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## New records of non-indigenous molluscs from the eastern Mediterranean Sea

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### Abstract

We report new findings of non-indigenous Indo-Pacific molluscs from shallow water habitats off Israel, Greece and Egypt, eastern Mediterranean Sea. The bivalves *Pillucina vietnamica* Zorina, 1978 and *Alveinus miliaceus* (Issel, 1869) were collected from sandy bottoms off Israel, whereas *Gregariella* cf. *ehrenbergi* (Issel, 1869) was recovered from a buoy originating from Port Said, Egypt, and stranded on the Israeli coast. The three species are first records for the Mediterranean Sea. Additionally, we report range extensions for several gastropods: *Varicopeza pauxilla* (A. Adams, 1855) is recorded from Israel, *Phidiana militaris* (Alder and Hancock, 1864) from southern Israel (Ashqelon), and *Viriola* cf. *bayani* Jousseaume, 1884 from Israel and Crete. Shells and valves of an unidentified lucinid bivalve morphologically distinct from any known Mediterranean species were found along the Israeli Mediterranean shore.

### Keywords

Lessepsian invasion; Israel; Greece; Egypt; Suez Canal; first records; range extensions

### Introduction

Biological invasions rank among the most serious threats to the world's biodiversity and constitute a major and pervasive element of global change (Galil 2007; Molnar et al. 2008; Occhipinti-Ambrogi and Galil 2010). The Mediterranean Sea, a hotspot of species richness and endemism (Bianchi and Morri 2000; Coll et al. 2010), is affected by the largest marine biological invasion—the so-called “Lessepsian invasion”—which followed the opening of the Suez Canal in 1869. The Suez Canal, a shallow artificial waterway connecting the Mediterranean and Indo-Pacific biogeographic provinces, is the most significant vector for introductions of non-indigenous species (NIS) to the basin, followed by shipping (Galil 2008; Galil et al. 2016; Zenetos 2017). Due to the geographic proximity and prevailing surface currents, the Levantine Sea in the southeastern Mediterranean is the region most

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affected by Lessepsian NIS (Galil 2008, 2017; Tzomos et al. 2012; Katsanevakis et al. 2014; Galil et al. 2016). Biological invasions have the potential to fundamentally alter the structure and functioning of recipient communities (Molnar et al. 2008; Ehrenfeld 2010; Fanelli et al. 2015); therefore, they not only affect local biodiversity, but may cause major ecological, economic and social damage (Galil 2007; Pyšek and Richardson 2010; Simberloff et al. 2013), particularly if NIS affect the provision of ecosystem services (Wallentinus and Nyberg 2007) or adversely affect human health (Mazza et al. 2014). Considering this and the rapid range expansions observed for many NIS originally restricted to the Levantine Basin (Galil 2009; Tzomos et al. 2012; Galil et al. 2016), the timely reporting of new findings is essential for better understanding the dynamics of the invasion and to recognize potential invasive species at an early stage, when mitigation measures are most effective (Crooks 2005; Simberloff et al. 2013).

As of 2016, 613 established and further 208 casual non-indigenous species representing most marine phyla have been recorded in the Mediterranean, with molluscs being the most diverse taxon (Galil 2009; Zenetos et al. 2017). Herein, we report new records and range extensions of non-indigenous molluscs of Indo-Pacific origin, further increasing the list of Lessepsian species in the Mediterranean Sea.

## Methods

The molluscs were collected along the Mediterranean coast of Israel, in southern Crete, Greece, and from a buoy originally moored at the entrance of the Suez Canal in Port Said, Egypt, but detached and stranded in 2014 near Shefayim, Israel, and subsequently transported to the Herzliya marina nearby (Captain M. Solomon and A. Tzindr, pers. comm.) (Figure 1).

In Israel, soft substrates were sampled in September 2016 and April 2017 off Ashqelon and Atlit (Figure 1, Table 1). Molluscan individuals and shells were recovered from bulk sediment samples taken at 10–41 m depth with a van Veen grab (36.5 × 31.8 cm) or boxcorer (25 × 25 cm) aboard RV “Mediterranean Explorer”. The sediment was sieved through a 0.5 mm mesh and the retained material fixed in ethanol. Additional molluscs were collected in spring 2018 from offshore reefs off Ashqelon, southern Israel, with a diver-operated airlift sampler equipped with a 0.5 mm mesh bag, and off Palmachim, central Israel, by snorkeling and overturning rocks (Figure 1).

In Crete, sampling took place off Plakias on the southern coast of the island in the framework of a survey of molluscan assemblages in *Posidonia oceanica* meadows. A diver-operated airlift sampler was used to collect on three replicate 1 m<sup>2</sup>-quadrats of *Posidonia* rhizomes at depths of 5, 10, 15 and 20 m, using 0.5 mm mesh bags.

The dry remains of fouling assemblages on the 13.5 m-long buoy in the Herzliya marina were scraped from 0.1 m<sup>2</sup> quadrats approximately every meter from the original water level to its lowermost end (originally 5.5 m water depth), plus a further quadrat in the hollow internal part of the buoy at ca. 5.5 m depth. Samples were sieved with a 0.5 mm mesh.

Molluscs from bulk samples were sorted and identified to the lowest possible taxonomic level. Detailed data for all sampling stations which yielded new records of non-indigenous species and georeferenced record data are provided in Table 1 and Supplementary material Table S1, respectively. Photographs were taken using a Zeiss SteREO Discovery.V20 stereomicroscope and stacked with Helicon Focus 6 (Helicon Soft Ltd., Roseau Valley, Dominica). Scanning electron microscopy (SEM) images were taken with a Fei Inspect S50 scanning electron microscope without coating. The illustrated specimens of the newly recorded non-indigenous species have been deposited as vouchers in the Naturhistorisches Museum Wien (NHMW). A subset of the specimens will be deposited at the Steinhardt Museum of Natural History (SMNH), Tel Aviv University.

#### *Abbreviations*

H: height; L: length (for bivalves); LV/s: left valve/s; RV/s: right valve/s; sh/s: empty shell/s (gastropod or complete bivalve); spcm/s: live collected specimen/s; v/s: valve/s; W: width (for gastropods).

## Results

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda Cox, 1960

Order unassigned

Family Cerithiidae J. Fleming, 1822

#### *Varicopeza pauxilla* (A. Adams, 1855)

(Figure 2)

**Material examined:** NG10 (21/09/2016, 3 shs); NG30 (20/09/2016, 37 spcms, 4 shs); SG20 (18/09/2016, 7 spcms; 27/04/2017, 2 spcms); SG30 (27/04/2017, 3 spcms); SG40 (18/09/2016, 88 spcms, 1 sh; 27/04/2017, 1 sh).

**Voucher specimens:** NHMW-MO-112644: NG30, 20/09/2016, 1 spcm, H 5.9 mm, W 2.3 mm (Figure 2A–C, H); NHMW-MO-112645: locality as previous, 1 juvenile sh, H 1.6 mm, W 0.9 mm (Figure 2D); NHMW-MO-112646: SG40, 27/04/2017, 1 sh, H 8.6 mm, W 2.9 mm (Figure 2E–G, I).

**Remarks:** *Varicopeza pauxilla* has a slender, rather straight-sided, turriiform shell with a strong sculpture consisting of spiral cords and slightly opisthocline axial ribs, forming tubercles at the intersections. The colour is variable, ranging from yellowish-white to brown (Figure 2), sometimes with a darker spiral band. A strong varix is present opposite the outer lip in adult specimens (Figure 2A, C, E and G; see also Houbrick 1980). In the Mediterranean, *V. pauxilla* may be confused with the invasive Lessepsian cerithiid *Rhinoclavis kochi*, particularly when dealing with juvenile specimens. The latter, however, lacks the wide sinus/posterior exhalant channel in the outer lip of adult *Varicopeza pauxilla*

(Figure 2H–I) as well as the prominent notch at the protoconch/teleoconch transition (Figure 2D). Further, the protoconch of *V. pauxilla* is smooth with only a faint spiral keel visible at high magnification, while two keels are present in *R. kochi*.

*Varicopeza pauxilla* has an Indo-West Pacific distribution, inhabiting soft substrates at continental shelf and upper slope depths (Houbrick 1980). In the northern Red Sea, it has been reported from the Gulf of Aqaba from 40–402 m depth, including locations off Elat (Houbrick 1980; Edelman-Furstenberg and Faershtein 2010), and from the Bay of Safaga, at the latter location mainly from mud at 39 m depth (Janssen et al. 2011). In August 2016, specimens were found along the Turkish Levantine coast at depths of 18–55 m, comprising the first record for the Mediterranean Sea (Öztürk et al. 2017). Herein, we extend its known distribution to the Israeli coast, where it was common on soft substrates at 30–40 m depth. The species was particularly abundant in samples collected in September 2016 at 41 m depth off Ashqelon, contributing 73.3% of living molluscan individuals. According to Houbrick (1980), *V. pauxilla* is a microphageous detritivore and perhaps also a filter feeder. It has a planktonic developmental strategy (Houbrick 1993). The numerous specimens in various growth stages and already wide distribution in the Levantine Sea suggest it is a well-established species in the eastern Mediterranean.

Family Triphoridae Gray, 1847

***Viriola* cf. *bayani* Jousseume, 1884**

(Figure 3)

**Material examined:** Rh10 (17/09/2017, 1 spcm); Rh20 (14/09/2017, 1 spcm); Palmachim, Israel, under rocks, –3 m (26/04/2018, 3 spcms); MNHN IM-2000-1388, New Caledonia (syntype, 1 sh).

**Voucher specimens:** NHMW-MO-112647: Rh10, 17/09/2017, 1 spcm, H 14.7 mm, W 2.8 mm (Figure 3).

**Remarks:** This striking shell cannot be misidentified with any native Mediterranean triphorid. It belongs to a taxonomically difficult group of *Viriola* species whose validity is still uncertain, such as *V. corrugata* (Hinds, 1843), *V. senafirensis* (Sturany, 1903) and *V. tricincta* (Dunker, 1882) (Albano and Bakker 2016; Albano et al. 2017). The Mediterranean specimens are closely similar to *V. bayani* in the colour pattern of white fletches on brown background and in the sculpture of obsolete orthocline axial riblets between the main spiral cords, a conclusion also shared by Angelidis and Polyzoulis (2018). *Viriola corrugata* and *V. tricincta* have usually stronger and prosocline axial ribs. *V. senafirensis* can be distinguished by its compressed pyriform shape.

Empty shells have been previously recorded as *V. corrugata* from Karpathos, Greece (Micali et al. 2017). Living individuals were recorded as *Viriola* sp. [cf. *corrugata*] from Iztuzu, western Turkey (Stamouli et al. 2017) but they clearly belong to this species. Very recently, *V. cf. bayani* has been reported also from Astypalaia, Greece, where several fresh dead specimens (one with operculum) were trawled in August 2017 at 35–50 m depth and two

shells were recovered from bioclastic sand sampled at 6–8 m depth in August 2016 (Angelidis and Polyzoulis 2018). This is the first record of living individuals for Greek and Israeli waters and confirms the species establishment in the eastern Mediterranean Sea and the Suez Canal as likely introduction vector. Due to the poor taxonomic knowledge of the genus, the native range is not known precisely but it is probably a widespread tropical Indo-Pacific species living in the shallow subtidal.

Subclass Heterobranchia Burmeister, 1837

Order Nudibranchia Cuvier, 1817

Family Facelinidae Bergh, 1889

***Phidiana militaris* (Alder and Hancock, 1864)**

(Figure 4)

**Material examined:** S12 (30/04/2018, 1 spcm, length ca. 10 mm).

**Remarks:** This nudibranch was found for the first time in the Mediterranean Sea in October 2016 in Haifa Bay, Israel (Rothman et al. 2017; see this paper also for diagnostic features of this species). This finding off Ashqelon extends its known range to southern Israel, suggesting that the Suez Canal may be the vector of introduction. Although this species has not yet been reported from the Red Sea, several nudibranch species were described from the Red Sea many decades after they had been described elsewhere in the Indo-West Pacific (Rothman et al. 2017).

Class Bivalvia Linnaeus, 1758

Subclass Pteriomorpha Beurlen, 1944

Order Mytilida Férussac, 1822

Family Mytilidae Rafinesque, 1815

***Gregariella cf. ehrenbergi* (Issel, 1869)**

(Figure 5)

**Material examined:** Port Said, Egypt, on a detached buoy stranded in 2014 in Shefayim, central coast of Israel, originally 0 to –5.5 m (sampled on 28/09/2016, 62 spcms, 1 sh, 32 vs).

**Voucher specimens:** NHMW-MO-112648: buoy stranded in Shefayim, Israel (see above), water level, 28/09/2016, 1 spcm collected with dried soft body, L 5.6 mm, H 2.9 mm (Figure 5A–B); NHMW-MO-112649: locality as previous, but –2 m, 1 spcm collected with dried soft body, L 8.8 mm, H 3.2 mm (Figure 5E–F).

**Material illustrated for comparison:** *Gregariella semigranata* (Reeve, 1858): PGA private coll. 1888, Wied-iz-Zurrieq, Malta, in sediment, -35 m, 03/07/1994, 1 RV (Figure 5C) and 1 LV (Figure 5D).

**Remarks:** This *Gregariella* was most abundant on the buoy at the water level, where it probably exploited the barnacle mat to settle, at 5.5 m depth on the ballast at the base of the buoy, where a mat of oysters formed another suitable substrate, and inside the buoy. Indeed, *Gregariella* often nest in crevices, empty date mussel burrows and similar microhabitats (Morton 1995).

This species differs from the native *G. semigranata* (Reeve, 1858) (Figure 5C–D) in its generally larger size, more inflated shell, more regularly oval profile, less acute anterior and posterior profiles, crenulations on the posterior margin that extend much deeper into the shell, and darker colour (Figure 5A–B, E–F). It can be readily distinguished from the native *G. petagnae* (Scacchi, 1832) by the branching periostracal bristles and its smaller size.

The taxonomy of genus *Gregariella* in the Indo-Pacific is unsettled (Oliver 1992) and we consider the attribution tentative until a revision is undertaken. Our specimens resemble material from Kuwait identified as *G. ehrenbergi* (G. Oliver, pers. comm.). The type specimen of *G. ehrenbergi* is stored in the Museo Civico di Storia Naturale “G. Doria” in Genoa, Italy. Two valves are present (likely belonging to different specimens) but unfortunately, they are badly affected by the Byne’s disease and most diagnostic characters cannot be observed any more. Moreover, these specimens are very small (the best-preserved one is just 3 mm long) and likely juvenile, thus the drawing by Issel (1869, Plate I, Figure 12) is of little assistance. Our specimens resemble *G. simplicifilis* Barnard, 1964 as illustrated by Bosch et al. (1995), though the latter lacks the branching periostracal bristles.

*Gregariella ehrenbergi* has not been recorded from the Mediterranean Sea but is known from the Suez Canal (Hoenselaar and Dekker 1998). The material is stored in Naturalis in Leiden, the Netherlands, but was unfortunately inaccessible during the preparation of this manuscript due to the ongoing renovation of the museum.

Subclass Heterodonta Neumayr, 1884

Order Lucinida Gray, 1854

Family Lucinidae J. Fleming, 1828

### **Lucinidae sp.**

(Figure 6)

**Material examined:** NG10 (21/09/2016, 2 shs, 19 vs); SG10 (19/09/2016, 19 vs; 27/04/2017, 1 v).

**Voucher specimens:** NHMW-MO-112650: SG10, 27/04/2017, 1 LV, L 4.6 mm, H 4.4 mm (Figure 6A, D, G, I); NHMW-MO-112651: SG10, 19/09/2016, 2 RVs, L 4.9 mm, H 4.7 mm (Figure 6B, E, H) and L 8.2 mm, H 7.9 mm (Figure 6C, F).

**Material illustrated for comparison:** *Loripes orbiculatus* Poli, 1791: University of Vienna, Dept. of Palaeontology collection: Staranzano, northeast Italy, outer tidal flat, –0.3–0.35 m, 10/1999, 1 RV (Figure 6J, L); PGA private coll. 1682: St. Julian's Bay, Malta, sand, –15 m, 29/06/1994, 1 sh (RV illustrated) (Figure 6K, M–N).

**Remarks:** We were unable to confidently assign this taxon to any species, but its shell morphology distinguishes it from all known Mediterranean Lucinidae. The alien status of this taxon could therefore not be clarified. The species is characterized by solid, rather tumid, subcircular valves, semi-translucent and waxy white in color (Figure 6). The outer surface is sculptured by several weakly-defined radial ribs which are also part of the internal shell structure and often more obsolete in larger specimens, as well as much finer, very densely spaced commarginal striae, most prominent in the dorsal part of the shell. Irregularly spaced growth marks are visible on the shell surface. The ligament is internal and rather short. Right valve with a single cardinal tooth (Figure 6H), left valve with two cardinal teeth (Figure 6G). The lateral teeth are weak in both valves, the inner shell margin is denticulate (Figure 6I). The characters of our lucinid are similar to *Chavania erythraea* (Issel, 1869), a species present also in the Gulf of Suez, however, the concentric sculpture of our shells is weaker than in illustrations of *C. erythraea*, and a posterior sulcus is not evident (e.g. Glover and Taylor 2001). Our unidentified lucinid resembles the Mediterranean *Loripes orbiculatus* Poli, 1791 (Figure 6J–N, specimens of similar size as the illustrated unidentified Lucinidae), particularly larger specimens with less obvious radial sculpture (Figure 6C, F). *L. orbiculatus*, however, lacks radial sculpture (although very fine radial striae might be present (Glover and Taylor 2001)) and the distinct marginal denticulation (Figure 6I – Lucinidae sp. – vs. Figure 6N – *Loripes orbiculatus*).

Genus *Pillucina* Pilsbry, 1921

***Pillucina vietnamica* Zorina, 1978**

(Figure 7)

**Material examined:** SG10 (19/09/2016: 1 spcm, 1 v); Abu Dhabi, United Arab Emirates, fine sediment on cap rock, seagrass (*Halophila ovalis*), –11 m (09/04/1999, 1 sh, 1 v)

**Voucher specimens:** NHMW-MO-112653: SG10, 19/09/2016, 1 RV, L 4.0 mm, H 3.7 mm (Figure 7A–B, D–E); NHMW-MO-112652: locality as previous, 1 spcm, L 2.8 mm, H 2.6 mm (Figure 7C, F).

**Material illustrated for comparison:** *Pillucina vietnamica* Zorina, 1978: University of Vienna, Dept. of Palaeontology collection: Abu Dhabi, United Arab Emirates, fine sediment on cap rock, seagrass (*H. ovalis*), –11 m, 09/04/1999, 1 LV (Figure 7G, J) and 1 sh (Figure 7H–I, K–L).

**Remarks:** The surface sculpture consisting of radial ribs most prominent in the anterior and posterior part of the shell, crossed by commarginal ribs, as well as the scalloped shell margins (Figure 7) distinguish this species at first glance from any Mediterranean lucinid. *P. vietnamica* has a wide geographic distribution, ranging from the Red Sea (here often referred

to as *P. fischeriana* (Issel, 1869), an unavailable name) to China and southern Queensland, Australia (Glover and Taylor 2001). It is reported to be common in the Gulf of Suez (Rusmore-Villaume 2008) and also occurs in the Great Bitter Lake (Hoenselaar and Dekker 1998). Here, we report the first Mediterranean record.

Order Venerida Gray, 1854

Family Kelliellidae P. Fischer, 1887

***Alveinus miliaceus* (Issel, 1869)**

(Figure 8)

**Material examined:** NG30 (20/09/2016, 1 sh, 1 v); SG10 (19/09/2016, 1 sh, 4 vs); SG20 (18/09/2016: 6 spcms, 5 shs, 14 vs; 27/04/2017, 1 spcm); SG30 (18/09/2016, 2 vs).

**Voucher specimens:** NHMW-MO-112655: SG20, 18/09/2016, 1 RV, L 0.9 mm, H 0.8 mm (Figure 8A, D, G) and 1 LV, L 0.9 mm, H 0.9 mm (Figure 8B, E, H); NHMW-MO-112654: SG20, 27/04/2017, 1 spcm, L 0.9 mm, H 1.0 mm (Figure 8C, F).

**Remarks:** This minute bivalve reaches a maximum shell size of only 2 mm (Oliver and Zuschin 2000), but may even be much smaller (e.g. specimens in Figure 8). It is a poorly known species, originally described from the Gulf of Suez (Issel 1869), and also known from the Bay of Safaga (Egypt) in the northern Red Sea and Oman (Oliver and Zuschin 2000). Here, we report the first record of *Alveinus miliaceus* for the Mediterranean Sea. The hinge (Figure 8G, H) is characteristic and allows a distinction from juveniles of other species, particularly the s-shaped cardinal complex of the left valve (Oliver and Zuschin 2000, Figures 3c, 4b, 7b; Figure 8H this study) makes it readily recognizable.

## Discussion

Since the opening of the Suez Canal, hundreds of Indo-Pacific species have successfully established populations in the Mediterranean Sea, and several new NIS are reported each year (Galil 2009; Zenetos et al. 2012; Galil et al. 2016; Zenetos 2017). Our findings of *Pillucina vietnamica* and *Alveinus miliaceus* in the Mediterranean meet the criteria for “records of confirmed alien species” as proposed by Marchini et al. (2015): i) the species must be unambiguously identified, ii) the native distribution is known, iii) the species has been introduced outside its natural distribution range by direct or indirect human agency, and iv) specimens were found in environments open to the sea. While *P. vietnamica* currently seems to be very rare, several living individuals of *A. miliaceus* from Ashqelon and the presence of shells also in sediments from northern Israel (Atlit) suggest that the latter species might have already established viable populations along a large stretch of the Israeli coast. *A. miliaceus* may represent a recently introduced NIS; however, a significant detection time lag (see e.g. Crooks 2005; Albano et al. 2018) could also be involved: due to its minute size, the species may have been missed in many benthic surveys using mesh sizes too large to retain it, or has been confused with juveniles or post-larval stages of other bivalves. Since the native ranges of *P. vietnamica* and *A. miliaceus* both include the Gulf of



Suez (and, for *P. vietnamica*, even the Great Bitter Lake (Hoenselaar and Dekker 1998)), it is likely that these species have entered the Levantine Sea via the Suez Canal, representing “Lessepsian migrants” in the strict sense (Por 1978; Zenetos et al. 2012). The Canal also seems the most likely vector of introduction for *Varicopeza pauxilla*, *Viriola* cf. *bayani*, *Phidiana militaris* and *Gregariella* cf. *ehrenbergi* considering that the new records here reported fill a geographical gap along the expected trajectory of spread from the Suez Canal into the eastern Mediterranean, following the prevalent counter clock-wise currents.

Once introduced outside their natural range, the fate of NIS may differ markedly between species, ranging from extinction to establishing viable populations and range expansion (e.g. Blackburn et al. 2011). The gastropods *Varicopeza pauxilla* and *Viriola* cf. *bayani* belong to the latter group: both species have first been collected in the Mediterranean in 2016, but our findings suggest that the species are widely distributed in its eastern basin. Both species are relatively large (to 1 cm) and have no Mediterranean congeners; considering the recent benthic surveys conducted in the Levantine Sea (e.g. Bakir et al. 2012; Çinar et al. 2012; Öztürk et al. 2015; Guarnieri et al. 2017) it seems unlikely, at least for the soft-bottom dwelling *V. pauxilla*, that they have been overlooked for a significant amount of time.

In the framework of our surveys in Israel, we found numerous valves of the unidentified lucinid bivalve in shelly death assemblages from sands at approximately 10 m depth. Due to the lack of species- and genus-level identifications, we were unable to assess the status of this species. However, considering the commonness of shells in the environment, their rather large (up to approx. 1 cm) size, and occurrence in very shallow water, we conjecture that the shells may be evidence for a newly introduced NIS rather than an undescribed native lucinid. We believe that publishing such records is nonetheless important pending the full identification of the species in order to raise awareness on their presence, especially when, as in this case, it is very similar to a native species.

Undoubtedly, the Suez Canal is the most significant vector of NIS introductions to the Mediterranean (Galil 2009), and major concerns were raised about the ecological consequences of the recent doubling of the Canal (Galil et al. 2015). While several studies highlighted the fast pace of NIS introductions to the eastern Mediterranean (Galil 2008; Zenetos et al. 2012; Guarnieri et al. 2017), it has been suggested that the introduction rate of new Lessepsian NIS has recently been on the decline (Zenetos et al. 2017). Our findings suggest caution in this respect as the invasion is evidently ongoing and detection time lags may conceal the actual introduction rates.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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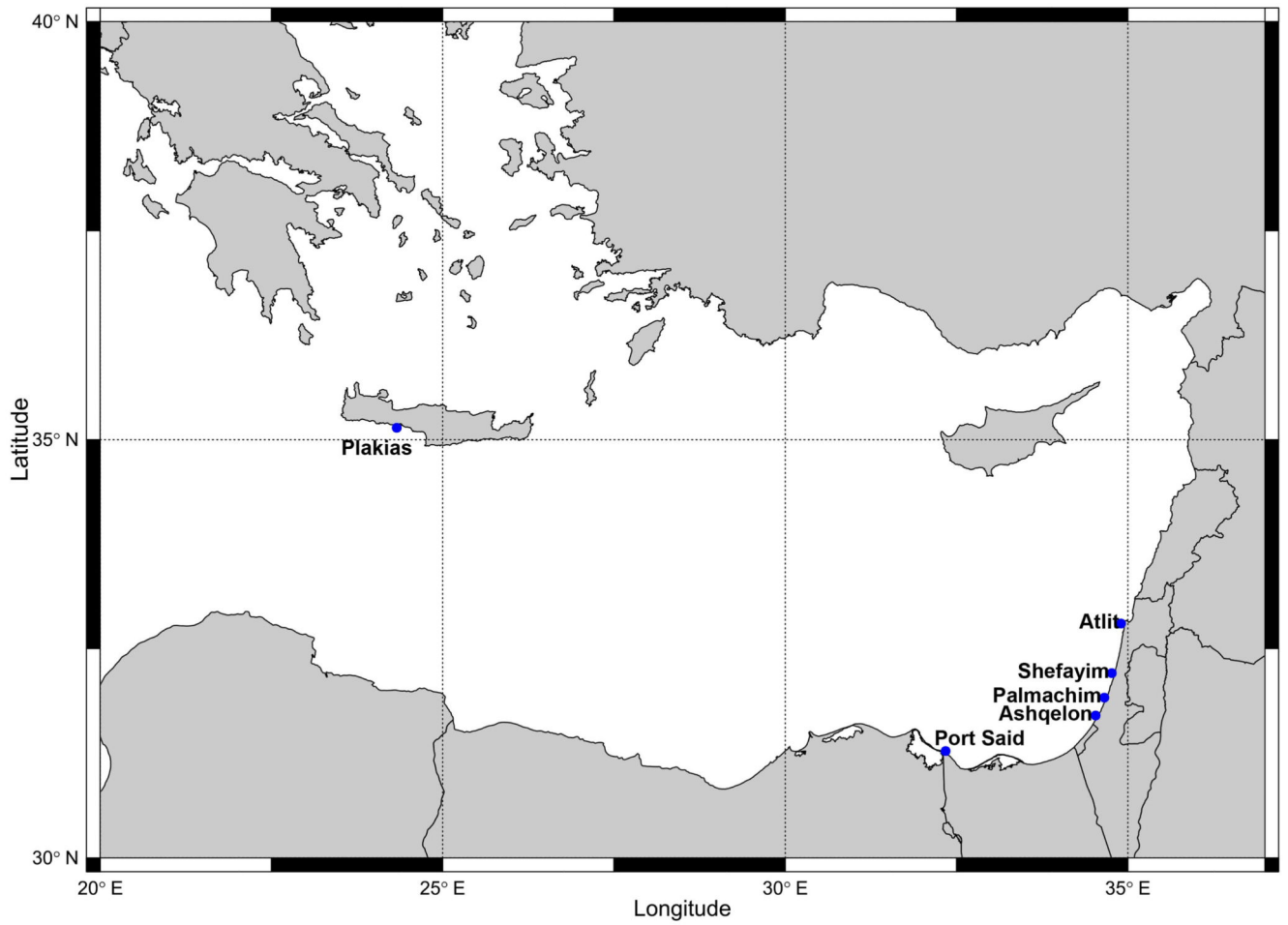
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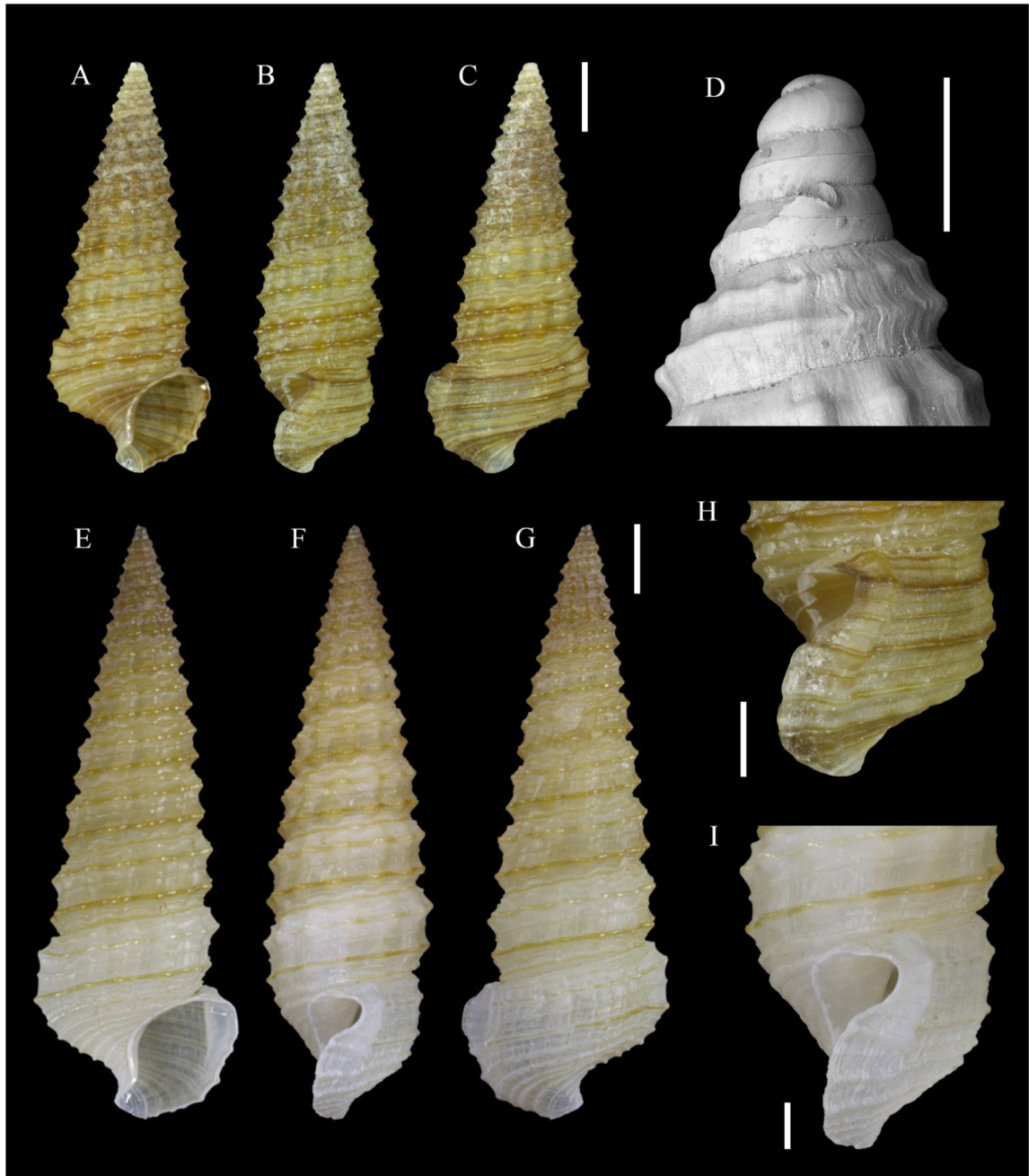
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**Figure 1.** Map of the eastern Mediterranean showing the sampling localities (see Table 1 for details).



**Figure 2.**

*Varicopeza pauxilla* (A. Adams, 1855). A–C, H. NHMW-MO-112644, NG30, N of Atlit, northern Israel, sand, –30 m, 20/09/2016, front (A), side (B) and back (C) view, side view of aperture (H). D. NHMW-MO-112645, locality as previous, protoconch. E–G, I. NHMW-MO-112646, SG40, off Ashqelon, southern Israel, mud, –41 m, 27/04/2017, front (E), side (F) and back (G) view, side view of aperture (I). Scale bars: 1 mm (A–C and E–G), 0.2 mm (D), 0.5 mm (H–I). Photo credit: J. Steger.

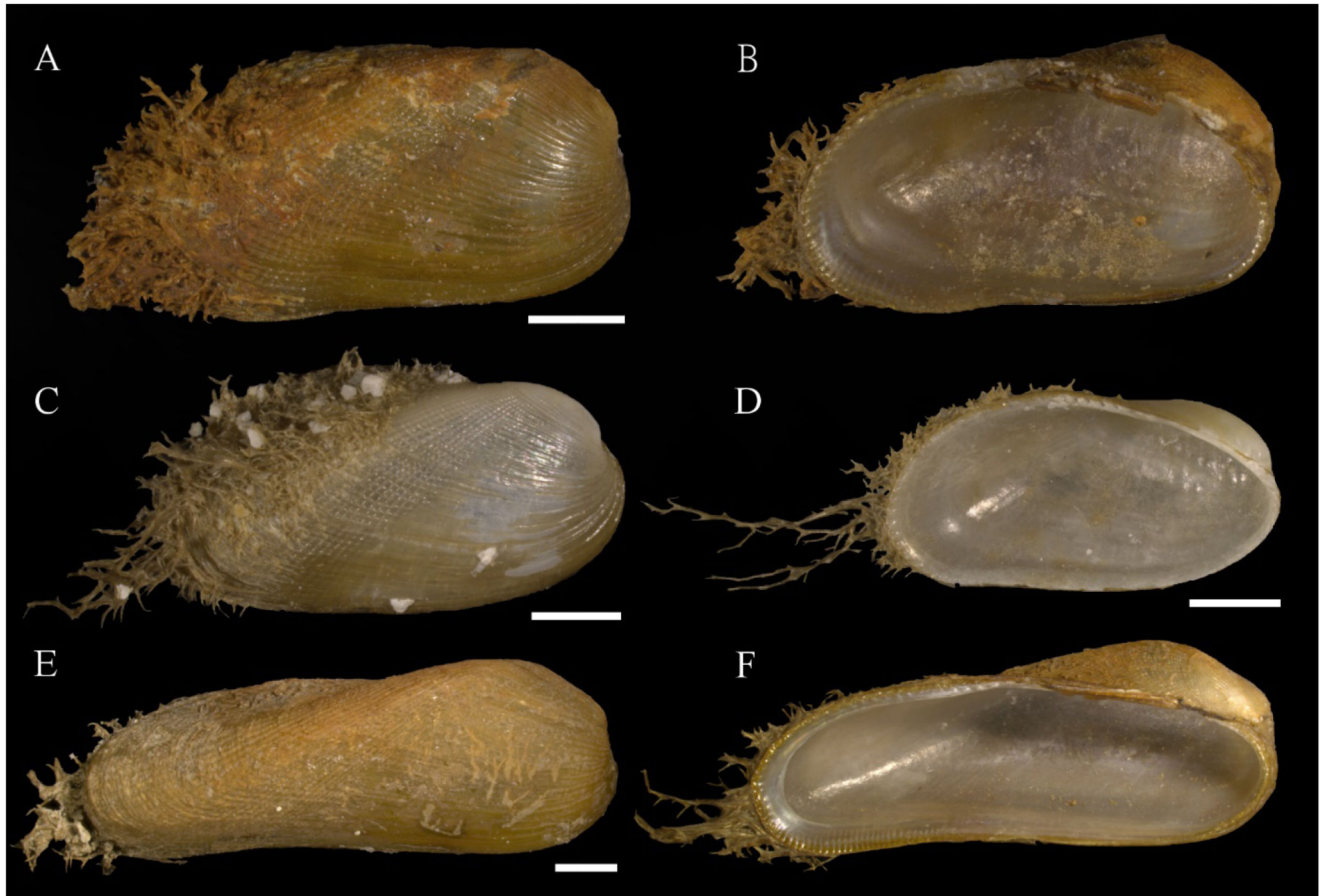


**Figure 3.**  
*Viriola* cf. *bayani* Jousseume, 1884. NHMW-MO-112647, Rh10, Plakias, Crete, Greece, among rhizomes of *Posidonia oceanica*, -10 m, 17/09/2017, front (A) and side (B) view. Scale bar: 2 mm. Photo credit: P.G. Albano.



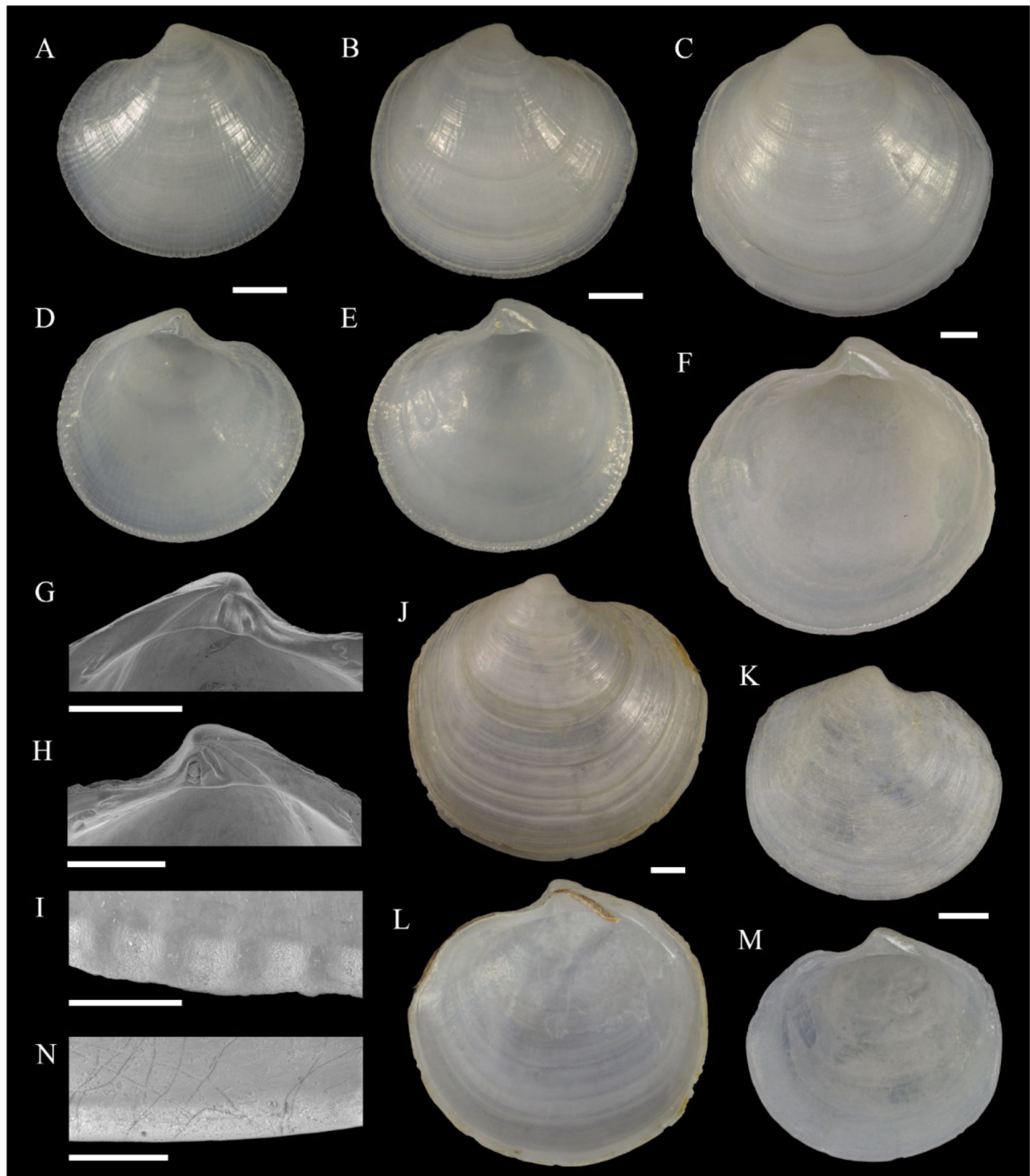
**Figure 4.**  
*Phidiana militaris* (Alder and Hancock, 1864). S12, off Ashqelon, Israel, offshore rocky reef, -12 m, 30/04/2018. Photo credit: P.G. Albano.





**Figure 5.**

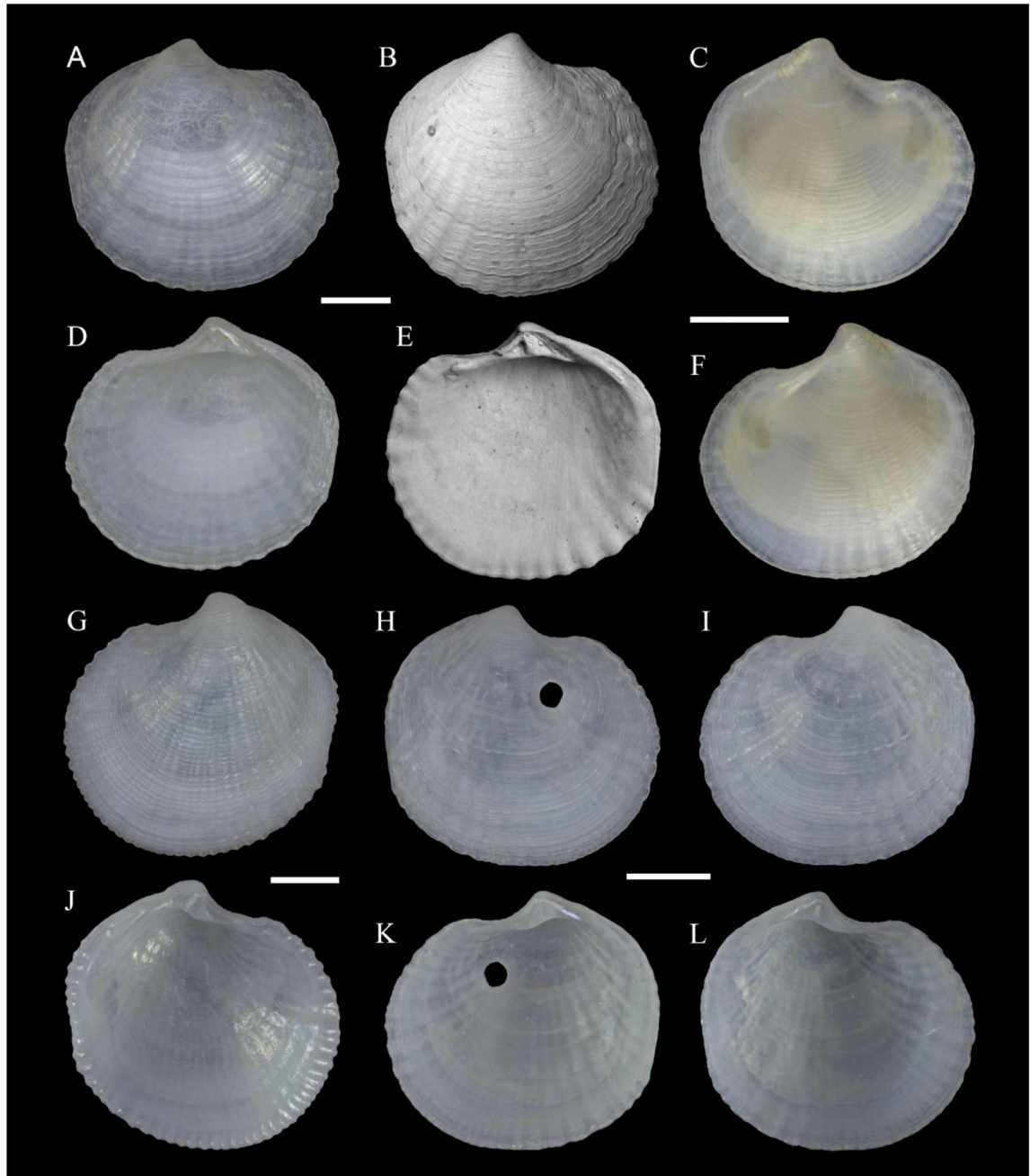
A–B. *Gregariella cf. ehrenbergi* (Issel, 1869), NHMW-MO-112648, buoy stranded in Shefayim, Israel (see text), water level, sampled on 28/09/2016, exterior RV (A), interior LV (B). C–D. *Gregariella semigranata* (Reeve, 1858). C. RV, PGA private coll. 1888, Wied-iz-Zurrieq, Malta, in sediment, -35 m, 03/07/1994, exterior. D. LV, as previous, interior. E–F. *Gregariella cf. ehrenbergi* (Issel, 1869), elongated form, NHMW-MO-112649, locality as A–B, but -2 m, exterior RV (E), interior LV (F). Scale bars: 1 mm. Photo credit: D. Di Franco, A. Ivki and P.G. Albano.



**Figure 6.**

A–I. *Lucinidae* sp. A, D, G, I. LV, NHMW-MO-112650, SG10, off Ashqelon, southern Israel, sand, -11 m, 27/04/2017, exterior (A), interior (D), hinge (G) and detail of ventral interior shell margin (I). B, E, H. RV, NHMW-MO-112651, locality as previous, but 19/09/2016, exterior (B), interior (E) and hinge (H). C, F. RV, as previous, but different valve, exterior (C) and interior (F). J–N. *Loripes orbiculatus* Poli, 1791. J, L. RV, University of Vienna, Dept. of Palaeontology collection, Staranzano, northeast Italy, outer tidal flat, -0.3–0.35 m, 10/1999, exterior (J) and interior (L). K, M–N. RV, PGA private coll. 1682, St.

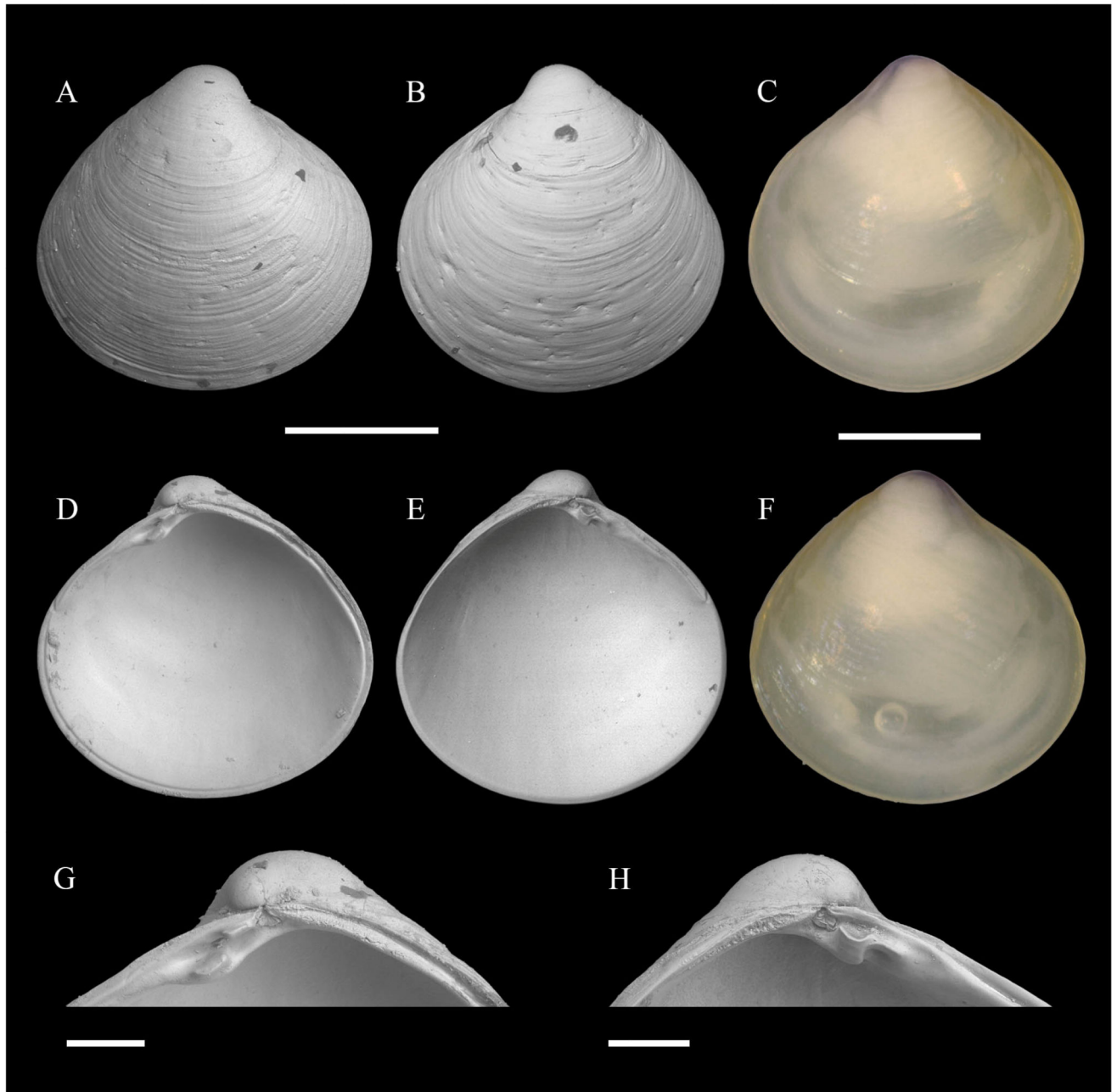
Julian's Bay, Malta, sand, -15 m, 29/06/1994, exterior (K), interior (M) and detail of ventral interior shell margin (irregular linear markings are traces of microbioerosion). Scale bars: 1 mm (A-H, J-M), 0.2 mm (I, N). Photo credit: J. Steger.



**Figure 7.**

*Pillucina vietnamica* Zorina, 1978. A–B, D–E. RV, NHMW-MO-112653, SG10, off Ashqelon, southern Israel, sand, –11 m, 19/09/2016, exterior (A, B) and interior (D, E); the slight anterior-posterior compression of images B and E compared to A and D is an artifact of very low magnification SEM-imaging. C, F. NHMW-MO-112652, locality as previous, exterior RV (C) and LV (F). G, J. LV, University of Vienna, Dept. of Palaeontology collection, Abu Dhabi, United Arab Emirates, fine sediment on cap rock, seagrass (*Halophila ovalis*), –11 m, 09/04/1999, exterior (G) and interior (J). H–I, K–L. As previous,

but sh, exterior RV (H) and LV (I), interior RV (K) and LV (L). Scale bars: 1 mm. Photo credit: J. Steger.



**Figure 8.**

*Alveinus miliaceus* (Issel, 1869). A, D, G. RV, NHMW-MO-112655, SG20, off Ashqelon, southern Israel, sand, -21 m, 18/09/2016, exterior (A), interior (D) and hinge (G). B, E, H. LV, as previous, exterior (B), interior (E) and hinge (H). C, F. NHMW-MO-112654, locality as previous, but 27/04/2017, exterior LV (C) and RV (F). Scale bars: 0.4 mm (A–F), 0.1 mm (G–H). Photo credit: J. Steger and P.G. Albano.

**Table 1**  
**List of stations (coordinates according to datum WGS84).**

Sample	Locality	Latitude	Longitude	Depth [m]	Substrate
Rh10	Greece, Crete, Plakias	35.1793	24.3956	10	<i>Posidonia oceanica</i> rhizomes
Rh20	Greece, Crete, Plakias	35.1793	24.3956	20	<i>Posidonia oceanica</i> rhizomes
NG10	Israel, N of Atlit	32.7820	34.9466	10	sand
NG30	Israel, N of Atlit	32.7422	34.9181	30	sand
S12	Israel, Ashqelon	31.6868	34.5516	12	offshore rocky reef
SG10	Israel, Ashqelon	31.6953	34.5588	11	sand
SG20	Israel, Ashqelon	31.7002	34.5498	21	sand
SG30	Israel, Ashqelon	31.7100	34.5406	30	muddy sand
SG40	Israel, Ashqelon	31.7487	34.4960	41	mud
–	Israel, Palmachim	31.9272	34.6964	3	rocks
–	originally Egypt, Port Said (but buoy detached and stranded near Shefayim, central Israel)	31.28	32.37	0–5.5	buoy