fossiliferous marl of layer 14b is moderately bioturbated with *A. carbonarius*, *Planolites* isp., and *Polykladichnus* isp. extending into the underlying shales. Among this trace fossil assemblage, the ichnogenus *Polykladichnus* is recorded for the first time in Egypt.

Arenicolites carbonarius (Binney, 1852)

Fig. 5A, B

Description: Endichnial, U- and J-shaped burrows, preserved as a full relief. Opening is with funnel shape. Burrow wall smooth with mud lining; fill identical to the surrounding matrix; diameter is constant throughout the burrow length.

Producers and ethology: Most *Arenicolites* resulted from the dwelling (domichnial) activity of suspension-feeding organisms, including polychaete worms, holothurians and amphipod crustaceans (Pearse, 1908; Howard, 1968; Hakes, 1976; Fillion and Pickerill, 1990; Gingras *et al.*, 2008).

Depositional environment: *Arenicolites* is known from a wide range of continental to deep-marine environments (e.g., Pemberton *et al.*, 2001). However, it is usually indicative of shallow-marine high-energy depositional settings (Fillion and Pickerill, 1990; Knaust, 2017; Hammersburg *et al.*, 2018).

Occurrence: Gharra Formation, beds 6 and 14b.

Ophiomorpha isp.

Fig. 5C, D

Description: Vertical and horizontal, cylindrical or subcylindrical burrows (commonly weathered). Tunnels branch and locally swell close to or at points of branching, unlined, unbranched cylindrical or subcylindrical infilled burrows straight to slightly curved, smooth trace fossil, with striae or annulations, horizontal to oblique to bedding planes.

Producers and ethology: It is interpreted as a feeding trace of deposit-feeder organisms, probably polychaetes (Pemberton and Frey, 1982) and/or shrimp or shrimp-like animals (Howard and Frey, 1984).

Depositional environment: *Ophiomorpha* is documented as a eurybathic trace fossil (e.g., Leaman *et al.*, 2015). It is regarded as a significant component of shallow-marine facies (Frey *et al.*, 1978; Pollard *et al.*, 1993), related to high-energy environments (Knaust, 2017).

Occurrence: Gharra Formation, beds 6 and 13.

Planolites isp.

Fig. 5E

Description: Relatively large, cylindrical or subcylindrical burrow, straight to slightly sinuous unlined, smooth-walled, horizontal to undulant. Individual segments may be parallel, oblique, or normal to the bedding. Sediment fills typically differ in colour from the surrounding sediments.

Producers and ethology: *Planolites* is interpreted as feeding burrows (fodinichnia) of deposit-feeders, including wormlike animals, arthropods, and bivalves (e.g., Pemberton and Frey, 1982; Knaust, 2017).

Depositional environment: It is found in marine and non-marine environments (Pemberton and Frey, 1982).

Occurrence: Gharra Formation, bed 14b.

Polykladichnus isp.

Fig. 5F

Description: Vertical to steeply oblique tubes with single or multiple Y- or U-shaped, upward branched bifurcation and slight enlargement at junctions; tubes usually connect to the bedding surface.

Producers and ethology: Possible tracemaker for marine *Polykladichnus* are polychaetes and cerianthid anemones (Schlirf and Uchman, 2005). Burrows are interpreted as dwelling or feeding structures of selective detritus-feeding crustaceans.

Depositional environment: *Polykladichnus* occurs in marine and non-marine environments (Schlirf and Uchman, 2005).

Occurrence: Gharra Formation, bed 14b.

Skolithos linearis Haldeman, 1840

Fig. 5G

Description: Burrows vertical to slightly inclined, cylindrical to sub-cylindrical, straight to slightly curved, unbranched burrow, more or less distinctly lined. Burrow-fill is structureless, commonly similar to the host rock.

Producers and ethology: It is interpreted as the domichnion of suspension- or deposit-feeding worms, most likely phoronids or polychaetes (Alpert, 1974).

Depositional environment: *Skolithos* is commonly occurs in relatively high-energy, shallow-water, nearshore to marginal-marine environments (Fillion and Pickerill, 1990; Knaust, 2017).

Occurrence: Gharra Formation, bed 6.

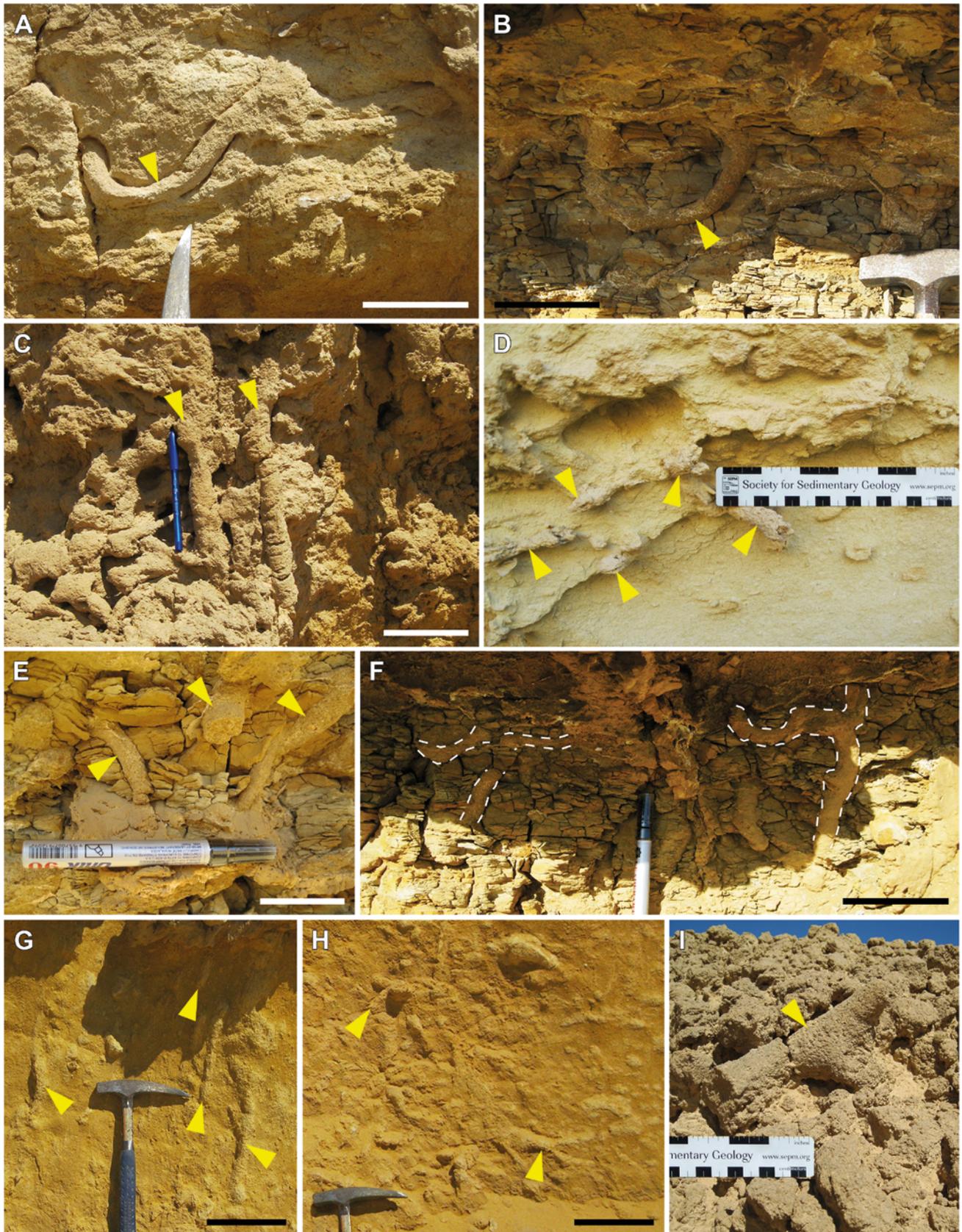


Fig. 5. The identified early Miocene ichnotaxa. **A, B.** *Arenicolites carbonarius* (arrows), Gh6, Gh14b, respectively. **C, D.** *Ophiomorpha* isp. (arrows), Gh6, Gh13, respectively. **E.** *Planolites* isp. (arrows), Gh14b. **F.** *Polykladichnus* isp., Gh14b. **G.** *Skolithos linearis* (arrows), Gh6. **H.** *Thalassinoides paradoxicus?* (arrows), Gh6. **I.** *Thalassinoides suevicus?* (arrow), Gh6. Scale bars equal 5 cm for A and E, 10 cm for B, C and F, and equal 15 cm for G and H.

Thalassinoides paradoxicus? Kennedy, 1967

Fig. 5H

Description: Smooth, cylindrical to subcylindrical, T-shaped burrows. Tunnels are straight to slightly curved; almost constant in diameter; horizontal tunnels bifurcate at angles ranged from 60° to 160°.

Producers and ethology: Burrows are interpreted as dwelling or feeding structures of selective detritus-feeding crustaceans (Ekdale, 1992).

Depositional environment: Herein, *Th. paradoxicus?* is a subordinate component in the less diversified assemblage, hardly preserved in the calcareous, egg yellow sandstone bed. *Thalassinoides paradoxicus* occurs preferably in fine-grained sediments of marginal-marine to shallow-marine deposits (e.g., Howard and Frey 1984; Knaust, 2021). It is a common component of the *Zoophycos*, *Cruziana* and *Glossifungites* ichnofacies (e.g., Knaust, 2021; El-Refaiy *et al.*, 2023).

Occurrence: Gharra Formation, bed 6.

Thalassinoides suevicus? (Rieth, 1932)

Fig. 5I

Description: Three-dimensional boxwork of branched, cylindrical burrows, interconnected by vertical shafts. Individual burrow shows Y- and T-shaped branches. Burrow fill is passive, composed of sands.

Producers and ethology: For Permian to modern *Thalassinoides*, the producers belong to thalassinidean shrimp (e.g., callianassids). For Palaeozoic *Thalassinoides*, in contrast, the tracemakers include other arthropods (e.g., trilobites), sea anemones and the acorn worms, i.e., enteropneusts (e.g., Ekdale and Bromley, 2003; Cherns *et al.*, 2006).

Depositional environment: *Thalassinoides* mostly registered in shallow-marine environment (e.g., Nickell and Atkinson, 1995), and can be found in brackish environments, e.g., in estuarine settings and fan deltas (e.g., Swinbanks and Luternauer, 1987).

Occurrence: Gharra Formation, bed 6.

Macrobenthic palaeocommunities**Faunal composition and distribution**

The Gebel Gharra succession contains, at specific horizons, a well-preserved and diversified macrobenthic fauna. Macrobenthic assemblages are mainly composed of molluscs (60.1%), corals (38.2%), and echinoids (1.6%). Molluscs include pectinids (28.1%), oysters (20.8%), other bivalves (9.5%), and gastropods (1.7%). Forty-five macrobenthic species have been identified, including pectinids (13), oysters (2), other bivalves (8), gastropods (8), echinoids (4), and corals (10). In general, epifaunal and suspension-feeding taxa predominate in the identified macrobenthic assemblages (Tab. 2).

Pectinids are the most common mollusc faunal element in the Gebel Gharra succession (Fig. 2). Sediments of the Gharra and Geniefa formations contain abundant and a relatively diverse assemblages of pectinids, including

Aequipecten, *Macrochlamis*, *Pecten*, *Amussiopecten*, *Flabellipecten*, *Oppenheimopecten*, and *Spondylus* species (Tab. 2). In addition, the lower Miocene Gharra Formation is characterised by the presence of three pectinid-rich marl beds (i.e., pectinid-shell accumulations; Fig. 2).

Oysters represent the second important mollusc group in sediments of the Gharra and Geniefa formations (Fig. 2). Several beds contain abundant *Lopha virleti* (Deshayes, 1833) and/or *Ostrea frondosa* (de Serres, 1829) associated with other macrobenthos. The presence of oyster accumulations was recorded in both the Gharra and Geniefa formations (Fig. 2).

Other bivalves are the third important mollusc group in the lower–middle Miocene succession studied (Tab. 2; Fig. 2). It shows relatively low species diversity. *Anomia* and *Lazariella* species were recorded only in the lower Miocene Gharra Formation. *Lucina*, *Myrtea*, and *Paphia* species exclusively occur in the middle Miocene Geniefa Formation. Furthermore, *Callista*, *Cerastoderma*, and *Lithophaga* species were recognised in both lower–middle Miocene formations.

Gastropods are sporadically recorded in the lower–middle Miocene succession studied, representing an assemblage with low species diversity, including *Conus*, *Globularia*, *Natica*, *Strombus*, *Turritella*, and *Xenophora* species (Tab. 2). They occur mainly in the lower Miocene Gharra Formation (Fig. 2). In contrast, *Natica*, *Turritella*, and *Xenophora* species also were observed in bed 20 in the upper part of the middle Miocene Geniefa Formation.

Echinoid tests and/or spines occur throughout the lower–middle Miocene succession studied (Fig. 2). Irregular echinoids are mainly represented by four species, including *Echinolampas amplus* Fuchs in Zittel, 1883, *Echinolampas* sp., *Clypeaster marginatus* Lamarck, 1816, and *Clypeaster* sp. (Tab. 2). In addition, moderate occurrences of cidaroid spines were recorded in the Gharra and Geniefa formations. In the middle part of the Geniefa Formation (bed 18), in contrast, spines occur, forming a relatively dense cluster.

Scleractinian corals are quite common in the lower–middle Miocene sediments of the Gebel Gharra section, occurring in low species diversity in different habits throughout the succession studied. They are mostly colonial (branched and massive forms), with only few solitary species. Solitary corals are represented mainly by the two species, *Ceratotrochus* sp. and *Desmophyllum* sp. (Tab. 2). Both species occur sporadically in the lower Miocene Gharra Formation (beds 2 and 14b), whereas *Ceratotrochus* sp. also was recorded in bed 23 of the topmost part of the middle Miocene Geniefa Formation (Fig. 2).

The branched *Acropora* sp. represents the most common scleractinian coral in the study area. Stratified deposits with accumulations of mainly redeposited branches of this species were recorded in the Gharra Formation in two levels (beds 9 and 14b), associated with other solitary coral taxa (Fig. 2). A similar feature also was observed in the Geniefa Formation in bed 22 that exclusively is dominated by *Acropora* sp. without any other coral species. *In situ* growth of colonies of *Acropora* sp. is scarce throughout the studied succession.

The genus *Tarbellastraea* represents the second common scleractinian coral in the studied succession.

Table 2

List of macrobenthic fauna in the lower–middle Miocene succession with data on life habits and feeding modes.

Family	Species	Life habit	Feeding mode
Bivalves			
Mytilidae Rafinesque, 1815	1. <i>Lithophaga lithophaga</i> (Linnaeus, 1758)	I	S
Ostreidae Rafinesque, 1815	2. <i>Lopha virleti</i> (Deshayes, 1833)	EC	S
	3. <i>Ostrea frondosa</i> (de Serres, 1829)	EC	S
Pectinidae Wilkes, 1810	4. <i>Aequipecten radians</i> (Nyst and Westendorp, 1839)	EM	S
	5. <i>Aequipecten submalvinae</i> (Blanckenhorn, 1901)	EM	S
	6. <i>Macrochlamis zizini</i> (Blanckenhorn, 1901)	EM	S
	7. <i>Pecten benedictus</i> Lamarck, 1819	EM	S
	8. <i>Pecten cristatocostatus</i> Sacco, 1897	EM	S
	9. <i>Pecten fraasi</i> Fuchs, 1883	EM	S
	10. <i>Pecten kochi</i> Locard, 1877	EM	S
	11. <i>Pecten subarcuatus</i> Tournouër, 1873	EM	S
	12. <i>Pecten</i> sp.	EM	S
	13. <i>Amussiopecten expansus</i> (Sowerby in Smith, 1847)	EM	S
	14. <i>Flabellipecten schweinfurthi</i> (Blanckenhorn, 1901)	E	S
	15. <i>Oppenheimiopecten josslingi</i> (Sowerby in Smith, 1847)	E	S
	Spondylidae Gray, 1826	16. <i>Spondylus</i> sp.	EC
Anomiidae Rafinesque, 1815	17. <i>Anomia ephippium</i> Linnaeus, 1758	EC	S
Lucinidae Fleming, 1828	18. <i>Lucina multilamellata</i> Deshayes, 1832	IM	D
	19. <i>Myrtea spinifera</i> (Montagu, 1803)	IM	D
Carditidae Férussac, 1822	20. <i>Lazariella hippopea</i> (Basterot, 1825)	IM	S
Cardiidae Lamarck, 1809	21. <i>Cerastoderma edule</i> (Linnaeus, 1758)	IM	S
Veneridae Rafinesque, 1815	22. <i>Callista</i> sp.	IM	S
	23. <i>Paphia vetula</i> Basterot, 1825	IM	S
Gastropods			
Turritellidae Lovén, 1847	24. <i>Turritella triplicata</i> (Brocchi, 1814)	SIM	S
	25. <i>Turritella vermicularis</i> (Brocchi, 1814)	SIM	S
	26. <i>Turritella</i> sp.	SIM	S
Ampullinidae Cossmann, 1918	27. <i>Globularia</i> sp.	E	G
Strombidae Rafinesque, 1815	28. <i>Strombus</i> sp.	E	Om/G
Naticidae Guilding, 1834	29. <i>Natica</i> sp.	SI	C
Xenophoridae Troschel, 1852	30. <i>Xenophora</i> sp.	E	G
Conidae Fleming, 1822	31. <i>Conus</i> sp.	E	C
Echinoids			
Echinolampadidae Gray, 1851	32. <i>Echinolampas amplus</i> Fuchs in Zittel, 1883	E	G/D
	33. <i>Echinolampas</i> sp.	E	G/D
Clypeasteridae Agassiz, 1836	34. <i>Clypeaster marginatus</i> Lamarck, 1816	SI	D
	35. <i>Clypeaster</i> sp.	SI	D
Corals			
Acroporidae Verrill, 1902	36. <i>Acropora</i> sp.	EC	S
Caryophylliidae Dana, 1846	37. <i>Ceratotrochus</i> sp.	EC	MC
	38. <i>Desmophyllum</i> sp.	EC	MC
Diploastraeidae Chevalier & Beauvais, 1987	39. <i>Thegioastraea roasendai</i> (Michelotti, 1871)	EC	MC
Faviidae Gregory, 1900	40. <i>Tarbellastraea reussiana</i> (Milne-Edwards and Haime, 1850)	EC	MC
	41. <i>Tarbellastraea</i> sp.	EC	MC
Merulinidae Verrill, 1866	42. <i>Dipsastraea</i> sp.	EC	S
	43. <i>Favites</i> sp.	EC	S
Montastraeidae Yabe & Sugiyama, 1941	44. <i>Montastraea</i> sp.	EC	MC
Siderastreidae Vaughan & Wells, 1943	45. <i>Siderastrea miocenica</i> Osasco, 1896	EC	S

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

Tarbellastraea reussiana (Milne-Edwards and Haime, 1850) and *Tarbellastraea* sp. occur as small colonial patches in the Gharra (bed 9) and Geniefa (beds 15, 16, and 23) formations, respectively. The reef-building species *Siderastrea miocenica* Osasco, 1896 appeared as an isolated *in situ* massive colonial corals in bed 18 in the Geniefa Formation, associated with *Dipsastraea* sp. and *Montastraea* sp. In addition, *Dipsastraea* sp. was also recorded in the middle Miocene Geniefa Formation in bed 15 associated with *Favites* sp. and *Tarbellastraea reussiana*. Furthermore, *Thegioastraea roasendai* (Michelotti, 1871)

was recorded sporadically in the upper part of the Geniefa Formation (beds 17 and 23; Fig. 2).

On the basis of the occurrences and temporal distributions of these macrobenthic taxa, 13 samples were selected from the Gebel Gharra section. Q-mode cluster analysis produced five macrofossil clusters (assemblages A–E) that are interpreted to represent the remnants of former communities (Fig. 6). The dominant macrobenthic group, epifaunal/infaunal abundances and substrate lithofacies represent major features characterising each assemblage. Furthermore, the Euclidean distances indicate the level of similarity among

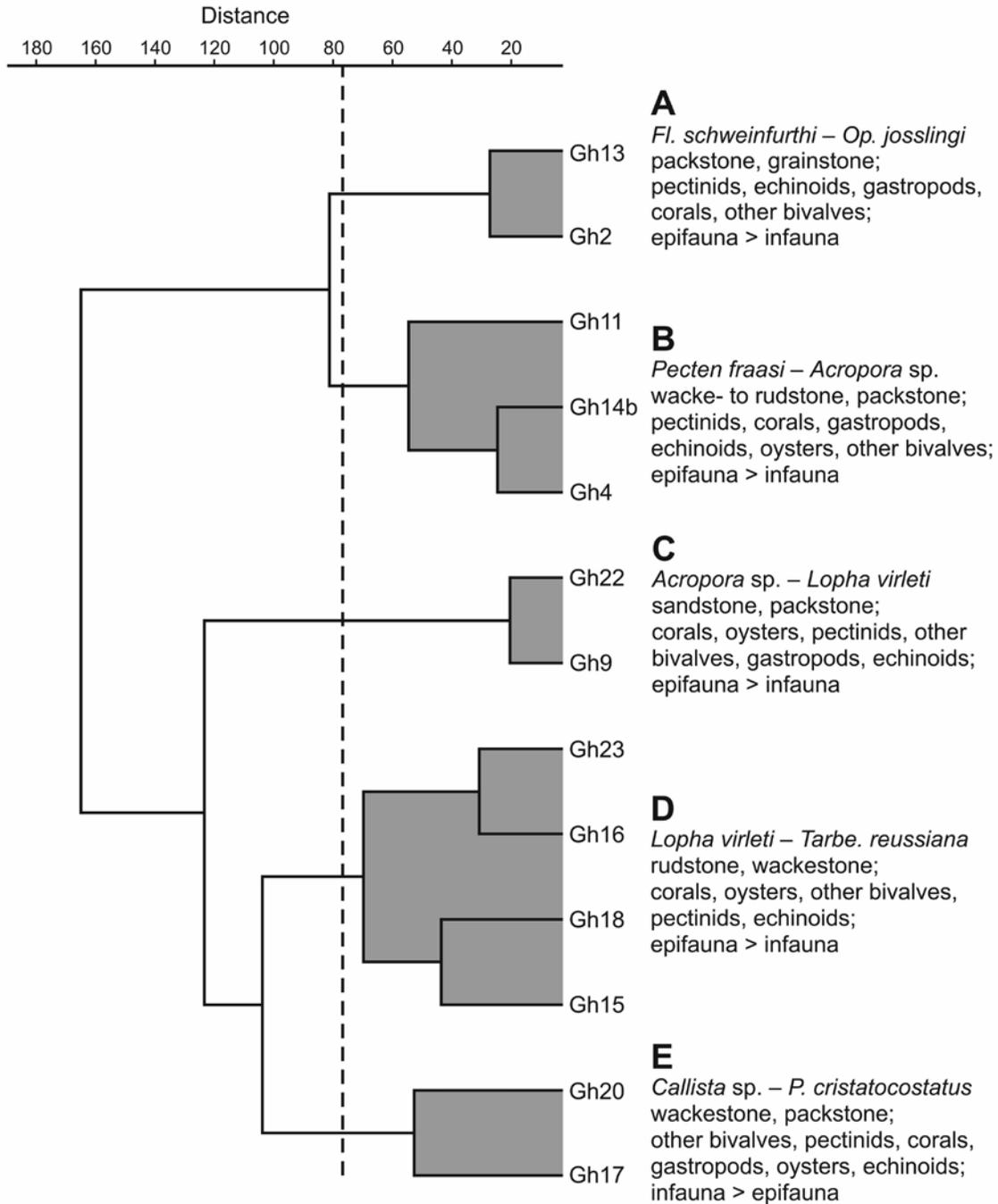


Fig. 6. Q-mode cluster analysis using Ward’s method. A–E represent five clusters of sample groups, based on species abundance data. The vertical dashed line is the cut-off for defining the five assemblages. Assemblages were named after two abundant species to avoid name duplication. Numbers of fossil samples in each cluster are prefixed by Gh for the Gebel Gharra section.

these assemblages (Fig. 7). For instance, assemblage C is quite similar to assemblages D and E, characterised by moderate evenness values (0.49–0.53). Assemblage B ranges in evenness values from 0.35 to 0.50 (mean: 0.43; Fig. 7). In assemblage A, evenness is low, varying between 0.22 and 0.34 (mean: 0.28; Fig. 7).

Two of the five assemblages identified are dominated by pectinids (> 69.0%; A, B), and one by other bivalves (62.6%; E; Fig. 8). The remainders (assemblages C and D) are dominated by two fossil groups, including corals (49.7 and 59.8%) and oysters (35.4 and 31.5%), respectively. With respect to life habits, four of the five assemblages (A–D) are remarkably dominated by epifaunal elements (94.5–98.4%). Assemblage E is dominated by both infaunal and epifaunal elements (62.6 and 31.3%, respectively; Fig. 8). In contrast, semi-infaunal elements play only a minor role in assemblages A, B, C, and E, reaching 6.1% in assemblage E (Fig. 8). In all assemblages, epifaunal elements are represented by solitary and colonial corals, cementing oysters, pectinid, spondylid and anomid bivalves, and some gastropods and echinoids. The infauna is represented mainly by infaunal bivalves. Semi-infaunal organisms are represented by some gastropods and echinoids (Tab. 2; Fig. 8). Concerning feeding modes, all benthic assemblages are strongly dominated by suspension-feeders, ranging between 64.8% in assemblage D and 98.9% in assemblage C (Fig. 8). The second important group is carnivores, which likewise occur in all assemblages and range from 0.5% in assemblage C to 34.0% in assemblage D. Similarly, deposit-feeders were recorded in all assemblages and range from 0.5% in assemblage C to 7.4% in assemblage E. Grazers, in contrast, rarely occurred in assemblage B (1.0%) and E (1.1%). Furthermore, omnivores occur only in assemblage B (0.3%). The distribution of feeding modes is closely related to the distribution of benthic groups (Fig. 8). Out of the 23 species of bivalves, 21 were suspension-feeders and only two deposit-feeders (Tab. 2). Corals are thought to have been microcarnivorous and suspension-feeders. Gastropods were suspension-feeders, carnivores, grazers and omnivores. The irregular echinoids were deposit-feeders.

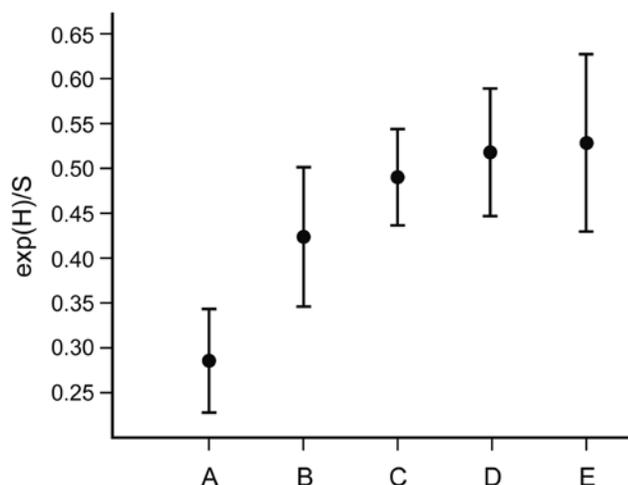


Fig. 7. Range and mean values of evenness of macrobenthic assemblages identified (A–E).

Taphonomic aspects

Taphonomic analysis of the macrofossil assemblages studied mainly referred to the state of preservation of specimens, including disarticulation, sorting, fragmentation, encrustation and bioerosion (Fig. 9). Noteworthy is the absence of evidence of any significant distortion in all fossil groups. The faunal elements with well-preserved shell structures are calcitic, including oysters, pectinids, corals, and echinoids (Fig. 9A–F); corals are partially recrystallised (Fig. 9E). In contrast, owing to diagenetic processes, aragonitic taxa, including infaunal bivalves, semi-infaunal and epifaunal gastropods are preserved exclusively as internal moulds (Fig. 9G, H). However, a single specimen of the gastropod *Turritella triplicata* (Brocchi, 1814) also is preserved as a composite mould (Fig. 9I, J). All infaunal bivalve moulds are articulated, unsorted, and rarely fragmented (7.9%), encrusted (1.3%), and bioeroded (2.0%); they are not in the life position. Gastropod moulds are unsorted, randomly oriented, mostly complete (96.3%), and rarely encrusted (Fig. 9I, J) and bioeroded (11.1% each).

A key feature of the Gharra section is the presence of three pectinid-shells (beds 2, 13 and 14b) and two oyster (beds 9 and 22) accumulations in the early–middle Miocene (Figs 2, 3F, G, 9K, M–O). Throughout the studied succession, oyster and pectinid shells are largely disarticulated (95.1 and 96.9% of total studied specimens, respectively), moderately to poorly sorted, and re-oriented (Fig. 9K, M–O). They mostly display a preferred convex-upward orientation (about 85%). Among the disarticulated oyster specimens, left and right valves are roughly equally abundant (48.6 and 46.5%, respectively). In the disarticulated pectinid specimens, in contrast, the average occurrence of left and right valves is distinctly unequal (30.9 and 66.0%, respectively). In general, oyster fossils are characterised by a relatively low percentage of breakage (13.7%). Commonly encrusted and bored (44.1 and 60.8%, respectively) oyster specimens also were recorded (Fig. 9P–S). On the other hand, pectinid specimens are highly fragmented (47.7%), moderately encrusted (27.9%) and rarely bored (9.0%; Fig. 9K, T, U).

Echinoid specimens are moderately sorted, mostly re-oriented, commonly broken (69.2%), moderately encrusted (19.2%), and rarely bored (7.7%). All specimens lack spines. Tests are parallel to the bedding, occurring both oral side down (35%; in life position) and oral side up (60%). Oblique specimens (5%) also occur (Fig. 9F, V, W).

Corals display a variety of taphonomic features, including fragmentation, abrasion, encrustations, and borings. The occurrence and distribution of these features within the corals studied differ greatly at each group (branched, massive, and solitary forms). Fragmentation is well obvious in the branched forms *Acropora* sp. (Fig. 9O, X). Their remains appeared as stratified deposits of small, reworked and resedimented specimens from reefs, ranging between 3 and 7 cm in diameter and between 8 and 10 cm in length. In addition, these fragments are greatly affected by bioerosion and abrasion. Furthermore, bioerosion is commonly observed in the massive forms, such as *Dipsastraea*, *Favites*, *Montastraea*, and *Tarbellastraea* species.

The macrobenthic specimens studied are greatly affected by various types of episkeletobionts. These encrusters

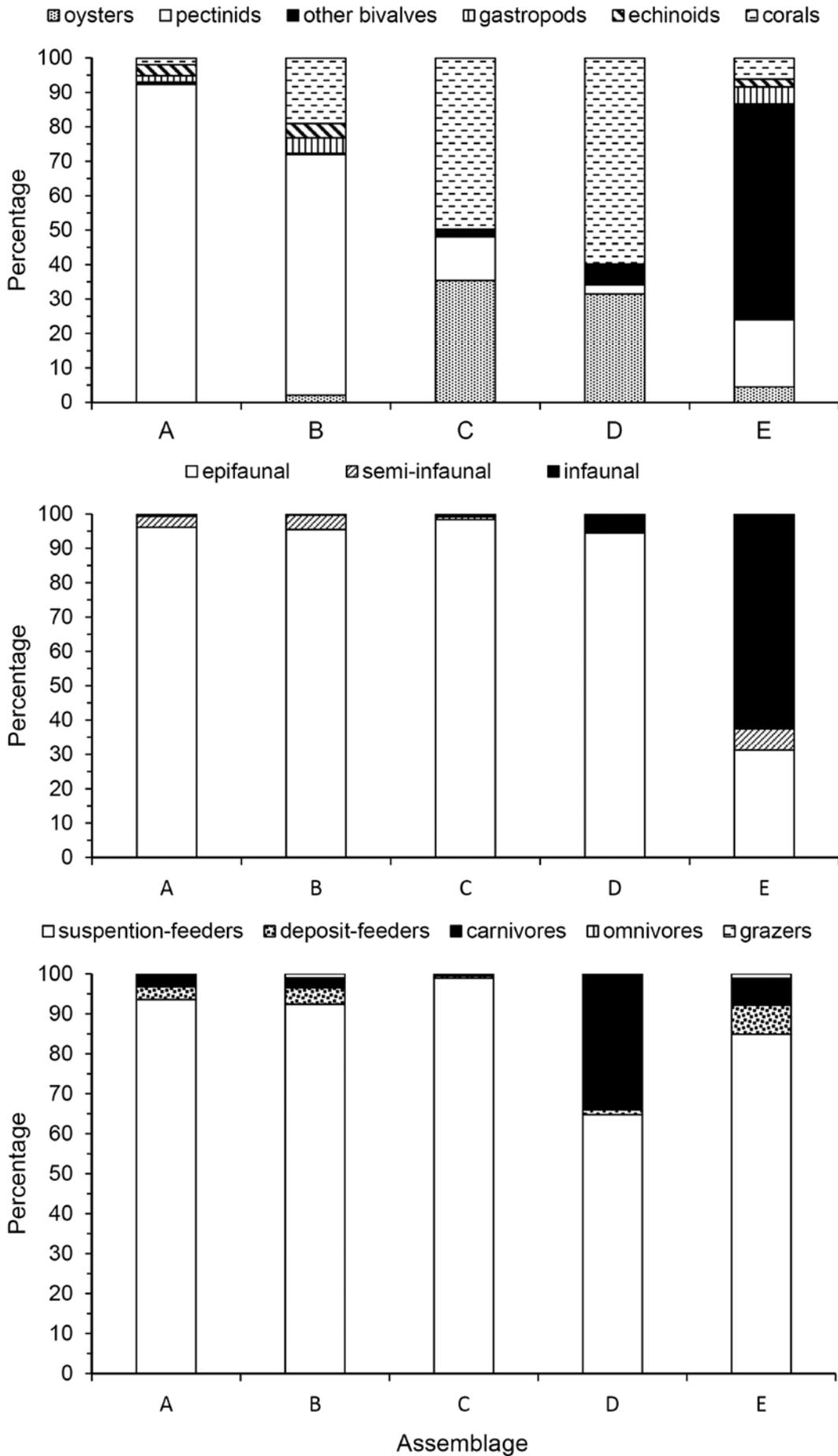


Fig. 8. Distribution of macrobenthic groups, life habits and feeding modes in assemblages A–E.

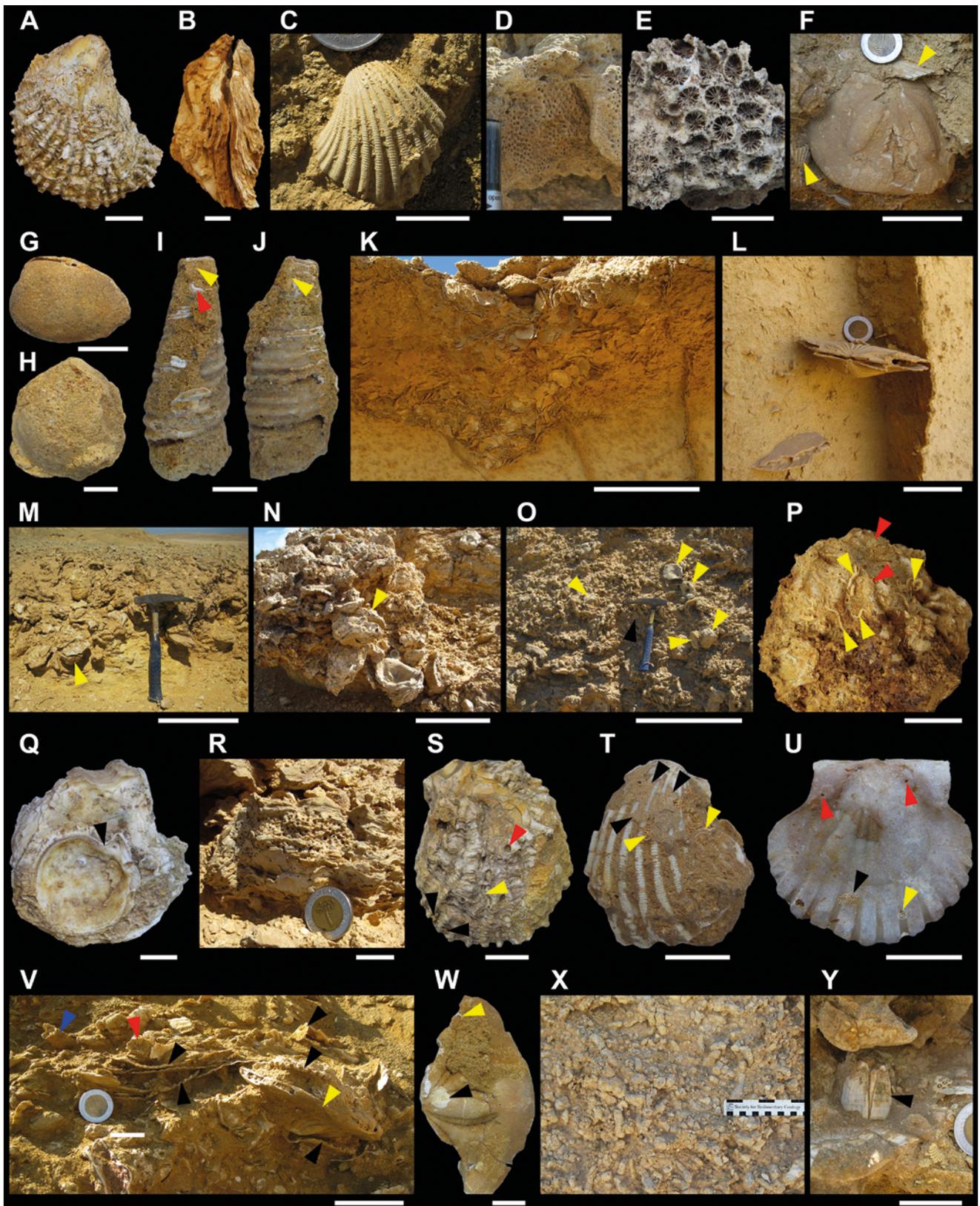


Fig. 9. Taphonomic aspects of the faunal assemblages studied. **A.** *Ostrea frondosa*, external view of well-preserved disarticulated left valve, Gh9O36. **B.** *Lopha virleti*, well-preserved articulated left and right valves, Gh9O33. **C.** *Pecten cristatocostatus*, external view of well-preserved disarticulated right valve, bed 14b, the Gharra Formation. **D.** Well-preserved *Montastraea* sp. specimen, bed 18, the Geniefa Formation. **E.** Well-preserved recrystallised *Tarbellastraea* sp. specimen, Gh9C82. **F.** *Clypeaster* sp. test in life position (oral side down) and some fragmented pectinid shells (arrows), bed 14b, the Gharra Formation. **G.** *Calista* sp., left valve view of well-preserved articulated internal mould, Gh20B57. **H.** *Myrtea spinifera*, right valve view of well-preserved articulated internal mould, Gh20B36. **I, J.** *Turritella triplicata*, moderately preserved composite mould with bryozoans and polychaete worm (yellow and red arrows, respectively), Gh14bG13.

were found abundantly attached to the shells of oysters and pectinids, but there are few other bivalves, gastropods, echinoids, and corals having rare episkeletobionts. Among oyster specimens, the sites of episkeletobiont assemblages vary a great deal, including oysters (52.4%), bryozoans (46.2%), polychaetes (31.5%), balanoid barnacles (15.4%), and pectinids (4.2%; Fig. 9P, Q, S). In contrast, the episkeletobiont assemblages on pectinid specimens include polychaetes (72.6%), bryozoans (66.1%), and oysters (22.6%). Rare occurrences of benthic foraminifera (*Planostegina* sp.) also were observed (Fig. 9T, U). The distribution and frequency of these encrusters vary considerably between species and commonly within the same species. The attached oysters are represented by different ontogenetic stages of the left valves. Bryozoans are represented mostly by sheet-like cheilostome types (Fig. 9T). Among polychaetes, adult and juvenile stages of serpulid, sabellid, and spirorbid worms were recorded (Fig. 9P, T; for details, see Mandor *et al.*, 2022). In many cases, different episkeletobionts show signs of bioerosion and they can be found growing over or within borings, as well.

Bioerosion traces are represented by chambers and/or tunnels, which are the product of varied endolithic communities, including sponges (ichnogenus *Entobia*), bivalves (*Gastrochaenolites*), polychaetes (*Caulostrepsis*, *Maeandropolydora*, and *Trypanites*), phoronid worms (*Talpina*), and acrothoracican cirripeds (*Rogerella*). Moreover, traces of gastropod activities, including *Oichnus* and *Renichnus*, were recorded. Collectively, all these traces belong to three ethological categories, including domichnia, fixichnia, and praedichnia (Fig. 9R, S, U).

Macrofossil assemblages and interpretations

On the basis of species richness, the clustered assemblages are considered as paucispecific. They were named after the most dominant two species to avoid name duplication (Fig. 6). As mentioned above, the macrobenthic fauna is dominated by moderately to well-preserved, moderately to densely packed, commonly disarticulated, poorly sorted, moderately fragmented, and re-oriented or re-sedimented

specimens. Consequently, these results confirm that the authors were 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 palaeo-ecosystem can be generated and inferred.

Flabellipecten schweinfurthi–*Oppenheimopecten josslingi* assemblage (A)

Description: This assemblage has been defined on the basis of two samples (Gh2, Gh13), 156 individuals and 17 species. It occurs in sandy highly porous packstone (FT7) and tightly-packed grainstone (FT11) of the lower Miocene Gharra Formation (Figs 2, 6). Pectinids are the most common faunal element (92.3%), followed by echinoids (3.2%), gastropods and corals (1.9% each), and other bivalves (0.6%; Fig. 8). Epifaunal species dominate (96.2%), while semi-infauna and infauna are rare (3.2 and 0.6%, respectively; Fig. 8). With respect to feeding habits, suspension-feeders are dominant in the assemblage at 93.6%, followed by deposit-feeders and carnivores (3.2% each; Fig. 8). The trophic nucleus consists of the pectinids *F. schweinfurthi* (Blanckenhorn, 1901; 37.8%), *O. josslingi* (Sowerby in Smith, 1847; 14.7%), *Macrochlamis ziziniiae* (Blanckenhorn, 1901; 14.1%), *Aequipecten submalvinae* (Blanckenhorn, 1901; 5.1%), *Pecten fraasi* Fuchs, 1883 and *A. radians* (Nyst and Westendorp, 1839; 4.5% each; Fig. 10). Specimens mostly are disarticulated, densely packed, re-oriented, highly fragmented, moderately encrusted and rarely bored (Tab. 3). In the upper part of sample (Gh13), in particular, some articulated pectinid specimens preserved in the life position also were recorded (Fig. 9L). The evenness value is obviously low and varies from 0.23 to 0.34 (mean: 0.28; Fig. 7).

Interpretation: Pectinids are widely distributed in shallow-marine environments (Cox, 1952; Fleming, 1957; Waller, 1969). The presence of corals and echinoids indicates euhaline conditions and a position probably within the photic zone (Smith *et al.*, 1988, 1995; Ayoub-Hannaa and Fürsich, 2012). The high percentage of suspension-feeders

K. Reworked accumulation of large specimens of *Flabellipecten schweinfurthi*, bed 13, the Gharra Formation. **L.** Articulated and well-preserved *F. schweinfurthi* specimen preserved in life position, bed 13, the Gharra Formation. **M, N.** Accumulations of disarticulated and re-oriented specimens of *L. virleti*; note the occurrence of rare articulated specimens preserved in life position (arrows), bed 9 (the Gharra Formation) and bed 22 (the Geniefa Formation), respectively. **O.** Abundant redeposited *Acropora* sp. fragments associated with disarticulated, partially fragmented and re-oriented *Lopho virleti* (yellow arrows) and pectinid (black arrow) shells, bed 22, the Geniefa Formation. **P.** Polychaete worms (yellow arrows) overgrowing bryozoans (red arrows) on the exterior surface of right valve of *L. virleti*, Gh14bO44. **Q.** Pectinid left valve on the interior surface of right valve of *Lopho virleti*, Gh16O85. **R.** Ventral margin of left valve of *L. virleti* with abundant *Entobia* borings, bed 22, the Geniefa Formation. **S.** External surface of left valve of *Ostrea frondosa* with small balanoid barnacles (black arrows), and borings of *Maeandropolydora* (yellow arrow) and *Gastrochaenolites* (red arrows), Gh22O253. **T.** External surface of right valve of *P. fraasi* with bryozoans (black arrows) and polychaete worms (yellow arrows), Gh14bP195. **U.** Internal surface of left valve of *P. kochi* with bryozoans, foraminifera, and *Trypanites* borings (black, yellow and red arrows, respectively), Gh14bP152. **V.** Marl of bed 14b (the Gharra Formation) with disarticulated and fragmented pectinid valves (black arrows), *Desmophyllum* sp. (red arrow), *Clypeaster marginatus* (yellow arrow), and echinoid spine (blue arrow). Note that the echinoid test occurs with oral side up. **W.** Incomplete *Clypeaster* sp. test with well-developed calcified scar of balanoid barnacle and polychaete traces (black and yellow arrows, respectively), Gh14bE16. **X.** Stratified accumulation of redeposited fragmented branches of *Acropora* sp., bed 22, the Geniefa Formation. **Y.** Large balanoid barnacle (arrow) in life position, bed 20, the Geniefa Formation. Scale bars equal 2 cm, except for F, L, and V, which are 5 cm, I, J, and U, which are 1.0 cm, K and O, which are 50 cm, and for M and N, which are 20 cm.

Table 3

Taphonomic attributes of the lower–middle Miocene macrofaunal assemblages A–E.

Assemblage	Formation & samples	Biofacies	No. of individ.	No. of species	Disart. ¹ %	Taphonomic characters				
						Sorting	Fragm. ²	Encrust. ³	Bioeros. ³	
						%				
A	<i>Flabellipecten schweinfurthi</i> – <i>Oppenheimopecten josslingi</i>	Gharra (Gh2, Gh13)	Densely packed, re-oriented fossils	156	17	91.1	Moderate-non	44.6	21.5	7.7
B	<i>Pecten fraasi</i> – <i>Acropora</i> sp.	Gharra (Gh4, 11, 14b)	Moderately to densely packed, re-oriented fossils	289	22	100.0	Non	43.4	34.7	11.8
C	<i>Acropora</i> sp.– <i>Lopha virleti</i>	Gharra, Geniefa (Gh9, 22)	Densely packed, re-oriented fossils	370	16	94.0	Moderate-non	15.6	42.6	59.6
D	<i>Lopha virleti</i> – <i>Tarbellastraea reussiana</i>	Geniefa (Gh15, 16, 18, 23)	Moderately packed, re-oriented fossils	585	14	95.7	Moderate-non	16.9	36.1	51.4
E	<i>Callista</i> sp.– <i>Pecten cristatocostatus</i>	Geniefa (Gh17, 20)	Moderately to loosely packed, re-oriented fossils	179	15	93.1	Non	9.1	4.5	3.2

¹Disarticulation percentages are calculated based on the total oyster and pectinid specimens in an assemblage.

²Fragmentation percentages are calculated based on the total oyster, pectinid, other bivalve, gastropod, and echinoid specimens in an assemblage.

³Encrustation and bioerosion percentages are calculated based on the total oyster, pectinid, other bivalve, gastropod, and echinoid specimens in an assemblage.

points to elevated water energy. In particular, *Macrochlamis* species typically occur in high-energy, shallow-marine environments (e.g., Ctyroky, 1969). In addition, the abundant highly sculptured inequivalve pectinid shells can resist these higher energy levels (e.g., Kauffman, 1969; Waller, 1969, 1991). This type of ornamentation also may represent an adaptation to ward off predators (e.g., Waller, 1969). In addition, the occurrence of highly disarticulated, re-oriented, and fragmented pectinid valves likewise confirms high-energy conditions (e.g., Mandic and Piller, 2001). Furthermore, sand dollars characterise shallow-water, higher-energy environments (e.g., Ebert and Dexter, 1975; Mooi and Telford, 1982). This increased water energy keeps organic nutrients in suspension, along with a low to moderate rate of sedimentation (e.g., Ayoub-Hannaa and Fürsich, 2012; El-Sabbagh *et al.*, 2021). The latter is also confirmed by the moderate signs of encrustation by polychaetes and bryozoans (Wilson and Taylor, 2001). In addition, this low to moderate rate of sedimentation permits the accumulation of food particles for deposit feeders. The dominance of epifauna suggests a firm substrate (packstone); corals also need a hard substrate for fixation. The occurrence of semi-infauna and infauna particularly may point to the presence of a slightly softer substrate. This assemblage lived in lagoon (FT7) and shoal (FT11) environments of the inner ramp setting. Apparently, the abundant epifauna may indicate a relatively stable low-stress environment (Fürsich, 1981; Fürsich *et al.*, 2012). However, the predominance of a single taxon (Fig. 10), along with low value of evenness, are most probably the result of a sample size effect (see Koch,

1987). Furthermore, the dissolution of aragonitic shells (e.g., Morse *et al.*, 1985) also may have affected the trophic structure of this assemblage.

***Pecten fraasi*–*Acropora* sp. assemblage (B)**

Description: This assemblage consists of three samples (Gh4, Gh11, Gh14b) with 22 species and 289 individuals from the Gharra Formation. It occurs in sandy bioturbated wacke-to rudstone (FT3), and sandy highly porous packstone (FT7; Figs 2, 6). The following fossil groups were recorded: pectinids (69.9% of the assemblage), corals (19.0%), gastropods (4.5%), echinoids (4.2%), oysters (2.1%), and other bivalves (0.3%; Fig. 8). Epifauna accounts for 95.5%, semi-infauna for 4.2%, and infauna for 0.3% (Fig. 8). Five trophic groups were recorded, including suspension-feeders (92.4%), deposit-feeders (4.2%), carnivores (2.1%), grazers (1.0%), and omnivores (0.3%; Fig. 8). The trophic nucleus consists of *P. fraasi* (28.4%), the branched coral *Acropora* sp. (18.0%), *O. josslingi* (17.0%), *P. kochi* Locard, 1877 (15.6%), and *A. submalvinae* (4.5%; Fig. 10). In sample Gh14b, highly fragmented *Acropora* sp. branches occur, associated with rare solitary corals *Ceratotrochus* and *Desmophyllum* species (Fig. 9V). In general, specimens are disarticulated. They are moderately to densely packed, re-oriented, unsorted, highly fragmented, commonly encrusted and rarely bored (Tab. 3). The evenness value varies from 0.35 to 0.50 (mean: 0.43; Fig. 7).

Interpretation: This assemblage lived in a shallow lagoon (FT3 and FT7) environment of the inner ramp setting. The occurrence of echinoids and corals indicate euhaline

conditions in the photic zone. Highly convex and sculptured pectinid shells (*P. fraasi*, *P. kochi*, and *O. josslingi*) are better adapted to a semi-sessile habit, resisting higher energy levels in a shallow-marine environment. The function of this type of pectinid ornamentation also may protect shells against predators. The presence of reworked and re-sedimented branches of *Acropora* sp. likewise confirms episodic elevated water-energy events (e.g., Schuster, 2000). The dominance of epifauna indicates a firm substrate (wacke- to packstone). The occurrence of semi-infauna and infauna points to a slightly soft and well oxygenated substrate. During these conditions, the dead shell materials acted as a secondary hard substrate for the settlement of the rare coral patches and oysters (e.g., Taylor and Wilson, 2003; Zuschin and Stachowitsch, 2009). The common occurrence of encrusting organisms, including bryozoans, polychaetes, and oysters, reflects reduced sedimentation rates. The abundant epifauna, along with the occurrence of semi-infaunal and infaunal taxa and the moderate value of evenness, may indicate a relatively stable low-stress environment. However, diagenetic sorting may also have affected the trophic structure of this assemblage.

Acropora sp.–*Lopha virleti* assemblage (C)

Description: Assemblage C includes 370 individuals and 16 species in two samples from the Gharra Formation (Gh9) and the Geniefa Formation (Gh22). It occurs in dolomite-cemented sandstone (FT2) and sandy highly porous packstone (FT7; Figs 2, 6). Corals are the dominant group, accounting for 49.7% of the assemblage (Fig. 8). The remainders are represented by oysters (35.4%), pectinids (12.7%), other bivalves (1.1%), gastropods and echinoids (0.5% each). Epifaunal species are predominant (98.4%), while infauna and semi-infauna are remarkably rare (0.8% each; Fig. 8). Suspension-feeders are dominant (98.9%). Other trophic groups are represented by rare deposit-feeders and carnivores (0.5% each; Fig. 8). The trophic nucleus consists of *Acropora* sp. (43.5%), *L. virleti* (29.5%), *Tarbellastraea* sp. (6.2%), and *Ostrea frondosa* (5.9%; Fig. 10). Corals are preserved as highly fragmented and recrystallised *Acropora* sp. Branches, associated with isolated massive *Tarbellastraea* sp. colonies. Specimens are mostly disarticulated, densely packed, re-oriented, moderately fragmented, and highly encrusted and bored (Tab. 3). The evenness value varies from 0.44 to 0.55 (mean: 0.49; Fig. 7).

Interpretation: The common corals indicate euhaline conditions in the photic zone. Oysters lived in very shallow-water environments (Stenzel, 1971; Bottjer, 1981). The dominance of epifauna and the nearly complete lack of infaunal and semi-infaunal elements and gastropods indicate a firm substrate and a relatively low sedimentation rate. The assemblage is characterised by the abundance of radially ribbed cemented oysters, i.e., ornamentation helped in the adhesion of organisms to the substrate (e.g., Seilacher, 1984) and to protect them against predators, such as some gastropods (e.g., Ayoub-Hannaa and Fürsich, 2012; El-Sabbagh *et al.*, 2021). A low rate of sedimentation also is confirmed by the abundant signs of encrusters (bryozoans, serpulids, oysters, and balanoid barnacles) and bioeroders (e.g., sponges, bivalves, polychaetes, and acrothoracican

cirripeds). The high percentage of suspension-feeders certifies that the turbulence level must have been sufficiently high to keep food particles suspended in the water column. Moreover, the densely packed, highly disarticulated and re-oriented oyster and pectinid valves confirm brief periods of high-energy conditions. These short-lived reworking events also are documented in the occurrence of abundant fragmented corals. In general, oysters thrived in high-energy, nutrient-rich and low-salinity waters, i.e., as opportunistic species that occur in very shallow and faunally restricted environments (e.g., Pufahl and James, 2006). However, sample size and/or diagenetic sorting also may have affected the trophic structure of this assemblage. Sediments were deposited in supratidal (FT2) and lagoonal (FT7) environments in an inner ramp setting.

Lopha virleti–*Tarbellastraea reussiana* assemblage (D)

Description: This assemblage includes 585 individuals and 14 species in four samples (Gh15, Gh16, Gh18, Gh23) from the Geniefa Formation. It occurs in coralline red algae rudstone (FT4) and sparry calcite wackestone (FT6; Figs 2, 6). Corals dominate this assemblage (59.8%), followed by oysters (31.5%), other bivalves (5.5%), pectinids (2.7%) and rare echinoids (0.5%; Fig. 8). Epifaunal species predominate (94.5%), while infauna is rare (5.5%; Fig. 8). Three trophic groups were recorded, including suspension-feeders (64.8%), carnivores (34.0%), and deposit-feeders (1.2%; Fig. 8). The trophic nucleus consists of *L. virleti* (20.5%), *Tarbellastraea reussiana* (18.8%), *Dipsastraea* sp. (16.2%), *Montastraea* sp. (12.3%), *Ostrea frondosa* (10.9%), and *Siderastrea miocenica* (5.3%; Fig. 10). Specimens are mostly disarticulated, moderately packed, re-oriented, moderately fragmented, and highly encrusted and bored (Tab. 3). In addition, corals occur as moderately to well-preserved isolated massive colonies. The evenness value is moderate and varies from 0.45 to 0.59 (mean: 0.52; Fig. 7)

Interpretation: Oysters lived in very shallow seas. The abundant corals document euhaline conditions. The occurrence of algae confirms a position probably within the shallow photic zone (Wray, 1977; Bucur and Săsăran, 2005). The predominance of epifauna indicates a firm substrate (rudstone and wackestone). In addition, the occurrence of infauna may point to a slightly softer substrate. In that condition, shells of infauna may provide a secondary hard substrate for the settlement of the cemented oysters and massive corals. The high percentage of suspension-feeders indicates high-energy conditions that kept organic nutrients in suspension, i.e., reduced sedimentation rates. These conditions also can be confirmed by the occurrence of moderately packed, highly disarticulated, and re-oriented oyster and pectinid shells with abundant signs of encrustation and bioerosion (Tab. 3). In addition, the abundant cidaroid spines (as in sample Gh18) and the complete absence of other skeletal elements may support these high-energy conditions. Robust cidaroid spines have a higher stability in comparison with the much thinner tests (Greenstein, 1992; Moffat and Bottjer, 1999; Nebelsick and Kroh, 2002). Furthermore, the rarity of deposit-feeders may be explained by the elevated water energy, and consequently, the by-passing of particulate organic matter (e.g., Abdelhady and Fürsich,

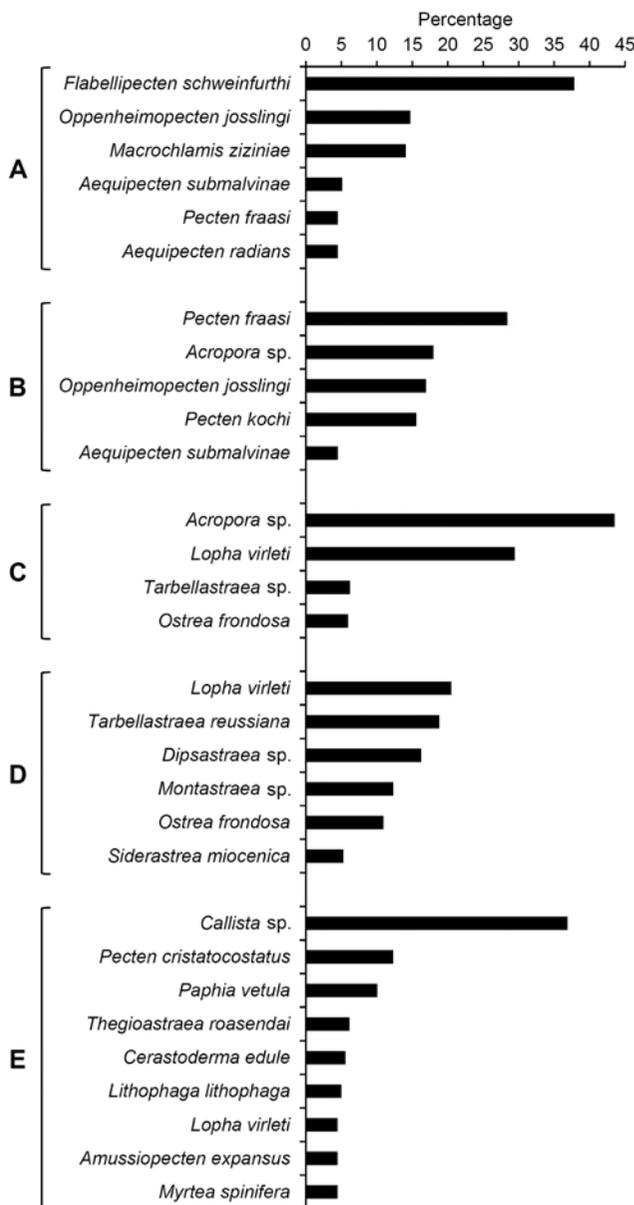


Fig. 10. Trophic nuclei (in %) of assemblages A–E.

2014). The environment deduced for this assemblage is a well oxygenated, shallow lagoon (FT4 and FT6) in an inner ramp setting. It is characterised by high water energy, a low rate of sedimentation, and high surface water productivity. The species diversity is relatively low, but evenness is moderate, certifying the effect of sample size and/or diagenetic sorting on the trophic structure of this assemblage.

Callista sp.–*Pecten cristatocostatus* assemblage (E)

Description: This assemblage was defined on the basis of two samples (Gh17, Gh20), 179 individuals and 15 species in the Geniefa Formation. It occurs in sparry calcite wackestone (FT6) and sandy highly porous packstone (FT7; Figs 2, 6). Other bivalves predominate (62.6% of the assemblage), followed by pectinids (19.6%), massive corals (6.1%), gastropods (5.0%), oysters (4.5%), and echinoids (2.2%; Fig. 8). Infaunal species predominate (62.6%), but epifaunal (31.3%)

and semi-infaunal (6.1%) taxa are also present (Fig. 8). Four trophic groups occur, including suspension-feeders (84.9%), deposit-feeders (7.3%), carnivores (6.7%), and grazers (1.1%; Fig. 8). The trophic nucleus consists of *Callista* sp. (36.9%), *P. cristatocostatus* Sacco, 1897 (12.3%), *Paphia vetula* Basterot, 1825 (10.1%), *Thegioastraea roasendai* (6.1%), *Cerastoderma edule* (Linnaeus, 1758; 5.6%), *Lithophaga lithophaga* (Linnaeus, 1758; 5.0%), and *L. virleti*, *Amussiopecten expansus* (Sowerby in Smith, 1847), and *Myrtea spinifera* (Montagu, 1803; 4.5% each; Fig. 10). Specimens are mostly disarticulated, moderately to loosely packed, re-oriented, and unsorted. In addition, fragmented, encrusted and bored specimens are remarkably rare (Tab. 2). The evenness is moderate, varying between 0.43 and 0.63 (mean 0.53; Fig. 7).

Interpretation: The presence of corals and echinoids indicates euhaline conditions in the photic zone. The fine-grained sediment (chalky limestone and marl) and the dominance of infauna indicate a well-oxygenated soft substrate. However, the occurrence of epifaunal taxa (mainly pectinids, oysters and corals) confirm a certain stability of the substrate. In addition, the complete and articulated internal moulds, and the low level of shell breakage (Tab. 3) indicate intermediate to low water energy (i.e., a relatively low degree of reworking; e.g., Fürsich, 1977, 1984). The occurrence of moderately to loosely packed, unsorted, and re-oriented fossils, along with the abundant suspension feeders, confirm at least moderate water energy that kept organic nutrients in suspension, and at the same time, permitted the accumulation of food particles for deposit feeders. The highly disarticulated pectinid and oyster valves (Tab. 3) confirms these brief periods of moderate-energy conditions. Re-oriented infaunal specimens, in addition, also may evidence the effect of bioturbation (e.g., Abdelhady and Fürsich, 2014; El-Sabbagh *et al.*, 2021). The moderate percentage of epifauna and the rare occurrence of encrusters and bioeroders also may support a possibly moderate to high sedimentation rate. The sediments were deposited in a lagoonal environment (FT6 and FT7) in an inner ramp setting. The abundant infaunal along with the occurrence of epifaunal and semi-infaunal taxa and the moderate value of evenness may indicate a relatively stable low-stress environment. However, dissolution of aragonitic shells and/or the sample size also may have affected the trophic structure of this assemblage.

DISCUSSION

Palaeoenvironments

In Egypt, the Oligocene–Miocene boundary is marked by dramatic tectonic events, including the Red Sea–Gulf of Suez rifting and the associated intense volcanic activity (Said, 1962, 1990). Consequently, the Miocene successions of Egypt are characterised by great facies variations, containing a large number of unconformities (e.g., Gindy and El Askary, 1969; Said, 1990; Abdel-Fattah *et al.*, 2013; Hewaidy *et al.*, 2018). During the Miocene Epoch, the Cairo–Suez District, including the study area, represents part of a characteristic neritic marginal zone, which was covered intermittently by the sea (Said, 1962, 1990; Issawi

et al., 1999). The lower Miocene marine transgression is confirmed by the change from fluvial sediments of the Oligocene Gebel Ahmar Formation to fine-grained, fossiliferous, shelf siliciclastics of the lower Miocene Gharra Formation (Said, 1990). The early Middle Miocene was a time of an extensive marine transgression, following a major drop of the sea level at the Burdigalian/Langhian transition (e.g., Haq *et al.*, 1987). In the study area, the middle Miocene Geniefa Formation is made up of detrital, richly fossiliferous carbonate beds. It is worth mentioning that this Miocene transgressive phase advanced toward the south and west of the study area and was recorded in several outcrops in the northern part of the Western Desert, Gulf of Suez and the Red Sea (e.g., Said, 1962, 1990; Gindy and El Askary, 1969; Abdel-Fattah and Assal, 2016).

Litho- and biofacies analyses revealed that the Gharra and Geniefa formations were deposited on an inner ramp setting, with dominance of a lagoonal environment that was characterised by some sort of water restrictions and proximally influenced by clastic input (Tab. 1; Figs 4, 11). The scarcity of open-marine biota as well as open-marine deposits confirms these depositional conditions. Several previous studies concluded that the entire Miocene succession in the Cairo-Suez District formed under shallow-marine conditions on a mixed siliciclastic and carbonate inner ramp setting (e.g., Abou Khadrah *et al.*, 1993; Piller *et al.*, 1998; Mandic and Piller, 2001; Nebelsick and Kroh, 2002; Kroh and Nebelsick, 2003; Tawfik *et al.*, 2015; El-Sorogy *et al.*, 2017; Mandor *et al.*, 2022). However, the present study differs in integrating, for the first time, different stratigraphical, sedimentological, and ichnological information in order to arrive at an accurate insight into the palaeoenvironmental and palaeoecological characteristics of the Gharra and Geniefa formations.

Facies associations of the Gebel Gharra section studied reflect a transgressive-regressive sequence. In the Gharra Formation, the facies types show a relatively wide spectrum of shallow-marine environments, ranging from supratidal, lagoonal to shoal settings (Tab. 1; Fig. 4), and confirming the early Miocene transgression. The noticeable variations in macrofaunal contents and trace fossils within this formation document potential environmental fluctuations under slightly elevated energy conditions (assemblages A–C; Figs 5, 8, 10, 11). The lagoonal interpretation of the sediments of the Gharra Formation is supported by the occurrence of muddy facies (packstone and wacke- to rudstone; Tab. 1; Figs 2, 4), bioturbated siltstone and shale, and the abundance of oysters, pectinids and corals (assemblages A–C). The supratidal depositional setting is documented in the presence of highly bioturbated calcareous sandstone with common trace fossils and abundant oysters (assemblage C). In addition, a highly agitated shoal depositional environment also is confirmed in the Gharra Formation by the occurrence of moderately sorted, reworked lime- and bioclasts, including pectinids, other bivalves, corals, and echinoids (assemblage A; Figs 4, 11; Flügel, 2010).

The sedimentary facies of the Geniefa Formation are likewise dominated by muddy and silty facies types (Tab. 1). However, their features mostly support deeper marine deposition on an inner ramp setting (Fig. 4). The occurrence of skeletal wackestone with bivalves, gastropods, corals, echinoid spines and tests (assemblages C–E; Figs 2, 8, 10, 11) indicate normal marine and moderate- to low-energy shallow-water environments (Wilson, 1975; Flügel, 2010). In addition, the presence of calcareous algae (assemblage D) evidences deposition under fully marine conditions within the shallow-water photic zone (e.g., Granier, 2012). Furthermore, common encrustation and bioerosion

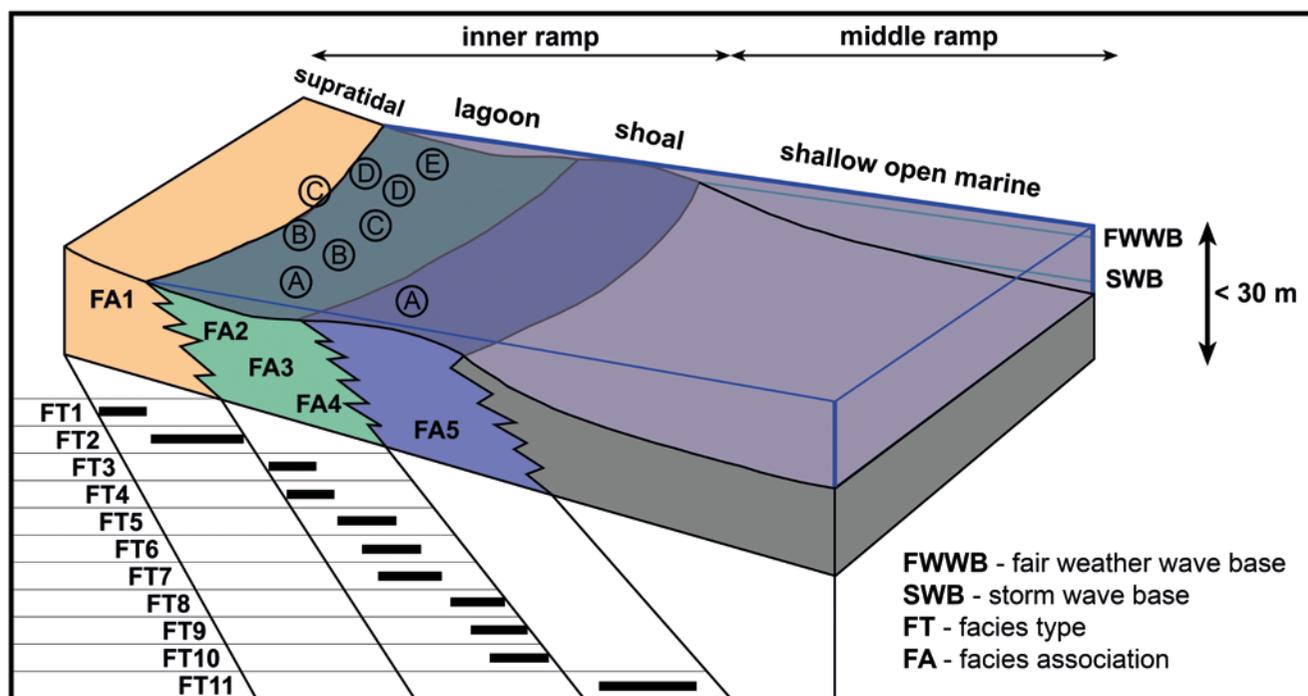


Fig. 11. Depositional ramp model of the lower–middle Miocene succession studied, showing the distribution of facies types (FT), facies associations (FA), and occurrences of assemblages A–E.

(assemblages C, D; Tab. 3) confirm continuous intervals of moderate- to low-rate sedimentation for a number of years (e.g., Edinger, 2001) in an inner ramp setting (e.g., Wilson and Taylor, 2001; Flügel, 2010).

Biotic response to environmental parameters

In general, environmental parameters played an important role in the distribution of the trace fossils and/or macrobenthic fauna, affecting the trophic structure of the assemblages recorded (Fürsich, 1977, 1984; Oschmann, 1988; Fürsich *et al.*, 1995, 2001; Pemberton *et al.*, 2001; MacEachern *et al.*, 2007; Wilmsen *et al.*, 2007; Ayoub-Hannaa and Fürsich, 2012; El-Sabbagh *et al.*, 2021; Rashwan *et al.*, 2022).

Trace fossils

Although less diversified, trace fossils are well preserved in the siliciclastic sediments of the studied Gharra Formation (Figs 2, 5), being dominated by vertical dwelling traces, like *Skolithos* and *Ophiomorpha*, co-occurring with *Thalassinoides*, *Arenicolites*, and *Polykladichnus*, and representing trace-fossil suites, attributable to the *Skolithos* ichnofacies (Seilacher, 1953a, b; Bromley, 1996; Pemberton *et al.*, 2001; MacEachern *et al.*, 2007). In the present work, the amount of bioturbation is lower than expected in comparison with modern shallow-marine siliciclastic environments (e.g., Zonneveld *et al.*, 2001; Joseph *et al.*, 2012). The trace fossils assemblages of the present account apparently represent an environmentally stressed, benthic community in a restricted marginal-marine setting, with low-marine salinity, nutrient-rich and high-energy waters and relatively oxygen-deficient bottom sediments (see below).

The *Skolithos* ichnofacies characterises intertidal to shallow subtidal, high-energy, sandy marine environments (Pemberton *et al.*, 2001; MacEachern *et al.*, 2007). *Arenicolites*, *Ophiomorpha*, and *Skolithos* are usually indicative of shallow-marine, high-energy depositional settings (Frey *et al.*, 1978; Fillion and Pickerill, 1990; Uchman *et al.*, 2004; Knaust, 2017; Hammersburg *et al.*, 2018). *Arenicolites* in low diversity, as in the present assemblage, is indicative of stressed environments, such as reduced and fluctuating salinity or increased organic productivity, and reflects opportunistic colonization (e.g., Price and McCann, 1990; Bradshaw, 2010). *Thalassinoides*, likewise, had a broader range of salinity tolerance, i.e., a brackish water ichnogenus (e.g., Swinbanks and Luternauer, 1987). The occurrence of large-diameter *Thalassinoides*, in addition, indicates a nutrient-rich and well-oxygenated water column, along with moderate-energy conditions (e.g., Abdel-Fattah *et al.*, 2016). All these observations are in accordance with results in the present account. Furthermore, the sediment supply seems to be high to enable the establishment of larger burrowing communities. Low oxygen concentrations in bottom and interstitial waters influence trace fossil size and diversity. The lower oxygen content may result in a noticeable reduction in the size of the burrows present and the diversity of organisms also decreases (see Rhoads and Morse, 1971; Savrda and Bottjer, 1989; Wignall, 1991; Savrda, 2007).

Pectinids

The results reveal that palaeoenvironmental parameters, controlling the distribution of pectinids, include bathymetry, water-energy, and rate of sedimentation (see assemblages A, B, and E). The studied lower–middle Miocene pectinid accumulations, similar to modern pectinids, were best developed in high-energy, shallow-marine water environment (20–50 m depth; e.g., Fuchs, 1900; Dakin, 1909; Brand, 1991). These are in accordance with the associated faunal elements (e.g., oysters, gastropods, corals, echinoids) and with facies characteristics, including packstones, rudstone, and grainstones. Consequently, the relative decrease in diversity in the middle Miocene Geniefa Formation supports relatively deeper marine deposition.

The pectinid-shell accumulation of bed 2 (assemblage A) is mainly composed of *F. schweinfurthi*, *O. josslingi*, and *Macrochlamis zizini* shells. In bed 14b (assemblage B), the pectinid-shell accumulation consists mostly of *P. fraasi*, *O. josslingi*, *P. kochi*, and *Aequipecten submalvinae*. It is worth mentioning that both shell accumulations occur above a sharp, intensively bioturbated boundary (Fig. 3A, B, H, I). They are characterised by the presence of mud clasts at the base (Fig. 3I), supporting the reworking of the underlying bed due to turbulent water. The two pectinid-shell accumulations are formed in shallow-marine environments that are characterised by high water energy and a low rate of sedimentation (see assemblages A and B above). Thus, these two beds can be categorised as a composite concentration (*sensu* Kidwell, 1991), representing accretion or amalgamation of multiple events.

On the other hand, the pectinid-shell accumulation in bed 13 (assemblage A) is mainly composed of large *F. schweinfurthi* shells with some associated unidentified pectinid shell fragments. It also occurs above a bioturbated base, representing a coquina of high and moderately convex, sub-horizontally oriented, and rarely encrusted valves (Figs 3G, 9K). It is proposed that this accumulation resulted from a single storm event, causing the high-density occurrence of these pectinid valves (i.e., reworked event-concentration of Kidwell, 1991). Above this concentration, the occurrence of some pectinid specimens preserved in the life position (Fig. 9L) may confirm this interpretation (cf. Mandic and Piller, 2001).

Oysters

The results in the present account confirm that oysters can tolerate a wide range of environmental perturbations. They are recorded in carbonate and siliciclastic substrates (assemblages C, D). To adapt the soft substrates, they changed their shell morphology and/or ornamentation (e.g., Seilacher, 1984). In addition, oysters occur in high energy, shallow (< 20 m; e.g., Pufahl and James, 2006) marine environments with low salinity, high nutrient levels and a turbid water column (see assemblages C, D).

The occurrence of oyster-rich layers (beds 9 and 22; assemblage C), forming oyster biostromes, also confirms these biotic stressed conditions in the Gebel Gharra section (e.g., Glenn and Arthur, 1990; Dhondt *et al.*, 1999; Pufahl and James, 2006). As a result of these high-energy conditions, assemblage C is characterised by abundant signs of

disarticulation (Tab. 3). However, the presence of some articulated and well-preserved oyster shells (Fig. 9M, N), the low level of shell breakage (Tab. 3), and the absence of large-scale transported oyster valves may document autochthonous to parautochthonous relicts of former oysters communities (Boucot *et al.*, 1958; Fürsich, 1977; Kidwell *et al.*, 1986; Fürsich *et al.*, 2004, 2009), representing “within-habitat time-averaged” oyster assemblage (Walker and Bambach, 1971; Fürsich and Aberhan, 1990; Kidwell and Bosence, 1991). On the other hand, owing to the occurrence of these oyster shells together with highly fragmented and redeposited branches of *Acropora*, this accumulation may be interpreted as a “within-habitat” environmentally condensed assemblage (e.g., Fürsich, 1975; Kidwell and Bosence, 1991).

Corals

In the section studied, corals occur at specific horizons, confirming a shallow, lagoonal environment that extends laterally over a relatively large area. The highly abundant and diversified corals in the middle Miocene Geniefa Formation (mostly massive forms), in comparison with those occurring in the lower Miocene Gharra Formation (mostly solitary and small colonial patches), may confirm the effect of terrigenous influx on the growth of corals. Corals presumably favoured the limited siliciclastic supply in an area (e.g., McCall *et al.*, 1994). In addition, corals mostly occur on a relatively firm substrate or on a soft substrate with secondary hard substrates, in the form of shells (see assemblages C–E; e.g., Ayoub-Hannaa and Fürsich, 2012).

In the Gebel Gharra section, *Acropora* sp. is recorded in three intervals, forming characteristic thin and stratified deposits with accumulations of mainly redeposited branches, co-occurring with other faunal elements (assemblages B and C; Figs 2, 3F, 8, 9O, X). These accumulations of *Acropora* sp. probably occurred in patchy, dense thickets, which were broken during high-energy (i.e., storm) events and redeposited in their present stratigraphic positions (Schuster, 2000). In general, the Miocene *Acropora* was rapidly emergent and speciated, occurring in high-energy, shallow-marine environments (e.g., McCall *et al.*, 1994). Modern *Acropora* species, likewise, are abundantly recorded in shallow, high-energy water in the northern Red Sea (Riegl and Piller, 1997) and in the Indo-Pacific area (Rosen, 1975).

CONCLUSIONS

The lower–middle Miocene succession in Gebel Gharra, NW of Suez, Egypt, was studied by integrating stratigraphical, sedimentological and palaeontological data. This succession represents part of the southern margin of the Mediterranean Sea. It comprises the Gharra and Geniefa formations, representing a mixed siliciclastic-carbonate succession, developed in response to a general early–middle Miocene transgression-regression cycle. Facies development of the studied section confirms depositional palaeoenvironments, ranging from supratidal, lagoonal, to shoal settings on an inner ramp that was influenced proximally by clastic input.

Seven ichnotaxa were recorded only in the lower Miocene siliciclastics of the Gharra Formation, representing suites of the *Skolithos* ichnofacies. Forty-five macrobenthic taxa, belonging to pectinids, oysters, other bivalves, gastropods, echinoids, and corals, were identified throughout the Gebel Gharra succession. The distribution of trace and/or macrofossils shows a strong relationship to the recognised facies characteristics. The macrobenthic taxa, identified in 13 statistical samples, are grouped into five assemblages (A–E) that are described to reconstruct the macrobenthic palaeo-communities and to interpret the different depositional environments.

Two of the assemblages are dominated by pectinids, one by other bivalves, and the remainders are dominated by corals and oysters. Epifaunal elements strongly dominate these assemblages, followed by infauna. Semi-infaunal elements, in contrast, play only a minor role. With respect to the feeding modes, all macrobenthic assemblages are strongly dominated by suspension-feeders, followed by carnivores and deposit-feeders. Other feeding groups, such as grazers and omnivores, occur sporadically. In general, the macrobenthic fauna is dominated by moderately to well-preserved, moderately to densely packed, commonly disarticulated, poorly sorted, moderately fragmented, and re-oriented or re-sedimented specimens, documenting slightly transported skeletons, deposited in the original life habitat, i.e., parautochthonous community relicts.

The faunal distribution and trophic structure of most of the assemblages recorded confirm relatively stable and low-stress conditions. However, the trophic structure of these assemblages reflects the influence of particular environmental parameters, dissolution of aragonitic shells and/or sample-size effects. Environmental parameters controlling the distribution of trace and/or body fossils include substrate consistency, bathymetry, water energy, productivity level, rate of sedimentation, salinity, and oxygen availability. The integrated litho- and biofacies results confirm that the succession studied was deposited in different environmental perturbations, providing perfect conditions for the occurrence and preservation of trace-fossil and macrobenthos assemblages.

Acknowledgements

We are grateful to Marcin Górka and an anonymous reviewer for their constructive comments and to the Editor-in-Chief, Alfred Uchman, Assistant Editor, Mariusz Salamon, and Frank Simpson for their insightful suggestions that immensely improved the manuscript. We would like to thank Nikolaos Tsaparas for his help with coral identification.

REFERENCES

- Abdel-Fattah, Z. A. & Assal, E. M., 2016. Bioerosion in the Miocene reefs of the northwest Red Sea, Egypt. *Lethaia*, 49: 398–412.
- Abdel-Fattah, Z. A., Gingras, M. K., Caldwell, M. W., Pemberton, S. G. & MacEachern, J. A., 2016. The *Glossifungites* ichnofacies and sequence stratigraphic analysis: A case study from middle to upper Eocene successions in Fayum, Egypt. *Ichnos*, 23: 157–179.

- Abdel-Fattah, Z. A., Kora, M. A. & Ayyad, S. N., 2013. Facies architecture and depositional development of Middle Miocene carbonate strata at Siwa Oasis, Northwestern Egypt. *Facies*, 59: 505–528.
- Abdelghany, O., 2002. Lower Miocene stratigraphy of the Gabal Shabrawet area, north Eastern Desert, Egypt. *Journal of African Earth Sciences*, 34: 203–212.
- Abdelghany, O. & Piller, E., 1999. Biostratigraphy of Lower Miocene sections in the Eastern Desert (Cairo-Suez District, Egypt). *Revue de Paléobiologie*, 18: 607–617.
- Abdelhady, A. A. & Fürsich, F. T., 2014. Macroinvertebrate palaeo-communities from the Jurassic succession of Gebel Maghara (Sinai, Egypt). *Journal of African Earth Sciences*, 97: 173–193.
- Abou Khadrah, A. M., Wali, A. M., Müller, A. M. A. & El Shazly, A. M., 1993. Facies development and sedimentary structures of synrift sediments, Cairo-Suez District, Egypt. *Bulletin of Faculty of Science, Zagazig University*, 15: 355–373.
- Ali, S. H., Abdullatif, O. M., Babalola, L. O., Alkhalidi, F. M., Bashir, Y., Talha Qadri, S. M. & Wahid, A., 2021. Sedimentary facies, depositional environments and conceptual outcrop analogue (Dam Formation, early Miocene) Eastern Arabian Platform, Saudi Arabia: a new high resolution approach. *Journal of Petroleum Exploration and Production Technology*, 11: 2497–2518.
- Alpert, S. P., 1974. Systematic review of the genus *Skolithos*. *Journal of Paleontology*, 48: 661–669.
- Ayoub-Hannaa, W. & Fürsich, F. T., 2012. Palaeoecology and environmental significance of benthic associations from the Cenomanian–Turonian of eastern Sinai, Egypt. *Beringeria*, 42: 93–138.
- Bashri, M., Abdullatif, O. & Salih, M., 2017. Sedimentology and facies analysis of Miocene mixed siliciclastic–carbonate deposits of the Dam Formation in Al Lidam area, eastern Saudi Arabia. *Arabian Journal of Geosciences*, 10: 472.
- Basterot, B., de, 1825. Description géologique du bassin tertiaire du Sud-Ouest de la France, (avec) description des coquilles fossiles des environs de Bordeaux. *Mémoires de la Société d'Histoire Naturelle de Paris*, 2: 1–100.
- Binney, E. W., 1852. On some trails and holes found in rocks of the Carboniferous strata, with remarks on the *Microconchus carbonarius*. *Memoirs of the Literary and Philosophical Society of Manchester; Series 2*, 10: 181–201.
- Blanckenhorn, M., 1901. Neues zur Geologie und Paläontologie Aegyptens. 3. Das Miocän. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 53: 52–132.
- Blanckenhorn, M., 1903. Die Vola-arten des ägyptischen und syrischen Neogens. *Neues Jahrbuch für Mineralogie, Geologie and Paläontologie*, 17: 163–186.
- Bottjer, D. J., 1981. Structure of Upper Cretaceous chalk benthic communities, southwestern Arkansas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 34: 225–256.
- Boucot, A. J., Brace, W. & Demar, R., 1958. Distribution of brachiopod and pelecypod shells by currents. *Journal of Sedimentary Petrology*, 28: 321–332.
- Bradshaw, M. A., 2010. Devonian trace fossils of the Horlick Formation, Ohio Range, Antarctica: systematic description and palaeoenvironmental interpretation. *Ichnos*, 17: 58–11.
- Brand, A. R., 1991. Scallop ecology: Distributions and behaviour. In: Shumway, S. E. (ed.), *Scallops: Biology, Ecology and Aquaculture. Developments in Aquaculture and Fisheries Science*, 21: 517–584.
- Brocchi, G. B., 1814. *Conchiologia fossile subapennina con osservazioni geologiche sugli Apennini e sul suolo adiacente*. Stamperia Reale, Milano, 472 pp.
- Bromley, R. G., 1996. *Trace Fossils: Biology, Taphonomy and Applications*. Chapman & Hall, London, 361 pp.
- Bucur, I. I. & Săsăran, E., 2005. Relationship between algae and environment: an early Cretaceous case study, Romania. *Facies*, 51: 274–286.
- Burchette, T. P. & Wright, V. P., 1992. Carbonate ramp depositional systems. *Sedimentary Geology*, 79: 3–57.
- Caracciolo, L., Gramigna, P., Critelli, S., Calzona, A. B. & Russo, F., 2013. Petrostratigraphic analysis of a Late Miocene mixed siliciclastic-carbonate depositional system (Calabria, Southern Italy): Implications for Mediterranean paleogeography. *Sedimentary Geology*, 284–285: 117–132.
- Cherns, L., Wheeley, J. R. & Karis, L., 2006. Tunneling trilobites: Habitual infaunalism in an Ordovician carbonate seafloor. *Geology*, 34: 657–660.
- Cox, L. R., 1952. The Jurassic Lamellibranch fauna of Kachh (Cutch), No. 3, families Pectinidae, Amussidae, Plicatulidae, Limidae, Ostreidae, and Trigoniidae. *Memoirs of the Geological Survey of India: Palaeontologia Indica*, 3: 1–128.
- Ctyroky, P., 1969. The family Pectinidae in the Burdigalian of Czechoslovakia. *Sbornik Geologických Ved: Paleontologie*, 10: 7–66.
- Dakin, W. J., 1909. *Pecten*. The edible scallop. *Proceedings and Transactions of the Liverpool Biological Society*, 23: 333–468.
- Dépéret, Ch. & Fourtau, R., 1900. Sur les Terrains Neogene de la Basse-Egypte et de l'Isthme de Suez. *Comptes Rendus de l'Académie des Sciences, Paris*, 131: 401–403.
- Deshayes, G. P., 1832. Histoire Naturelle des Vers. Par Bruguiere et De Lamarck, Continué par Mr. PG Deshayes. Tome Second, Part 2. In: *Encyclopédie Méthodique (Dictionnaire Encyclopédique Méthodique), ou par Ordre de Matieres*. Imprimeur-Libraire, Paris, pp. 185–271.
- Deshayes, G. P., 1833. *Description des coquilles fossiles des environs de Paris, II. Mollusques*. L'auteur, chez Bechet, Paris, pp. 291–426.
- Dhondt, A. V., Malchus, N., Boumaza, L. & Jaillard, E., 1999. Cretaceous oysters from North Africa: origin and distribution. *Bulletin de la Société géologique de France*, 170: 67–76.
- Du, X., Ye, M., Xie, X., Zhao, K., Jia, J. & Du, X., 2022. Why is it easy to form high-quality reservoirs in a mixed siliciclastic-carbonate system? Evidence from diagenetic characteristics. *Journal of Petroleum Science and Engineering*, 212: 110339.
- Dunham, R. J., 1962. Classification of carbonate rocks according to depositional texture. In: Ham, W. E. (ed.), *Classification of Carbonate Rocks. American Association of Petroleum Geologists, Memoir*, 1: 108–121.
- Ebert, T. A. & Dexter, D. M., 1975. A natural history study of *Encope grandis* and *Mellita grantii*, two sand dollars in the Northern Gulf of California, Mexico. *Marine Biology*, 32: 397–407.
- Edinger, E. N., 2001. Bioerosion. In: Briggs, D. G. & Crowther, P. R. (eds), *Palaeobiology II*. Blackwell, Oxford, pp. 275–278.

- Ekdale, A. A., 1992. Muckraking and mudslinging: the joys of deposit-feeding. In: Maples C. G. & West, R. R. (eds), *Trace Fossils. Short Courses in Paleontology* 5. The Palaeontological Society, Knoxville, Tennessee, pp. 145–171.
- Ekdale, A. A. & Bromley, R. G., 2003. Paleoethologic interpretation of complex *Thalassinoides* in shallow-marine limestones, Lower Ordovician, southern Sweden. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192: 221–227.
- El Haddad, A., Aissaoui, D. M. & Soliman, M. A., 1984. Mixed carbonate-siliciclastic sedimentation on a Miocene fault-block, Gulf of Suez, Egypt. *Sedimentary Geology*, 37: 185–202.
- El-Refaïy, A., El-Sabbagh, A., El Hedeny, M., Mansour, A. & El-Barkooky, A., 2023. Stratigraphical, microfacies, and ichnological characteristics and depositional environments of the Permo–Carboniferous Aheimer Formation, western side of the Gulf of Suez, Egypt. *Facies*, 69: 8.
- El-Sabbagh, A., Nagm, E., Mansour, A., El Hedeny, M., Abdelaal, A., Mansour, H. & Rashwan, M., 2021. Palaeoecological and palaeoenvironmental analyses of Cenomanian–early Turonian macrobenthic faunas from the northern Eastern Desert of Egypt. *Cretaceous Research*, 125: 104853.
- El-Sorogy, A., Abd-Elmoneim, M., Mowafi, A., Al-Kahtany, K. & Gahlan, H., 2017. Facies analysis and biostratigraphy of the Miocene sequence, Cairo-Suez District, Egypt. *Journal of African Earth Sciences*, 28: 1–8.
- Embry, A. F. & Klovan, J. E., 1971. A Late Devonian reef tract on Northeastern Banks Island, NWT. *Canadian Petroleum Geology Bulletin*, 19: 730–781.
- Fernández-López, S. R., 1991. Taphonomic concepts for a theoretical biochronology. *Revista Española de Paleontología*, 6: 37–39.
- Fernández-López, S. R., 2011. Taphonomic analysis and sequence stratigraphy of the Albarracinites beds (Lower Bajocian, Iberian Range, Spain): an example of shallow condensed section. *Bulletin de la Société géologique de France*, 182: 405–415.
- Fernández-López, S. R., Fernández-Jalvo, Y. & Alcalá, L., 2002. Accumulation: taphonomic concept and other palaeontological uses. In: De Renzi, M., Alonso, M. V. P., Belinchon, M., Penalver, E. & Montoya, P. (eds), *Current Topics on Taphonomy and Fossilization. Proceedings of the International Conference Taphos 2002, Valencia*, pp. 37–47.
- Fillion, D. & Pickerill, R. K., 1990. Ichnology of the Upper Cambrian? to Lower Ordovician Bell Island and Wabana groups of Eastern Newfoundland, Canada. *Palaeontographica Canadiana*, 7: 1–83.
- Fleming, C. A., 1957. The genus *Pecten* in New Zealand. *New Zealand Geological Survey Paleontological Bulletin*, 26: 1–70.
- Flügel, E., 2010. *Microfacies of Carbonate Rocks: Analysis, Interpretation and Application*. Springer, Heidelberg, 984 pp.
- Fourtau, R., 1920. *Catalogue des Invertébrés Fossiles de l’Égypte. Terrains Tertiaires. 2^{de} partie: Echinodermes Néogènes*. Geological Survey of Egypt, Cairo, 100 pp.
- Fraas, O. F., 1867. *Aus dem Orient: Geologische Beobachtungen am Nil, auf der Sinai Halbinsel, und in Syrien*. Ebner & Seubert, Stuttgart, 222 pp.
- Frey, R. W., Howard, J. D. & Pryor, W. A., 1978. *Ophiomorpha*: its morphologic, taxonomic, and environmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 23: 199–229.
- Fuchs, Th., 1883. Beiträge zur Kenntniss der Miocänfauna Ägyptens und der libyschen Wüste. *Palaeontographica*, 30: 18–66.
- Fuchs, Th., 1900. Über die bathymetrischen Verhältnisse der sogenannten Eggenburger und Gaudemdorfer Schichten des Wiener Tertiärbeckens. *Sitzungsberichte der Akademie der Wissenschaften Wien*, 109: 478–489.
- Fürsich, F. T., 1975. Trace fossils as environmental indicators in the Corallian of England and Normandy. *Lethaia*, 8: 151–172.
- Fürsich, F. T., 1977. Corallian (Upper Jurassic) marine benthonic associations from England and Normandy. *Palaeontology*, 20: 337–385.
- Fürsich, F. T., 1981. Salinity-controlled benthic associations from the Upper Jurassic of Portugal. *Lethaia*, 14: 203–223.
- Fürsich, F. T., 1984. Palaeoecology of boreal invertebrate faunas from the Upper Jurassic of Central East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 48: 309–364.
- Fürsich, F. T. & Aberhan, M., 1990. Significance of time-averaging for palaeocommunity analysis. *Lethaia*, 23: 143–152.
- Fürsich, F. T., Berndt, R., Scheuer, T. & Gahr, M., 2001. Comparative ecological analysis of Toarcian (Lower Jurassic) benthic faunas from southern France and east-central Spain. *Lethaia*, 34: 169–199.
- Fürsich, F. T., Freytag, S., Röhl, J. & Schmid, A., 1995. Palaeoecology of benthic associations in salinity-controlled marginal marine environments: examples from the Lower Bathonian (Jurassic) of the Causses (southern France). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 113: 135–172.
- Fürsich, F. T., Oschmann, W., Pandey, D. K., Jaitly, A. K., Singh, I. B. & Liu, C., 2004. Palaeoecology of middle to lower Upper Jurassic macrofaunas of the Kachchh Basin, western India: an overview. *Journal of the Palaeontological Society of India*, 49: 1–26.
- Fürsich, F. T., Werner, W., Delvene, G., García-Ramos, J. C., Bermúdez-Rochas, D. D. & Piñuela, L., 2012. Taphonomy and palaeoecology of high-stress benthic associations from the Upper Jurassic of Asturias, northern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 358–360: 1–18.
- Fürsich, F. T., Werner, W. & Schneider, S., 2009. Autochthonous to parautochthonous bivalve concentrations within transgressive marginal marine strata of the Upper Jurassic of Portugal. *Palaeobiodiversity and Palaeoenvironments*, 89: 161–190.
- Gilinsky, N. L. & Bennington, J. B., 1994. Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record. *Paleobiology*, 20: 245–258.
- Gindy, A. R. & El-Askary, M. A., 1969. Stratigraphy, structure and origin of Siwa depression, Western Desert of Egypt. *American Association of Petroleum Geologists Bulletin*, 53: 603–625.
- Gingras, M. K., Dashtgard, S. E., MacEachern, J. A. & Pemberton, S. G., 2008. Biology of shallow marine ichnology: a modern perspective. *Aquatic Biology*, 2: 255–268.

- Glenn, C. R. & Arthur, M. A., 1990. Anatomy and origin of a Cretaceous phosphorite-green sand giant, Egypt. *Sedimentology*, 37: 123–148.
- Goldhammer, R. K., 1978. Mixed siliciclastic and carbonate sedimentation. In: Fairbridge, R. W. & Bourgeois, J. (eds), *Encyclopedia of Sedimentology. Encyclopedia of Earth Science Series*. Springer, Berlin, pp. 724–732.
- Granier, B., 2012. The contribution of calcareous green algae to the production of limestones: a review. *Geodiversitas*, 34: 35–60.
- Greenstein, B. J., 1992. Taphonomic bias and the evolutionary history of the family Cidaridae (Echinodermata: Echinoidea). *Paleobiology*, 18: 50–79.
- Hakes, W. G., 1976. Trace fossils and depositional environment of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas. *University of Kansas Paleontological Contributions*, 63: 1–60.
- Haldeman, S. S., 1840. *Supplement to Number One of "A Monograph of the Limniades, or Freshwater Univalve Shells of North America", Containing Descriptions of Apparently New Animals in Different Classes, and the Names and Characters of the Subgenera in Paludina and Anculosa*. J. Dobson, Philadelphia, 3 pp.
- Hammer, O., Harper, D. A. T. & Ryan, P. D., 2001. PAST: Paleontological Statistical software package for education and data analysis. *Palaeontologia Electronica*, 4: 1–9.
- Hammersburg, S. R., Hasiotis, S. T. & Robison, R. A., 2018. Ichnotaxonomy of the Cambrian Spence Shale Member of the Langston Formation, Wellsville Mountains, northern Utah, USA. *University of Kansas Paleontological Contributions*, 20: 1–66.
- Hamza, F. H., 1992. Contribution to the Neogene biostratigraphy in the eastern part of Egypt. *Middle East Research Center, Ain Shams University, Earth Science Series*, 6: 151–166.
- Handford, C. R. & Loucks, R. G. 1993. Carbonate depositional sequences and systems tracts – Responses of carbonate platform to relative sea-level changes: Chapter 1. In: Loucks, R. G. & Sarg, J. F. (eds), *Carbonate Sequence Stratigraphy: Recent Developments and Applications. American Association of Petroleum Geologists Memoir*, 57: 3–41.
- Haq, B. U., Hardenbol, J. & Vail, P. R., 1987. Chronology of fluctuating sea levels since the Triassic. *Science*, 235: 1156–1167.
- Hassan, H. F. & Hany, S. M., 2012. Sequence stratigraphic analysis of the carbonate-siliciclastic Miocene sediments, North Eastern Desert, Egypt. *Journal of Petroleum and Mining Engineering*, 15: 84–103.
- Hermina, M., Klitzsch, E. & List, F. K., 1989. *Stratigraphic Lexicon and Explanatory Notes to the Geological Map of Egypt 1:500,000*. Conoco/Egyptian General Petroleum Corporation, Cairo, 264 pp.
- Hewaidy, A. A., Abd El-Moghny, M. W., Ayyad, H. M. & Gameel, O., 2018. Biostratigraphy, microfacies analysis and sequence stratigraphy of the Miocene successions in Cairo-Suez district, Egypt. *Al Azhar Bulletin of Science*, 29: 39–59.
- Howard, J. D., 1968. X-ray radiography for examination of burrowing in sediments by marine invertebrate organisms. *Sedimentology*, 11: 249–258.
- Howard, J. D. & Frey, R. W., 1984. Characteristic trace fossils in nearshore to offshore sequences, Upper Cretaceous of east-central Utah. *Canadian Journal of Earth Sciences*, 21: 200–219.
- Issawi, B., El Hinnawi, M., Francis, M. & Mazhar, A., 1999. The Phanerozoic geology of Egypt: a geodynamic approach. *Geological Survey of Egypt*, 76: 1–462.
- Joseph, J. K., Patel, S. J. & Bhatt, N. Y., 2012. Trace fossil assemblages in mixed siliciclastic-carbonate sediments of the Kaladongar Formation (Middle Jurassic), Patcham Island, Kachchh, Western India. *Journal of the Geological Society of India*, 80: 189–214.
- Kauffman, E. G., 1969. Form, function and evolution. In: Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology. Part N. Mollusca 6. Bivalvia, Volum 1*. Geological Society of America and University of Kansas Press, New York, pp. 129–205.
- Kennedy, W. J., 1967. Burrows and surface traces from the Lower Chalk of Southern England. *Bulletin of the British Museum (Natural History), Geology*, 15: 125–167.
- Kidwell, S. M., 1991. The stratigraphy of shell concentrations. In: Allison, P. A. & Briggs, D. E. (eds), *Taphonomy: Releasing the Data Locked in the Fossil Record*. Plenum Press, New York, pp. 211–290.
- Kidwell, S. M. & Bosence, D. W., 1991. Taphonomy and time-averaging of marine shelly fauna. In: Allison, P. A. & Briggs, D. E. (eds), *Taphonomy: Releasing the Data Locked in the Fossil Record*. Plenum Press, New York, pp. 115–209.
- Kidwell, S. M., Fürsich, F. T. & Aigner, T., 1986. Conceptual framework for the analysis and classification of shell concentrations. *Palaios*, 1: 228–238.
- Kleesmenta, A., Kirsimäe, K., Martmaa, T., Shogenovaa, A., Urtsona, K. & Shogenova, K., 2012. Linkage of diagenesis to depositional environments and stratigraphy in the northern part of the Baltic basin. *Estonian Journal of Earth Sciences*, 61: 15–32.
- Knaust, D., 2017. *Atlas of Trace Fossils in Well Core: Appearance, Taxonomy and Interpretation*. Springer, Switzerland, 209 pp.
- Knaust, D., 2021. The paradoxical ichnotaxonomy of *Thalassinoides paradoxicus*: a name of different meanings. *Paläontologische Zeitschrift*, 95: 179–186.
- Koch, C. F., 1987. Prediction of sample size effects on the measured temporal and geographic distribution patterns of species. *Paleobiology*, 13: 100–107.
- Kroh, A. & Nebelsick, J., 2003. Echinoid assemblages as a tool for palaeoenvironmental reconstruction - an example from the Early Miocene of Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 201: 157–177.
- Lamarck, J. B. M., 1816. *Histoire naturelle des animaux sans vertèbres*. Deterville/Verdière, Paris, 612 pp.
- Lamarck, J. B. M., 1819. *Histoire naturelle des animaux sans vertèbres*. Verdière, Paris, 343 pp.
- Leaman, M., McIlroy, D., Herringshaw, L. G., Boyd, C. & Callow, R. H. T., 2015. What does *Ophiomorpha irregularis* really look like? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 439: 38–49.
- Linnaeus, C., 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th edition*. Laurentii Salvii, Holmiae, 824 pp. [In Latin.]
- Locard, A., 1877. Description de la faune des terrains tertiaires moyens et supérieurs de la Corse. *Annales de la Société d'Agriculture et d'Histoire Naturelle de Lyon, ser. 4*, 9: 1–374.
- MacEachern, J. A., Pemberton, S. G., Gingras, M. K. & Bann, K. L., 2007. The ichnofacies paradigm: A fifty-year retrospective.

- In: Miller, W., III (ed.), *Trace Fossils: Concepts, Problems, Prospects*. Elsevier, Amsterdam, pp. 52–77.
- Mandic, O. & Piller, W., 2001. Pectinid coquinas and their palaeoenvironmental implications – examples from the Early Miocene of northeastern Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 172: 171–191.
- Mandor, M., Vinn, O., El Hedeny, M., El-Sabbagh, A., Abdelaal, A. & Rashwan, M., 2022. Calcareous tube-dwelling encrusting polychaetes from a lower–middle Miocene sedimentary succession, Cairo-Suez District, Egypt. *Bulletin of Geosciences*, 97: 203–217.
- McCall, J., Rosen, B. R., & Darrell, J., 1994. Carbonate deposition in accretionary prism settings: Early Miocene coral limestones and corals of the Makhran Mountain Range in southern Iran. *Facies*, 31: 141–178.
- Michelotti, G., 1871. Matériaux pour servir à la paléontologie du terrain tertiaire du Piémont. *Memorie della Regia Accademia delle Scienze di Torino*, 25: 257–361.
- Milne Edwards, H. & Haime, J., 1850–1851. Recherches sur les polypiers. Mémoire 4. Monographie des Astréides (1) (suite). *Annales des Sciences Naturelles, Zoologie, Series 3*, 12: 95–197.
- Moffat, H. A. & Bottjer, D. J., 1999. Echinoid concentration beds: Two examples from the stratigraphic spectrum. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 149: 329–348.
- Montagu, G., 1803. *Testacea Britannica, or, Natural History of British Shells, Marine, Land, and Fresh-water, Including the Most Minute: Systematically Arranged and Embellished with Figures*. J. White, London, 291 pp.
- Mooi, R. & Telford, M., 1982. The feeding mechanisms of the sand dollar *Echinarachnius parma* (Lamarck). In: Lawrence, J. M. (ed.), *Echinoderms. Proceedings of the 4th International Conference, Tampa Bay*. Balkema, Rotterdam, pp. 51–58.
- Morse, J. W., Zullig, J. J., Bernstein, L. D., Millero, F. J., Milne, P., Mucci, A. & Chopin, G. R., 1985. Chemistry of calcium-rich shallow water sediments in the Bahamas. *American Journal of Science*, 285: 147–185.
- Mount, J. F., 1984. Mixing of siliciclastic and carbonate sediments in shallow shelf environments. *Geology*, 12: 432–435.
- Nagm, E., Bamoussa, A., Memesh, A., Babikir, I. & Dini, S., 2018. Relative sea-level changes and sedimentary facies development of the lowermost Cretaceous (Berriasian–Valanginian) cycles in the north of Ar Riyad city, Saudi Arabia. *Journal of Asian Earth Sciences*, 163: 163–176.
- Nebelsick, J. H. & Kroh, A., 2002. The stormy path from life to death assemblages: The formation and preservation of mass accumulations of fossil sand dollars. *Palaos*, 17: 378–393.
- Neyman, A. A., 1967. Limits to the application of the trophic group concept in benthic studies. *Oceanology of the Academy of Sciences of the USSR*, 7: 149–155.
- Nickel, L. A. & Atkinson, R. J. A., 1995. Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. *Marine Ecology Progress Series*, 128: 181–197.
- Nyst, H. & Westendorp, G. D., 1839. Nouvelles recherches sur les coquilles fossiles de la province d'Anvers. *Bulletins de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles*, 6: 1–3.
- Osasco, E., 1896. Di alcuni corallari miocenici del Piemonte. *Atti Della Reale Accademia Delle Scienze di Torino*, 32: 436–449.
- Oschmann, W., 1988. Upper Kimmeridgian and Portlandian marine macrobenthic associations from southern England and northern France. *Facies*, 18: 49–84.
- Patton, T. L., Moustafa, A. R., Nelson, R. A. & Abdine, S. A., 1994. Tectonic evolution and structural setting of the Suez Rift. In: Landon, S. M. & Coury, A. B. (eds), *Interior Rift Basins. American Association of Petroleum, Memoir*, 59: 9–55.
- Pearse, A. S. 1908. Descriptions of four new species of amphipodous Crustacea from the Gulf of Mexico. *Proceedings of the United States National Museum*, 34: 27–32.
- Pemberton, S. G. & Frey, R. W., 1982. Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma. *Journal of Paleontology*, 56: 843–881.
- Pemberton, S. G., Spila, M. V., Pulham, A. J., Saunders, T., MacEachern, J. A., Robbins, D. & Sinclair, I., 2001. Ichnology and sedimentology of shallow and marginal marine systems: Ben Nevis and Avalon reservoirs, Jeanne D'Arc Basin. St. John's, Newfoundland. *Geological Association of Canada, Short Course Notes*, 15: 1–353.
- Piller, W. E., Abdelghany, O., Kroh, A., Mandic, O., Nebelsick, J. H., Schlaf, J. & Schuster, F., 1998. Transgressive Folgen und Lumachellenbildungen in einer untermiozänen Abfolge der Östlichen Wüste (Gebel Gharra, W' Suez, Ägypten). *Erlanger Geologische Abhandlungen*, 2: 74–75.
- Pollard, J. E., Goldring, R. & Buck, S. G., 1993. Ichnofabrics containing *Ophiomorpha*: significance in shallow-water facies interpretation. *Journal of the Geological Society of London*, 150: 149–164.
- Price, S. & McCann, T., 1990. Environmental significance of *Arenicolites* ichnosp. in Pliocene lake deposits of southwest Turkey. *Neues Jahrbuch für Geologie und Paläontologie*, 11: 687–694.
- Pufahl, P. K. & James, N. P., 2006. Monospecific Pliocene oyster buildups, Murray Basin, South Australia: brackish water end member of the reef spectrum. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 233: 11–33.
- Rashwan, M., El-Sabbagh, A., El Hedeny, M., Vinn, O. & Mansour, H. 2022. Taphonomy and its significant role in palaeoenvironmental reconstruction of the upper Turonian actaeonellid gastropod concentrations of Abu Roash, Western Desert, Egypt. *Lethaia*, 55: 1–18.
- Rhoads, D. C. & Morse, J. W., 1971. Evolutionary and ecologic significance of oxygen-deficient marine basins. *Lethaia*, 4: 413–428.
- Riegl, B. & Piller, W. E., 1997. Distribution and environmental control of coral assemblages in northern Safaga Bay (Red Sea, Egypt). *Facies*, 36: 141–162.
- Rieth, A., 1932. Neue Funde Spongeliomorpher Fucoiden aus dem Jura Schwabens. *Geologische und Paläontologische Abhandlungen*, 19: 257–294.
- Roopzpykar, A., Maghfouri-Moghaddam, I., Yazdi, M. & Yousefi-Yegane, B., 2019. Facies and paleoenvironmental reconstruction of early–middle Miocene deposits in the north-west of the Zagros Basin, Iran. *Geologica Carpathica*, 70: 75–87.
- Rosen, B. R., 1975. The distribution of reef corals. *Report of the Underwater Association*, 1: 1–16.

- Sacco, F., 1897. *I Molluschi dei terreni Terziarii del Piemonte e della Liguria. Parte 24 (Pectinidae)*. Carlo Clausen, Torino, 116 pp.
- Sadek, H., 1959. *The Miocene in the Gulf of Suez Region (Egypt)*. Egyptian Geological Survey, Cairo, 118 pp.
- Said, R., 1962. *The Geology of Egypt*. Elsevier, Amsterdam, 377 pp.
- Said, R., 1990. *The Geology of Egypt*. Balkema Publishers, Rotterdam, 734 pp.
- Said, R. & Yallouze, M., 1955. Miocene fauna from Gebel Oweibed, Egypt. *Bulletin of Faculty of Science, Cairo University*, 33: 61–81.
- Savrdra, C. E., 2007. Trace fossils and marine benthic oxygenation. In: Miller, W., III (ed.), *Trace Fossils: Concepts, Problems, Prospects*. Elsevier, Amsterdam, pp. 149–158.
- Savrdra, C. E. & Bottjer, D. J., 1989. Trace fossil model for reconstruction of palaeo-oxygenation histories of ancient bottom waters: application to Upper Cretaceous Niobrara Formation, Colorado. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 74: 49–74.
- Schlirf, M. & Uchman, A., 2005. Revision of the ichnogenus *Sabellarifex* Richter, 1921 and its relationship to *Skolithos* Haldeman, 1840 and *Polykladichnus* Fürsich, 1981. *Journal of Systematic Palaeontology*, 3: 115–131.
- Schuster, F., 2000. Oligocene and Miocene examples of *Acropora*-dominated palaeoenvironments: Mesohellenic Basin (NW Greece) and northern Gulf of Suez (Egypt). *Proceedings 9th International Coral Reef Symposium, Volume 1, 23–27 October 2000*. Bali, Indonesia, pp. 1–6.
- Scotese, C. R., 2013. *Map Folio 7, Early Miocene, (Aquitainian & Burdigalian, 19.5 Ma)*, PALEOMAP PaleoAtlas for ArcGIS, Volume 1, Cenozoic. PALEOMAP Project, Evanston, IL.
- Seilacher, A., 1953a. Studien zur Palichnologie. I. Über die Methoden der Palichnologie. *Neues Jahrbuch für Geologie und Paläontologie*, 98: 87–124.
- Seilacher, A., 1953b. Über die Methoden der Palichnologie. II, Studien von Palichnologie. *Neues Jahrbuch für Geologie und Paläontologie*, 96: 421–452.
- Seilacher, A., 1984. Constructional morphology of bivalves: evolutionary pathways in primary versus secondary soft-bottom dwellers. *Palaeontology*, 27: 207–237.
- Serres, M., de, 1829. *Géognosie des Terrains Tertiaires: Ou, Tableau des Principaux Animaux Invertébrés des Terrains Marins Tertiaires, Du Midi de la France*. A Montpellier, Chez Pomathio-Durville, Paris, 277 pp.
- Smith, J., 1847. On the age of Tertiary beds of the Tagus, with a catalogue of the fossils. *Quarterly Journal of the Geological Society*, 3: 410–422.
- Smith, A. B., Morris, N. J., Gale, A. S. & Rosen, B. R., 1995. Late Cretaceous (Maastrichtian) echinoid-mollusc-coral assemblages and palaeoenvironments from a Tethyan carbonate platform succession, northern Oman Mountains. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 119: 155–168.
- Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K., 1988. Cenomanian and Lower Turonian echinoderms from Wilmington, south-east Devon, England. *Bulletin of the British Museum (Natural History) Geology*, 42: 1–245.
- Souaya, F., 1963. On the foraminifera of Gabal Gharra (Cairo-Suez road) and some other Miocene samples. *Journal of Paleontology*, 37: 433–457.
- Spalletti, L. A., Franzese, J. R., Matheos, S. D. & Schwarz, E., 2000. Sequence stratigraphy of a tidally-dominated carbonate-siliciclastic ramp: the Tithonian–Early Berriasian of the southern Neuquén Basin, Argentina. *Journal of the Geological Society of London*, 157: 433–446.
- Stenzel, H. B., 1971. Oysters. In: Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology, Part N, Volume 3, Mollusca 6, Bivalvia*. Geological Society of America and University of Kansas Press, Boulder/Lawrence, pp. N953–N1224.
- Swinbanks, D. D. & Luternauer, J. L., 1987. Burrow distribution of thalassinidean shrimp on a Fraser Delta tidal flat, British Columbia. *Journal of Paleontology*, 61: 315–332.
- Tawfik, M., El-Sorogy, A. S., Mowafi, A. & Al-Malky, M., 2015. Facies and sequence stratigraphy of some Miocene sediments in the Cairo-Suez District, Egypt. *Journal of African Earth Sciences*, 101: 84–95.
- Taylor, P. D. & Wilson, M. A., 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews*, 62: 1–103.
- Tuomisto, H., 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia*, 164: 853–860.
- Tournouër, R., 1873. Note sur les terrains miocènes des environs de Sos et de Gabarret (Lot-et-Garonne et des Landes). *Actes de la Société linnéenne de Bordeaux*, 29: 119–169.
- Uchman, A., Drygant, D., Paszkowski, M., Porębski, S. J. & Turnau, E., 2004. Early Devonian trace fossils in marine to non-marine redbeds in Podolia, Ukraine: palaeoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 214: 67–83.
- Van Siclen, D. C., 1958. Depositional topography – examples and theory. *American Association of Petroleum Geologists Bulletin*, 42: 1897–1913.
- Walker, K. R. & Bambach, R. K., 1971. The significance of fossil assemblages from fine-grained sediments: time-averaged communities. *Geological Society of America, Abstracts with Programs*, 3: 783–784.
- Waller, T. R., 1969. The evolution of the *Argopecten gibbus* stock (Mollusca: Bivalvia), with emphasis on the Tertiary and Quaternary species of eastern North America. *Journal of Paleontology, Paleontological Society Memoir*, 3: 1–125.
- Waller, T. R., 1991. Evolutionary relationships among commercial scallops (Mollusca: Bivalvia: Pectinidae). In: Shumway, S. E. (ed.), *Scallops: Biology, Ecology and Aquaculture*. Elsevier, Amsterdam, pp. 1–73.
- Whittaker, R. H., 1972. Evolution and measurement of species diversity. *Taxon*, 21: 213–251.
- Wignall, P. B., 1991. Dysaerobic trace fossils and ichnofabrics in the Upper Jurassic Kimmeridge Clay of southern England. *Palaaios*, 6: 264–270.
- Wilmsen, M. & Nagm, E., 2012. Depositional environments and facies development of the Cenomanian–Turonian Galala and Maghra el Hadida formations of the southern Galala plateau (upper Cretaceous, Eastern Desert, Egypt). *Facies*, 58: 229–247.

- Wilmsen, M., Niebuhr, B., Wood, C. J. & Zawischa, D., 2007. Fauna and palaeoecology of the Middle Cenomanian *Praeactinocamax primus* Event at the type locality, Wunstorf quarry, northern Germany. *Cretaceous Research*, 28: 428–460.
- Wilson, J. L., 1967. Cyclic and reciprocal sedimentation in Virgilian strata of southern New Mexico. *Geologic Society of America Bulletin*, 78: 805–818.
- Wilson, J. L., 1975. *Carbonate Facies in Geological History*. Springer-Verlag, Berlin, 471 pp.
- Wilson, M. A. & Taylor, P. D., 2001. Palaeoecology of hard substrate faunas from the Cretaceous Qahlah Formation of the Oman Mountains. *Palaeontology*, 44: 21–41.
- Wray, J. L., 1977. *Calcareous Algae*. Elsevier, Amsterdam, 185 pp.
- Zittel, K. A., 1883. Beiträge zur Geologie und Paläontologie der libyschen Wüste und der angrenzenden Gebiete von Aegypten. I. Geologischer Theil. *Palaeontographica*, 30: 1–147.
- Zonneveld, J.-P., Gingras, M. K. & Pemberton S. G., 2001. Trace fossil assemblages in a Middle Triassic mixed siliciclastic carbonate marginal marine depositional system, British Columbia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 166: 249–276.
- Zuschin, M. & Stachowitsch, M., 2009. Epifauna-dominated benthic shelf assemblages: lessons from the modern adriatic sea. *Palaios*, 24: 211–221.

