

Calcareous tube-dwelling encrusting polychaetes from a lower–middle Miocene sedimentary succession, Cairo-Suez District, Egypt

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This work represents the first systematic study of fossil calcareous tube-dwelling encrusting polychaetes to be conducted in Egypt. A total of 396 polychaete specimens were reported from the lower and middle Miocene Gharra and Geniefa formations, respectively, exposed at the Gebel Gharra section, Cairo-Suez District, Egypt. The tubeworms have been found attached to shells of oysters followed by pectinid shells, but there are few other gastropods and corals having rare attached tubes. At least nine polychaete taxa, belonging to eight genera, have been identified and systematically described. The tubeworm association is dominated by *Hydroides* (39.9% of the total polychaete specimens), *Filograna* (25.8%), *Spirobranchus* (12.6%), *Hyalopomatus* (10.6%), and *Glomerula* (8.1%). Stratigraphically, *Hydroides* sp. and spirorbid worms were exclusively reported from the lower Miocene succession; *Protula*? sp. from the middle Miocene, whereas the remaining species (*Filograna* cf. *implexa*, *Hyalopomatus*? sp., *Hydroides* cf. *elegans*, *Protis*? sp., *Spirobranchus* cf. *triqueter* and *Glomerula*? sp.) were reported from lower–middle Miocene sediments. Only fully marine polychaete species occur in the association, characterizing shallow subtropical marine conditions. The species reported show palaeobiogeographical affinities with the Miocene of Italy, Austria, and Slovakia and are characteristic of present-day Atlantic-Mediterranean regions. • Key words: polychaetes, systematics, palaeoecology, palaeobiogeography, Miocene, Northeast Africa.

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Encrusting polychaetes occur in many marine environments (e.g. Gosselin & Sewell 2013) from the Permian (Sanfilippo *et al.* 2017) to the present day (e.g. Rouse & Pleijel 2001). Most tube-building polychaete worms are benthic and sedentary suspension feeders (e.g. Díaz-Castañeda & Reish 2009). Serpulid-like calcareous tubes displayed a rapid diversification throughout the Jurassic and Cretaceous until the Holocene (Jäger 1983, 2004, 2012, 2014; Ippolitov 2007a, b, 2010; Sklenář *et al.* 2013; Ippolitov *et al.* 2014; Kočí & Ledvák 2014; Kočí *et al.* 2017). They secrete and inhabit a permanent calcareous tube that can be attached to both biogenic and inorganic hard substrates. They are most commonly found as post-mortem encrusters (e.g. Garberoglio & Lazo 2011, Sklenář *et al.* 2013, El-Sabbagh & El Hedeny 2016, El-Sabbagh *et al.* 2016, Veselská *et al.* 2021) but may also be colonizers of living hosts (*in vivo*; e.g. El Hedeny *et al.* 2021).

Hard substrates in the modern oceans are often heavily encrusted by polychaetes. They are common in all marine settings, ranging from the intertidal down to hadal depths (e.g. Hill 2013, Ippolitov *et al.* 2014). In addition, they were important encrusting organisms in the geological past (e.g. El-Sabbagh & El Hedeny 2016, El-Sabbagh *et al.* 2016). Hence, the study of ancient representatives could provide information on palaeoecology and palaeoenvironment.

Sediments of the lower–middle Miocene succession exposed in the Cairo-Suez District yield a significant polychaete assemblage, which, together with bivalves (oysters, pectinids and others), gastropods and echinoids, constitute the characteristic fossil assemblage in that area. Other common fossils include corals and bryozoans. So far, little attention has been paid to fossil calcareous tube-dwelling encrusting polychaetes in Egypt (e.g. El-Sabbagh & El Hedeny 2016, El-Sabbagh *et al.* 2016). Therefore, this

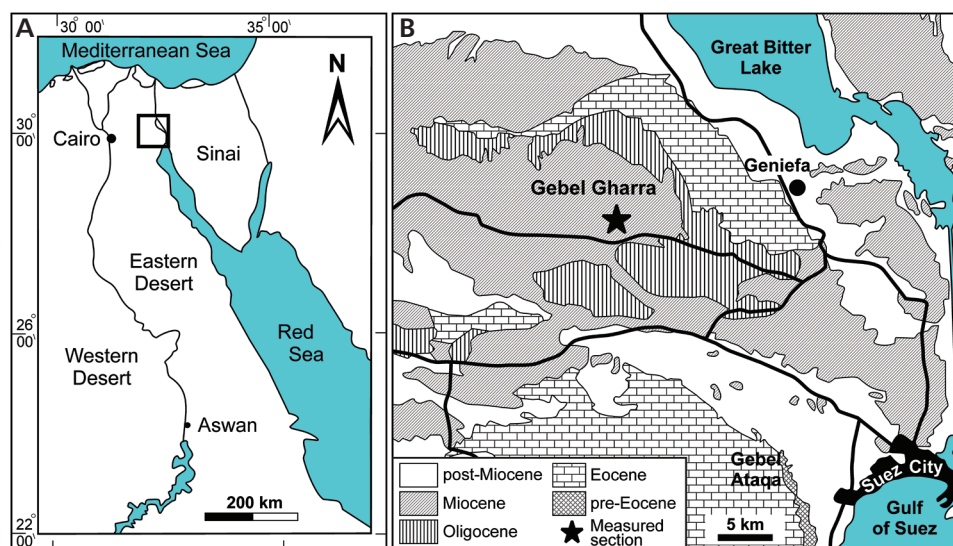


Figure 1. Geographic and geologic framework of the study area. • A – geographic overview. • B – simplified geological map of the study area (modified after Mandic & Piller 2001) with the location of the measured section at Gebel Gharra.

study aims, for the first time, to describe the systematics of a polychaete assemblage (mainly serpulids) from a lower–middle Miocene succession exposed in the Gebel Gharra section, Cairo-Suez District, Egypt, and to interpret its palaeoecology and palaeoenvironment.

Geological setting

Miocene successions are well exposed in the Cairo-Suez District in the northern part of the Eastern Desert of Egypt, forming the remarkable hills of that area (*e.g.* Depéret & Fourtau 1900; Sadek 1959; Souaya 1961, 1963; Said, 1962, 1990). The Gebel Gharra hill lies about 30 km NW of Suez City, Egypt (Fig. 1). It extends from longitude 32° 11' 00" to 32° 13' 20" E, and from latitude 30° 02' 12" to 30° 03' 18" N. The studied Miocene succession measures a total thickness of about 140 m. It is subdivided into lower siliciclastic- and upper carbonate-dominated intervals, representing the lower Miocene Gharra (Said 1962) and the middle Miocene Geniefa (Said 1990) formations, respectively (Fig. 2). The Gharra Formation attains a thickness of about 65 m. It consists of shale, sandstone, siltstone and sandy marl interbeds, partly bioturbated. The Geniefa Formation rests unconformably on the Gharra Formation, attaining a thickness of about 75 m. It consists of chalky and reefal limestones with few siltstone and marl intercalations (Fig. 2).

Sediments of the two formations are characterized by highly abundant macrobenthic faunas, including molluscs (oysters, pectinids, other bivalves and gastropods), echinoid tests and spines, corals (solitary, branched and massive species), bryozoans, sponges, polychaete worms and balanoid barnacles. In addition, they contain remarkable oyster and pectinid shell concentrations and firmground

discontinuity surfaces. In general, the diverse macrofossil assemblages support a late Burdigalian age for the Gharra Formation and a Langhian–Serravallian age for the Geniefa Formation (Souaya 1963, 1966; Abdelghany & Piller 1999; Mandic & Piller 2001; Abdelghany 2002; Kroh & Nebelsick 2003; El-Sorogy *et al.* 2017).

Material and methods

In the section studied, the lower–middle Miocene succession was measured bed-by-bed. Lithologies, textures, sedimentary structures, nature of contacts, macrofossil contents and taphonomic features were documented. Bivalves (oysters, pectinids and others) and echinoids are the main tools for delineating the stage and substage boundaries of the interval studied. Macrofossils have been recovered throughout the succession at specific horizons. Shells were marked with arrows to indicate *in-situ* orientations within the rock. In the laboratory, all macrofossil specimens were gently cleaned under running water, scrubbing with a soft toothbrush in order to remove adhering matrix.

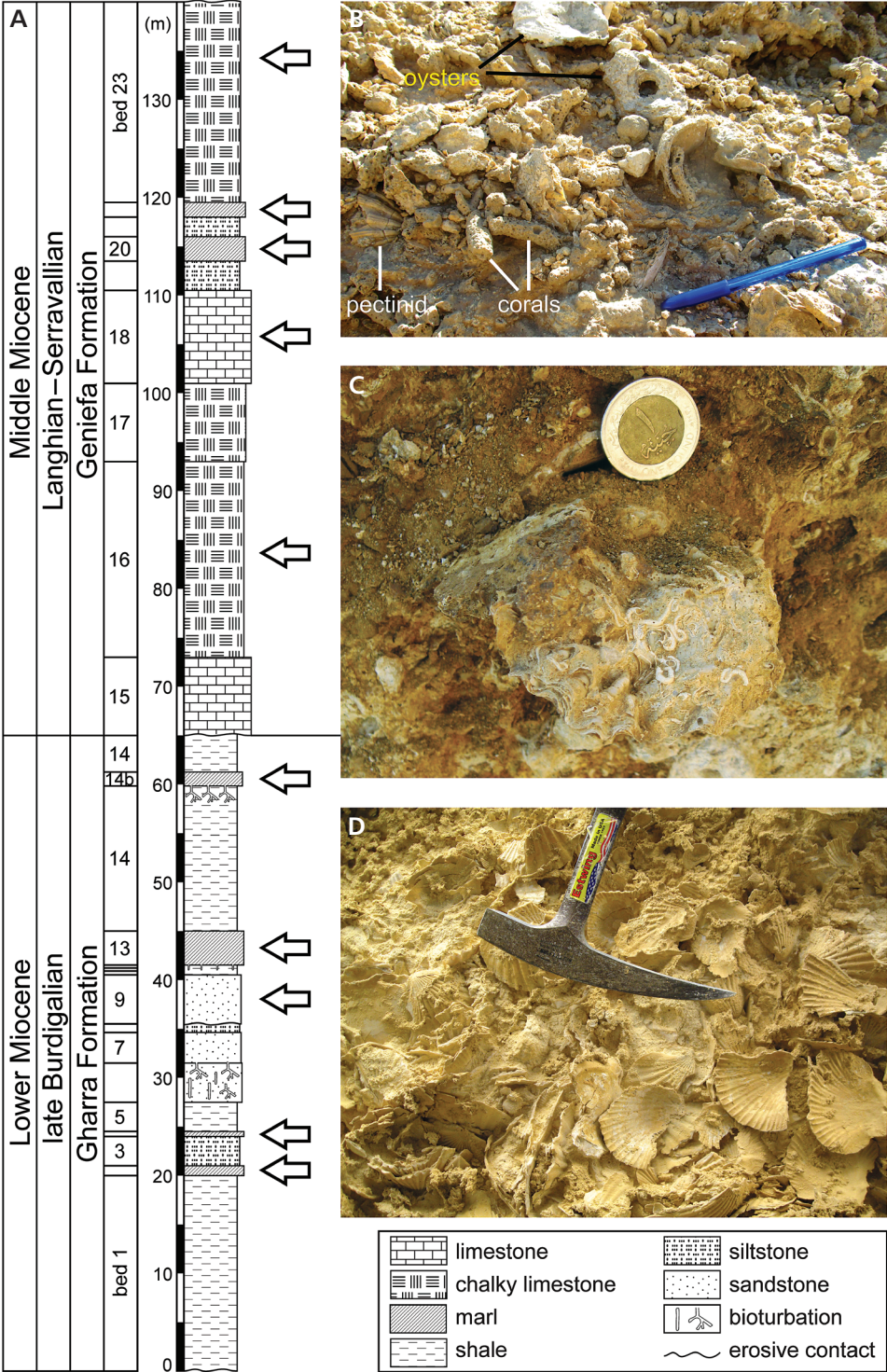
The present study is mainly based on 758 moderately to well-preserved oysters (43.4% of the total specimens), pectinids (30.5%), other bivalves (19.8%), gastropods (3.3%), echinoids (1.8%), and corals (1.2%). Each specimen was systematically screened for polychaete worms using both a hand lens and a binocular microscope. Specimens were photographed with a Canon Power-Shot A3000 digital camera. Measurements of tubes (diameter and wall thickness) were made using a digital calliper (accurate to 0.1 mm).

Terminology and systematic classifications of Schmidt (1955), Jäger (1983, 2004) and ten Hove & Kupriyanova (2009) are applied here. Although taxonomic identification

to species level was possible for some polychaete worm specimens, most specimens are worn and could only be identified to generic level. The palaeobiogeographical distributions of the identified polychaete worm taxa are mainly based on analogy with modern distributions of polychaetes (ten Hove & Kupriyanova 2009).

All macrofossil specimens were collected during field work for a Ph.D. study of 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

Figure 2. Stratigraphic log and photos of the outcrop. • A – lithological descriptions of the measured Gebel Gharra section. Arrows mark occurrences of serpulid worms. • B – marl of the Geniefa Formation (bed 22 at 119m) fossiliferous with pectinids, oysters and corals. • C – cluster of serpulid worms on the exterior surface of left valve of “*Ostrea*” *virleti* (Deshayes, 1835) in the thin marl bed (14b) at 60m. • D – at Gebel Gharra, the middle part of the Gharra Formation contains abundant, moderately preserved, and disarticulated pectinid specimens in the marl bed (13) at 42m.



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.

Systematic palaeontology

More than 396 polychaete specimens belonging to at least nine species and eight genera could be identified, described, and illustrated (Figs 3–5). They were recorded attached to shells or skeletons of the macrofaunal assemblage (76 out of 758 specimens), including oysters (51.3% of the total affected specimens), pectinids (46.1%), and gastropods and corals (1.3% each). They mostly encrust the exterior and interior surfaces of both left and right valves of oyster and pectinid shells. Six of the identified taxa are recorded for the first time in Egypt (Tab. 1).

Herein, the studied polychaete assemblages predominately consist of moderately to poorly preserved tubes. In many of them the upper part of the tube is partially abraded so that only the lower part cemented to the substrate is preserved (Figs 3E, 4H, 5E), while others were preserved as internal moulds (Fig. 4F, I). The tubes were probably originally circular in cross section and are deformed in some specimens due to sediment compression after burial.

Phylum Annelida Lamarck, 1802
Class Polychaeta Grube, 1850
Order Sabellida Levinsen, 1883
Family Sabellidae Latreille, 1825

Genus *Glomerula* Brünnich Nielsen, 1931

Type species. – *Glomerula gordialis* von Schlotheim, 1820.

Glomerula? sp.

Figure 3A–D

Material. – Thirty-one partially preserved tubes attached to eight oyster shells (GH22O205, 220, 222, 226, 227, 237, 246, 259) and a single occurrence on a pectinid shell (GH14bP310).

Description. – Somewhat loosely coiled to regular helically coiled tubes reaching up to 1.2 mm in diameter. Tubes have smooth surfaces without any ornamentation and show no flattened attachment surfaces.

Remarks. – Tube diameter and spiral shape resemble somewhat *Spiraserpula* Regenhardt, 1961, but the studied tubes differ in having no flattened attachment surface and widened tube base. The specimens described herein show most of the morphological characters of the sabellid

Glomerula but our specimens are too regularly spirally coiled for typical *Glomerula*. So, this identification is uncertain.

Occurrence. – *Glomerula* ranges from the Carboniferous? (Ippolitov *et al.* 2014) or Permian (Sanfilippo *et al.* 2017) to the Recent (Vinn *et al.* 2008). In the section studied, *Glomerula?* is common in the lower–middle Miocene sediments (Tab. 1).

Family Serpulidae Rafinesque, 1815

Genus *Filograna* Berkeley, 1835

Type species. – *Filograna implexa* Berkeley, 1835 (subjective synonym *Serpula filograna* Linnaeus, 1767).

Filograna cf. *implexa* Berkeley, 1835

Figure 3E, F

Material. – One-hundred-and-two partially preserved tubes attached to a single oyster (GH22O250) and three pectinid (GH14bP318, 319, 321) shells.

Description. – Small, smooth somewhat curved tubes with diameter ranging from 1.0 to 1.8 mm. Tubes increase slowly in diameter.

Remarks. – Size and morphology resembles *Salmacina incrustans* Claparède, 1870 (p. 176, pl. 30, fig. 5). Alternatively, studied tubes can be assigned to *Filograna* Berkeley, 1835 because of their similar diameter and morphology. In fossil specimens, it is impossible to distinguish between *S. incrustans* and *F. implexa*, because the only reliable difference is the presence in *Filograna* versus lack in *Salmacina* of two opercula or rarely one operculum, and fossil opercula of *Filograna* are normally not preservable (ten Hove & Kupriyanova 2009 and references therein). Furthermore, within the genus *Filograna*, the studied tubes with diameter from 1.0 to 1.8 mm are rather large, at least if compared to the tubes of specimens living today. Even the tubes of the most common and most wide-spread fossil *Filograna* species, *F. socialis* (Goldfuss, 1831) (Jurassic, Cretaceous and Paleocene) only occasionally reach 1.1 or 1.2 mm, but not much more. Consequently, the authors prefer *Filograna* cf. *implexa*, simply because this is the older name and therefore, if zoologists would decide to unite the two genera or species, the valid name.

Occurrence. – In Gebel Gharra, *Filograna* cf. *implexa* occurs in the lower–middle Miocene sediments (Tab. 1). The species is recorded in the Suez Canal, Egypt (Ben-Eliahu & ten Hove 2011). Modern species has a global

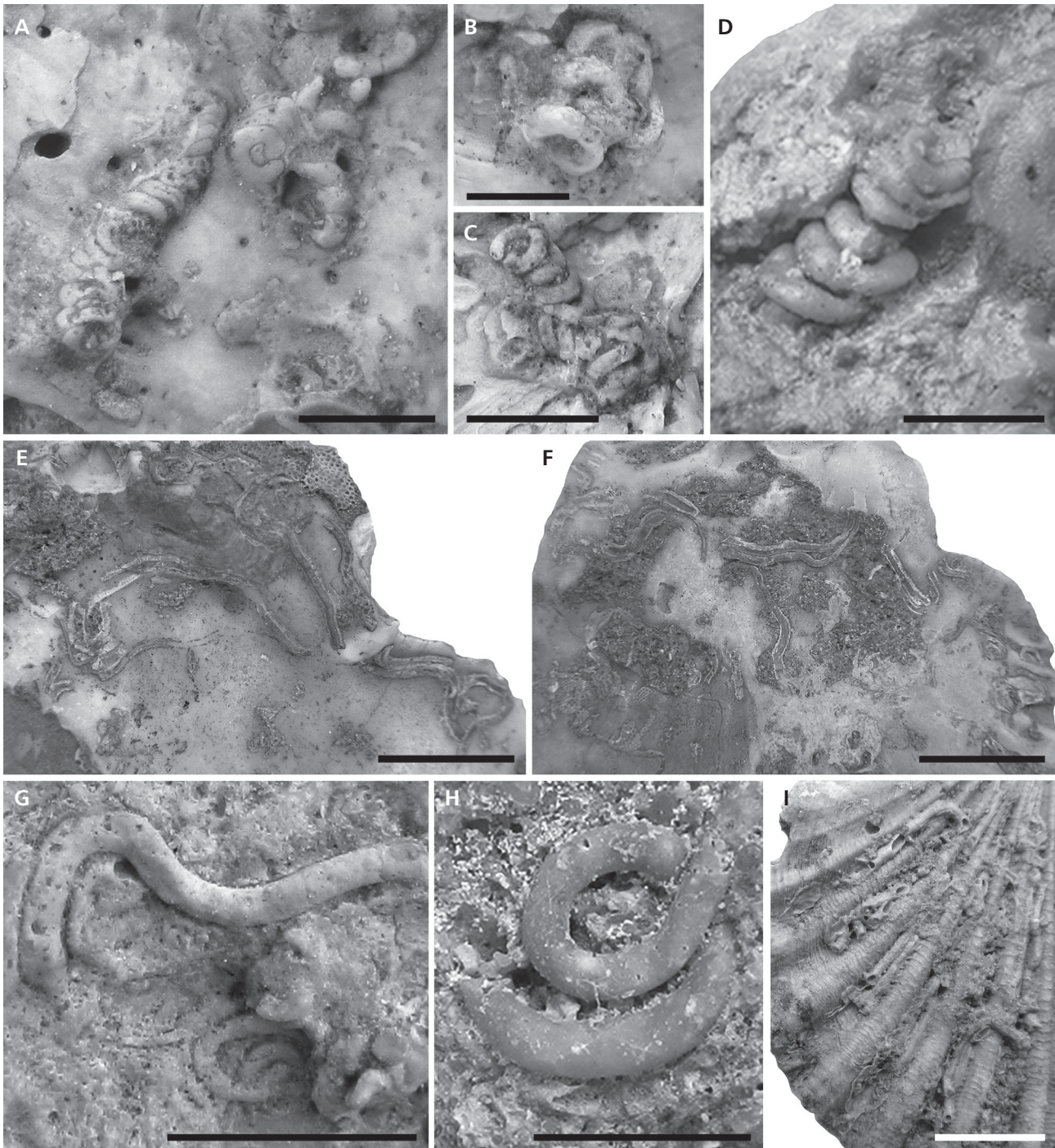


Figure 3. Identified serpulids from the studied lower-middle Miocene. • A–D – *Glomerula?* sp., GH22O227, 246, 205, 222. • E, F – *Filograna* cf. *implexa* Berkeley, 1835 (GH14bP318, 321). • G, H – *Hyalopomatus?* sp., GH22O202, GH20G1. • I – *Hydroides* cf. *elegans* (Haswell, 1883), GH04P08. Scale bars = 5 mm (A–D, G, H), 10 mm (E, F, I).

distribution, but it may constitute a complex of species (ten Hove & Kupriyanova 2009).

Genus *Hyalopomatus* Marenzeller, 1878

Type species. – *Hyalopomatus clapedii* Marenzeller, 1878.

Hyalopomatus? sp.

Figure 3G, H

Material. – Forty-two partially preserved tubes attached to four oyster (GH22O194, 202, 237, 257), four pectinid (GH02P01, GH04P100, GH13P200, GH14bP313), and

Table 1. Age of strata and numbers and percentages of the recorded calcareous tube worms attached to different faunal elements collected from the studied section. Abbreviations: l. – lower; m. –middle; LV – left valve; RV – right valve; * – taxa recorded for the first time in Egypt; Gastro. – Gastropods.

Polychaete species	Miocene age of strata	Occurrences											
		Total		Percentage on different hosts									
		No.	%	Oysters		Pectinids				Gastro.		Corals	
				Exterior surface	Interior surface	Exterior surface	Interior surface						
				LV	RV	LV	RV	LV	RV	LV	RV		
<i>Filograna</i> cf. <i>implexa</i>	l.–m.	102	25.8	0.0	0.0	3.9	0.0	21.6	0.0	74.5	0.0	0.0	0.0
* <i>Hyalopomatus</i> ? sp.	l.–m.	42	10.6	7.1	4.8	9.5	7.1	0.0	50.0	14.3	0.0	2.4	4.8
<i>Hydroides</i> cf. <i>elegans</i>	l.–m.	146	36.9	0.0	21.9	1.4	8.2	2.1	37.0	2.1	27.4	0.0	0.0
* <i>Hydroides</i> sp.	l.	12	3.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Protis</i> ? sp.	l.–m.	8	2.0	0.0	37.5	0.0	62.5	0.0	0.0	0.0	0.0	0.0	0.0
* <i>Protula</i> ? sp.	m.	1	0.3	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Spirobranchus</i> cf. <i>triqueter</i>	l.–m.	50	12.6	0.0	0.0	0.0	4.0	16.0	0.0	80.0	0.0	0.0	0.0
* Serpulidae unidentified	m.	1	0.3	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
* Spirorbid	l.	2	0.5	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
* <i>Glomerula</i> ? sp.	l.–m.	32	8.1	25.0	65.6	6.3	0.0	0.0	3.1	0.0	0.0	0.0	0.0

a single gastropod (GH14bG20) and coral (GH22C2) specimens. Six fragments of free tube parts.

Description. – Small curved tubes with diameter ranging from 0.4 to 2.0 mm. Tube wall very thin and smooth without any ornamentation. Base is not widened and concave.

Remarks. – The tube diameter (about 2.0 mm) is rather large for a *Hyalopomatus*, and therefore we have assigned our specimens only tentatively to the genus.

Occurrence. – *Hyalopomatus* has a relatively wide stratigraphic range (middle Miocene to Recent). In Gebel Gharra, *Hyalopomatus*? sp. occurs in the lower–middle Miocene sediments (Tab. 1). Although this genus is considered a deep-water serpulid (e.g. Sanfilippo 2009), it has been recorded in shallow depths (15 to 130 m) in association with *Hydroides* Gunnerus, 1768, *Pseudovermilia* Bush, 1907 and a vermetid shell (Bastida-Zavala 2012). Modern occurrences of *Hyalopomatus* include the Atlantic Ocean, the Indian Ocean and the Mediterranean Sea (ten Hove & Kupriyanova 2009).

Genus *Hydroides* Gunnerus, 1768

Type species. – *Hydroides norvegica* Gunnerus, 1768.

Hydroides cf. *elegans* (Haswell, 1883)

Figures 3I, 4A–C

1883 *Eupomatus elegans*; Haswell, p. 633, pl. 12, fig. 1.

Material. – One-hundred-and-forty-six partially preserved tubes attached to four oyster (GH14bO44, GH18O128, GH22O208, 257) and seven pectinid (GH04P08, 16, 30, GH13P201, GH14bP302, 309, 315) shells.

Description. – Curved to meandering tubes with trapezoidal cross-sections. Tube diameter ranges from 0.5 to 2.2 mm. Median surface is flattened and bordered by moderately developed edges, which do not form true keels. Poorly developed perpendicular growth lines are visible on tube side. Base is without flanges and the wall is relatively thin.

Occurrence. – The present-day *Hydroides elegans* is circumglobal, characterizing the warm-temperate zone of the Mediterranean Sea (Zibrowius 1992, Bianchi 1981, Koçak *et al.* 1999, El Hedeny *et al.* 2021). In the Gebel Gharra section, *Hydroides* cf. *elegans* occurs in the lower–middle Miocene sediments (Tab. 1). Fossils of this species were also recorded from the Miocene of Austria (e.g. Vinn 2020).

***Hydroides* sp.**

Figure 4D

Material. – Twelve partially preserved tubes attached to an oyster shell (GH14bO44).

Description. – Curved to meandering tubes with trap-ezoidal cross-sections and diameter ranging from 0.6 to 1.2 mm. Exterior surface has a faint median keel and two lateral keels, all located on top of the tube. Base slightly widened without well-developed flanges. Tube is covered with moderately developed perpendicular growth lines.

Remarks. – The studied specimens somewhat resemble *H. alatalateralis* (Jones, 1962) (Jones 1962: p. 205, figs 139–146) because of their similar diameter and presence of three faint longitudinal keels. However, we have assigned our specimens neither to *H. alatalateralis*, which today lives in the western Atlantic Ocean, nor to any other of the many extant *Hydroides* species (e.g. Bastida-Zavala & ten Hove 2002, 2003).

Occurrence. – In Gebel Gharra, *Hydroides* sp. occurs in the lower Miocene sediments (Tab. 1).

Genus *Protis* Ehlers, 1887

Type species. – *Protis simplex* Ehlers, 1887.

***Protis*? sp.**

Figure 4E

Material. – Eight partially preserved tubes attached to three oyster shells (GH09O29, GH23O311, 321).

Description. – Small smooth tubes with circular cross-sections and up to 0.9 mm in diameter. Tubes are curved, but do not form loops. Tube diameter increases relatively slowly. Base is not widened and does not form flanges. Aperture is plain without any protruding parts. Tube wall is thin.

Remarks. – Several different serpulid genera have similar tubes. Small smooth tubes with similar diameters occur also in the genus *Apomatus* Philippi, 1844, which is a possible alternative identification for the studied specimens. Thus, our specimens are assigned to *Protis* very tentatively.

Occurrence. – In Gebel Gharra, *Protis*? sp. occurs in the lower–middle Miocene sediments (Tab. 1). The genus has been recorded before in the middle Miocene succession of Siwa Oasis, Western Desert of Egypt (El Hedeny &

El-Sabbagh 2018) and in the upper Miocene of northern Italy (Vinn et al. 2012). Modern occurrences include the Atlantic Ocean and the Mediterranean Sea (ten Hove & Kupriyanova 2009).

Genus *Protula* Risso, 1826

Type species. – *Protula rudolphi* Risso, 1826, accepted as *Protula tubularia* (Montagu, 1803).

***Protula*? sp.**

Figure 4F

Material. – A single partially preserved tube attached to an oyster shell (GH18O100).

Description. – A coiled tube of moderate size, diameter ranging from 3.5 to 5.5 mm. Exterior surface of the internal mould is smooth without any ornamentation. Base is not widened and shows no flanges. Tube increases relatively fast in diameter.

Remarks. – This single specimen is among the largest in tube diameter of the entire studied polychaete fauna. By large size, coiling of posterior tube portion and smooth surface this specimen matches the genus *Protula* well. Moreover, large tubes of the genus *Protula* are widespread and common in Cenozoic faunas. However, this specimen is only an inner mould, a steinkern, and nothing is known about the outer surface of the now dissolved tube. Had the surface been smooth as in *Protula* or ornamented as in other large-sized Cenozoic serpulid genera? For this reason, we have added a question mark after *Protula*.

Occurrence. – *Protula* is a subtidal serpulid worm; generally living partly buried in sediment or attached to a hard substrate (Hayward 1977). This genus is recorded from the lower Miocene of North Auckland, New Zealand (Hayward 1977) and the Miocene (Badenian) of Austria (Vinn 2007). In the Gebel Gharra section, *Protula* occurs in the middle Miocene sediments (Tab. 1). Modern occurrences of the genus include the Atlantic Ocean, the Mediterranean Sea and the Indian Ocean (ten Hove & Kupriyanova 2009).

Genus *Spirobranchus* de Blainville, 1818

Type species. – *Spirobranchus giganteus* (Pallas, 1766).

***Spirobranchus* cf. *triqueter* (Linnaeus, 1758)**

Figure 4G, H

1758 *Serpula triquetra*; Linnaeus, p. 787.

1955 *Pomatoceros triqueter*. – Schmidt, pp. 51–53.

Material. – Fifty partially preserved tubes attached to a single oyster (GH18O159) and two pectinid (GH02P01, GH14bP304) shells.

Description. – Almost straight tubes of moderate size and triangular cross-section. There is a prominent thin slightly undulating median keel. Peristomes which are strongly curved forward at the median keel may occur. Otherwise the exterior surface is smooth. Tube diameter ranges from 1.8 to 4.8 mm.

Remarks. – The studied specimens are assigned tentatively to *Spirobranchus triqueter* due to the similar triangular cross-section and shape of the prominent median keel.

Occurrence. – In Gebel Gharra, *Spirobranchus* cf. *triqueter* occurs in the lower–middle Miocene sediments (Tab. 1). Modern occurrences include the Mediterranean Sea, the Atlantic Ocean and the Black Sea (ten Hove & Kupriyanova 2009). In Egypt, the species was collected from the intertidal zone of the Alexandria coast, south-eastern Mediterranean Sea (Dorham *et al.* 2013).

Serpulidae unidentified

Figure 4I

Material. – A single partially preserved tube attached to an oyster shell (GH16O81).

Description. – An almost U-shaped tube of moderate size. Exterior surface of the internal mould is smooth without any ornamentation. Cross-section is circular; base is not widened and lacks flanges. Tube wall is relatively thick. Diameter reaches up to 2.8 mm.

Remarks. – The described specimen is relatively small for *Neovermilia* Day, 1961 and may be immature. Alternatively, it could be assigned to *Protula* Risso, 1826 as morphologically similar smooth tubes are common in this genus.

Occurrence. – In the section studied, this unidentified serpulid specimen occurs in the middle Miocene sediments (Tab. 1).

Family Spirorbidae Pillai, 1970

Genus and species indet.

Figures 4J, 5F

Material. – Two specimens attached to an oyster shell (GH14bO44).

Description. – Tiny spirally coiled tubes (0.2–0.3 mm in

diameter). Tubes are tightly and sinistrally coiled. Base is not widened.

Remarks. – The present specimens show the typical characters of spirorbid worms; however, owing to the relatively small size and poor preservation, they could not be determined even at the generic level.

Occurrence. – In the Gebel Gharra section, spirorbid specimens occur in the lower Miocene sediments (Tab. 1).

Discussion

Palaeoecology

When compared to other Miocene localities, the studied oysters are encrusted by a moderately diverse polychaete fauna, represented by at least eight genera (Tab. 1). Nine species of polychaetes have been identified, but the actual number of species in the association is likely higher. The tubeworm association is dominated by *Hydroides* (40.0% of the total polychaete specimens), *Filograna* (25.8%), *Spirobranchus* (12.6%) and *Hyalopomatus*? (10.6%). Other tubeworms present are *Glomerula*? (8.1%), *Protis*? (2.0%), spirorbid (0.5%), *Protula*? and unidentified serpulid (0.3% each; Tab. 1). All polychaete species identified in the present study exclusively or at least usually live in normal marine waters. In general, the studied serpulids are characteristic of shallow water, subtropical and/or tropical environments. Most of the modern *Hydroides* species live on continental shelves, mainly in tropical to subtropical seas (Bastida-Zavala & ten Hove 2002, 2003; ten Hove & Kupriyanova 2009; El Hedeny *et al.* 2021). The known species of the present-day *Hyalopomatus* are morphologically very similar and mostly inhabit bathyal depths in all climatic zones (Zibrowius 1969). Modern species of *Spirobranchus* commonly occur in subtropical and tropical waters (ten Hove & Kupriyanova 2009).

Usually, numerous specimens of serpulids occur on the same substrate. Up to three serpulid species can occur on the same substrate, but most often each substrate is being encrusted by a single or less often by two species of serpulids. A single oyster shell is often encrusted by several generations of *Hydroides* cf. *elegans* and *Hyalopomatus*? sp. This indicates that substrates have been colonized repeatedly by larvae produced by the previously settled specimens on the same substrate or by larvae produced by mature specimens on nearby substrates. Polychaetes often occur in aggregations on oyster shells, which are common trait also in the present-day serpulid associations, for instance, in case of *Spirorbis* Daudin, 1800 (Knight-Jones 1951) and *Spirobranchus triqueter* (e.g. ten Hove & Kupriyanova 2009). It is possible that larvae of previously

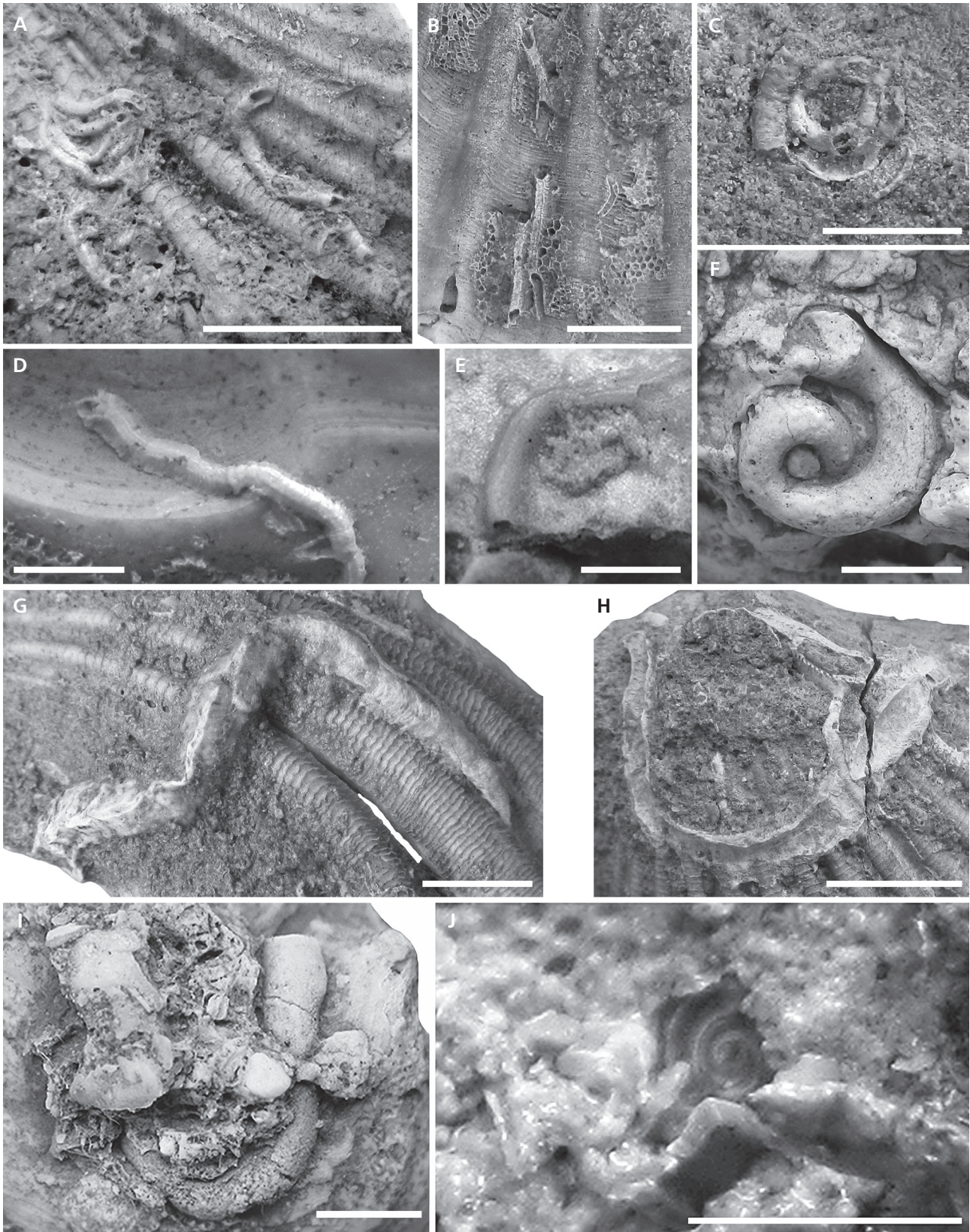


Figure 4. Identified polychaetes from the studied lower–middle Miocene. • A–C – *Hydroides* cf. *elegans* (Haswell, 1883), GH04P08, 30, GH13P201. • D – *Hydroides* sp., GH14bO44. • E – *Protis*? sp., GH09O29. • F – *Protula*? sp., GH18O100. • G, H – *Spirobranchus* cf. *triqueter* (Linnaeus, 1758), GH14bP304. • I – Serpulidae unidentified, GH16O81. • J – spirorbid worm, GH14bO44. Scale bars = 10 mm (A, F–H), 5 mm (B, C, I), 2.5 mm (D, E, J).

settled serpulids may have attracted the settling of next generations.

Polychaetes encrust both the exterior and interior surfaces of oyster shells (Fig. 5A–C). The interior surfaces were definitely encrusted post-mortem, but some oyster exteriors may have been encrusted by polychaetes already during their life based on the analogy with modern oyster associations. In pectinids, polychaetes are found mostly aggregated, composed of numerous specimens oriented subparallel to each other and also overgrowing each other (Fig. 5D). Sometimes polychaete tubes are growing parallel to radial ribs of pectinid shells because in the interspace between two ribs the polychaetes save calcareous material for tube building, and because in such a position they are a bit better sheltered from being destroyed by grazers. Such a preference of orientation parallel to pectinid ribs may be more often displayed in juvenile than in adult portions of the same specimen (Figs 4G, H; 5D). In this case, the orientation of the last part of the tube suggests that the aperture and final tube portion were vertical and elevated from the substrate (Radwańska 2004, Jäger & Kočí 2007). In oysters, in contrast, the encrustation pattern of polychaetes is rather random and there is no preference for the shell regions where polychaetes could have benefitted from water currents produced by the living bivalves.

Taphonomy of the encrusting calcareous worms

In the assemblage studied, the calcareous tube-dwelling polychaetes appeared as encrusting forms, cemented to bivalves (particularly oysters and pectinids), forming an important group of sclerobionts. Polychaetes may have colonized the living hosts or they may represent a post-mortem colonization. This phenomenon is common through the mid-late Mesozoic and the Cenozoic (Taylor 2016). The common occurrence of encrusted polychaetes reported in this study on the interior sides of organic substrate shells (Tab. 1; Figs 5A, B, E, F; 6) indicates a post-mortem colonization. In addition, the dense aggregation on some exterior surfaces of pectinid shells (Fig. 5D) likely did not form during the life of pectinids, because it would have

affected their swimming capability. However, pectinid swimming tends to be episodic and it is possible that heavily encrusted individuals may have been able to survive in some situations, for example, where asteroid predators were scarce.

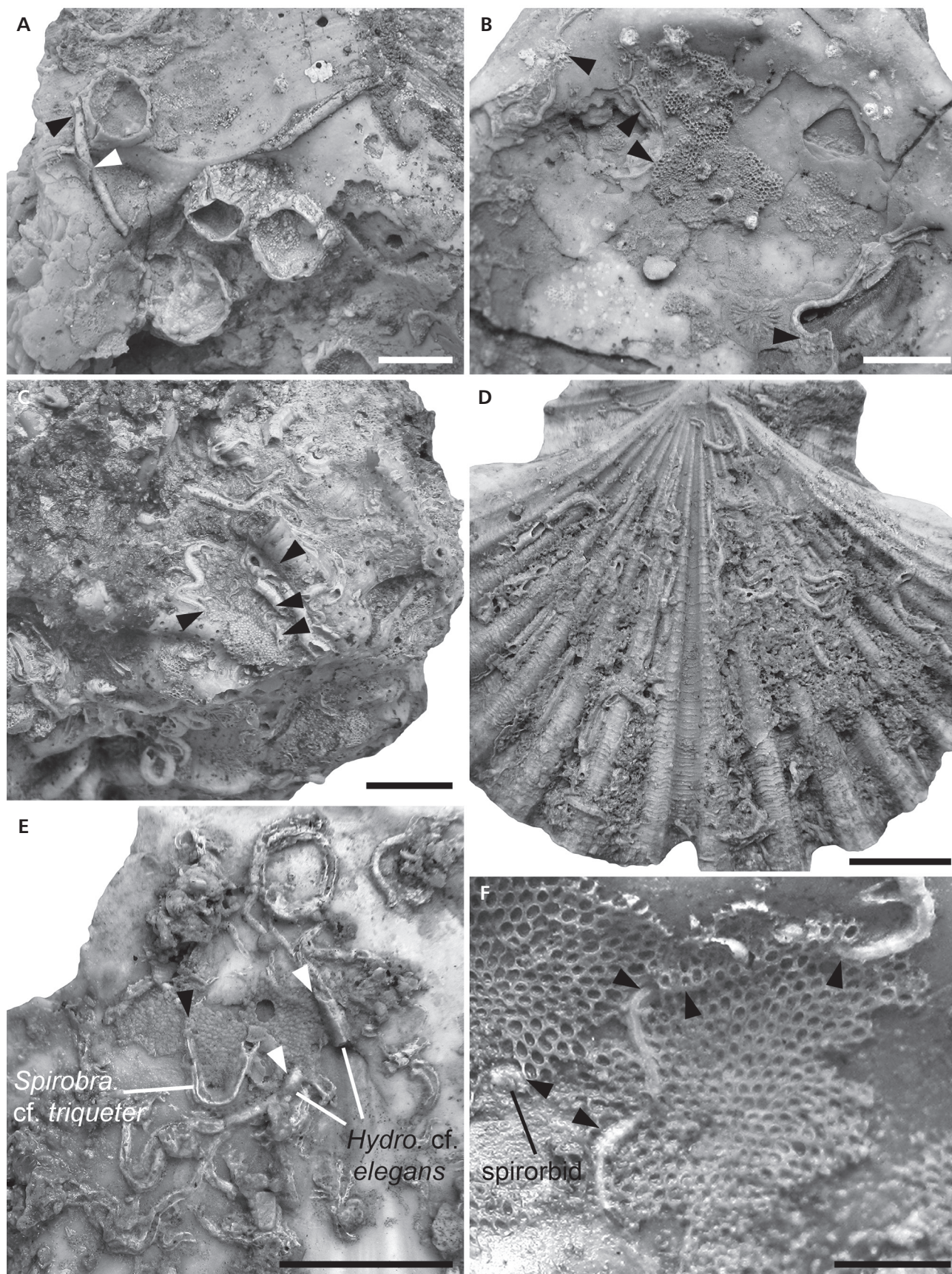
Besides the studied calcareous tube-dwelling encrusting polychaetes, other encrusters are also observed, including balanoid barnacles and bryozoans (Fig. 5A, F). Marginal encounters occur when two of these encrusters shared the same substrate and come into contact during their growth (Taylor 2016). Some serpulids display marginal competitive interactions (*i.e.* overgrowth) for space on the studied organic substrates. The marginal encounters are clearly observed between serpulids and balanoid barnacles in the interior surface of some oyster shells (*e.g.* Fig. 5A). However, the growing of tubeworms never ceases when it encounters another encruster, the tubeworms just change their growth direction.

Serpulids are sometimes overgrown by other serpulids (Fig. 5D), but most often they have been partially overgrown by bryozoans (Fig. 5B, E, F). In addition, a few reciprocal overgrowths were also observed between serpulids and bryozoans. Due to their occurrence on the interior sides of the valves, overgrowth took place post-mortem. In general, overgrowth involving serpulids is rare in the association indicating that there was no deficiency of hard substrate and oyster shells were sufficiently abundant on the seafloor to provide enough space for settlement and growth for all encrusting sclerobionts, without making spatial competition necessary. In general, bioerosional activity is restricted to a few, often relatively rare, ichnospecies (*e.g.* *Entobia* Bromley, 1970; Fig. 3H).

Palaeobiogeography

In the early to middle Miocene, there was a connection between the Indian Ocean and the Atlantic Ocean via the Mediterranean Sea (*e.g.* Golonka 2009). Palaeontological data based on macrofaunal distribution and tectonic considerations have allowed broad constraints on the closure of the Mesopotamian Seaway and the termination of a continuous Tethyan Seaway connectivity between the

Figure 5. Taphonomic aspects of the serpulid faunal assemblage studied. • A – the reciprocal overgrowth between encrusters on the interior surface of left valve of an oyster shell, GH220194; note *Hyalopomatus?* sp. overgrows a balanoid barnacle (black arrow), whereas another balanoid barnacle overgrows this serpulid (white arrow). • B – bryozoans overgrow serpulid specimens (arrows) on the interior surface of right valve of an oyster shell, GH220257. • C – *Hydroides* cf. *elegans* (Haswell, 1883) overgrows bryozoans (arrows) on the exterior surface of right valve of an oyster shell, GH14bO44. • D – cluster of the serpulid worms *Hydroides* cf. *elegans* (Haswell, 1883) on the exterior surface of left valve of a pectinid shell, GH04P08. • E – *Spirobranchus* cf. *triqueter* (Linnaeus, 1758) and *Hydroides* cf. *elegans* (Haswell, 1883) encrusted the interior surface of left valve of a pectinid shell, GH02P01. Note the reciprocal overgrowth between a sheet of bryozoan and specimens of these two serpulid species; the bryozoan overgrows *S.* cf. *triqueter* (Linnaeus, 1758) (black arrow), whereas to the right *H.* cf. *elegans* (Haswell, 1883) overgrows this bryozoan sheet (white arrows). • F – bryozoan sheet overgrows *Hydroides* sp. and a spirorbid specimen (arrows) on the interior surface of right valve of an oyster shell, GH14bO44. Scale bars = 10 mm (A–E), 2.5 mm (F).



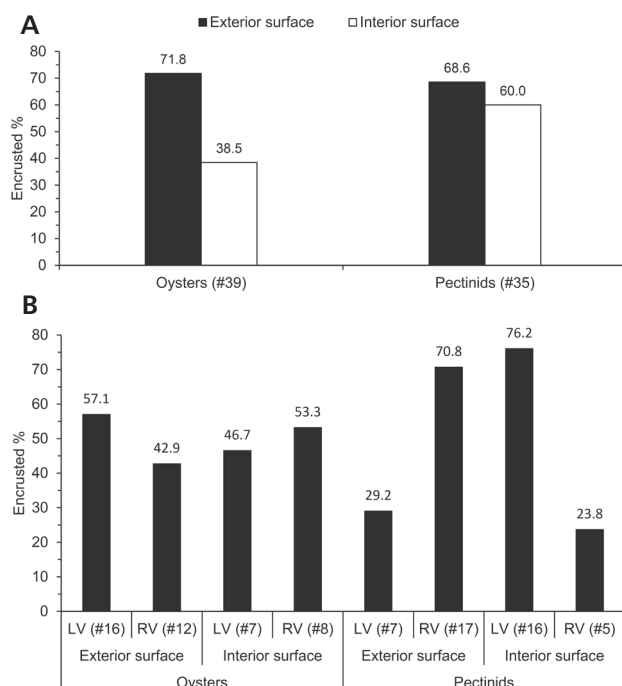


Figure 6. Distribution of polychaetes encrusting oyster and pectinid shells. • A – percentage of encrusting calcareous-tube worms on the exterior and interior surfaces of all encrusted oyster and pectinid shells. • B – comparison (in %) between the polychaete worms on the exterior and interior surfaces of both left and right valves (LV and RV, respectively) of all encrusted oyster and pectinid shells.

Indian and the Atlantic oceans to a time between the Late Oligocene and the Middle Miocene (*ca.* 23–14 Ma; Bialik *et al.* 2019). There was also a second connection across the Red Sea that may still have existed until at least the Aquitanian, but the feasibility and evolution of significant exchange of water masses between the Mediterranean Sea and the Indo-Pacific oceans is still debated (Bialik *et al.* 2019). Thus, considering the palaeogeographic setting one would expect to see both Atlantic and Indian Ocean influences on the faunal composition of calcareous polychaetes in the early and middle Miocene of Egypt. The studied calcareous polychaete fauna has most in common with the modern fauna of the Mediterranean-Atlantic region (ten Hove & Kupriyanova 2009). Some of the described genera occur both in the Indian and the Atlantic oceans, but the fauna lacks definitely Indian Ocean components. Thus, the studied species most likely had an Atlantic-Mediterranean origin. The global fauna of the Miocene serpulids is not well known, but there are some similarities between the serpulid faunas of Miocene of Italy and Egypt (*Hydroides*, *Spirobranchus triqueter* and *Protula*) (*e.g.* Rovereto 1904) and Miocene of Austria, Slovakia, and Egypt (*Hydroides elegans*, *Spirobranchus triqueter*, and *Protula*) (*e.g.* Schmidt 1955, Vinn 2007, Kočí & Ledvák 2014). This is not surprising as the Miocene basins of Italy and Austria had direct connections to the basin in Egypt.

Conclusions

This account represents the first description of polychaetes from a lower-middle Miocene succession exposed at the Gebel Gharra section, Cairo-Suez District, Egypt. Nine taxa were identified and described, comprising *Filigrana cf. implexa*, *Hyalopomatus?* sp., *Hydroides cf. elegans*, *Hydroides* sp., *Protis?* sp., *Protula?* sp., *Spirobranchus cf. triqueter*, unidentified serpulid, and a spirorbid. In addition, one further possible *Glomerula* species from the same strata is described. Six of the identified taxa are recorded for the first time in Egypt. Polychaetes displayed marginal competitive interactions for space on the organic substrate studied. Palaeoecologically, polychaete species characteristic of normal marine salinities occur in the association, characterizing shallow subtropical marine water. Biogeographically, the fauna has most in common with the modern fauna of the Mediterranean-Atlantic region and the Miocene fauna of Italy, Austria, and Slovakia.

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