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doi: 10.12681/mms.36181

Short Communication

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
www.hcmr.gr
DOI: https://doi.org/10.12681/mms.36181

Re-appearance of the gregarious gastropod *Dendropoma anguliferum* (Vermetidae) on abrasion platforms in the Carmel coast (Northern Israel)

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Contributing Editor: Serge GOFAS

Received: 13 December 2023; Accepted: 28 April 2024; Published online: 12 June 2024

Abstract

After three decades of sharp decline in the *Dendropoma* populations in Israel and genuine concern for their extinction, we affirm the re-appearance of the gregarious gastropod *Dendropoma anguliferum* on abrasion platforms in the Carmel coast (Northern Israel). A visual survey conducted during December 2020 and February 2021 along the rims of abrasion platforms in the Carmel coast area revealed 195 living clusters of live *D. anguliferum*. DNA sequences from tissue samples unambiguously supported the identity of our material as the Levantine Sea member *D. anguliferum* of the *Dendropoma petraeum* species complex, with 99-100% identity to sequences obtained from *D. anguliferum* from Southern Lebanon.

Keywords: *Dendropoma*; Abrasion platform; Mediterranean Sea; Israel.

Introduction

Vermetid reefs are bioconstructions commonly found in the Southern Mediterranean Sea (Chemello & Silenzi, 2011). A typical vermetid biogenic reef is the outcome of complex synergistic building activity by gregarious vermetid gastropods of the genus *Dendropoma* and encrusting red algae *Neogoniolithon brassica-florida* (Harvey) Setchell and Mason, 1943. Other species such as the vermetid *Vermetus (V.) triquetrus* A. Bivona, 1832 and other algae species may also support *Dendropoma* spp. and *N. brassica-florida* in these processes (Chemello & Silenzi, 2011).

Recent studies regarding genetic diversity and reproductive traits (Calvo *et al.*, 2009; Templado *et al.*, 2016; Usvyatsov & Galil, 2012) have shown that *D. petraeum* (Monterosato, 1884), previously considered a single species endemic to the warmest parts of the Mediterranean Sea, is in fact a complex of at least four cryptic species with a clear west-east geographic separation coinciding with the sub-basins of the Mediterranean Sea (Calvo *et al.*, 2009). The newly-detected genetic differences led Templado *et al.*, (2016) to an 'a posteriori' search for phenotypic characters that may enable the differentiation of the cryptic species and to formally describe and name them. These efforts yielded the designation of three *Dendropoma* species: *Dendropoma lebeche* Templado, Richter & Calvo, 2016 (Western Mediterranean clade), *Dendropoma cristatum* (Biondi, 1857) (Sicilian-Tyrrhenian clade) and *Dendropoma anguliferum* (Monterosato, 1878) (Levantine Sea clade) while a fourth putative species (Ionian-Aegean clade) still remains pending description (Templado *et al.*, 2016).

Along the Israeli Mediterranean coast, the abrasion platforms are one of the most significant and productive rocky habitats. These are made up of horizontal and sub horizontal ledges that can be continuous with the coastal "kurkar" ridge or detached from it. The latter form, may appear as broad platforms surrounded by water found dozens of meters from shore (Lipkin & Safriel, 1971). Abrasion platforms were recorded from Rosh Hanikra in the northern part of the Israeli coast, to Michmoret and Jaffa in the central coast and to Palmachim, further south (Safriel, 1966). One of the most noticeable features of the abrasion platforms are the elevated rims that surround them. These rims are actually the major biogenic portion of each platform, constructed by shells of the gregarious vermetids of the genus *Dendropoma* and cemented to the substrate by encrusting red algae (Safriel, 1966). The contorted shells of *D. anguliferum* snails are closely cemented to each other, forming a structure of densely packed interstices which features a combination of hardness and porosity (Ben Eliahu & Safriel, 1982). Each generation grows on top of the previous one and therefore the surface of the bioconstruction comprises both live (occupied) and dead (empty) gastropod shells. The actively developing rims increase the three-dimensional complexity of the platform and enable water to remain on the platform, thus modifying the physical and ecological features of this biogenic habitat and supporting greater ecological diversity (Chemello & Silenzi, 2011; Galil, 2013; La-Marca *et al.*, 2018). The contribution of *Dendropoma* spp. to these changes is so profound that this genus was labeled a biogenic engineer (see Templado *et al.*, 2016; La Marca *et al.*, 2018). Safriel (1966) reported that along the central coast of Israel the raised rims of the platforms are coated by *D. anguliferum* shells but that the majority of these are empty, and living individuals are confined to patches clear of sea-weeds. These patches are mainly found around burrows inhabited by the brachyuran crab *Pachygrapsus* that feeds on the surrounding algae. Lipkin & Safriel (1971) reported that during the 1960s and 1970s living patches of *Dendropoma* spp. constituted 3% of the raised rim areas.

During the 1990s, *D. anguliferum* was abundant at many of the vermetid reef sites along the coast, though some rim degradation was reported (Rilov, 2016). In the early 2000s *D. anguliferum* was still present (Usvyatsov & Galil, 2012) but during 2012 extreme reduction of the population was recorded in surveys conducted at several sites along the coast (Akhziv-Rosh Hanikra, Shiqmona and Atlit) (Galil, 2013). Fine *et al.*, (2017) surveyed six sites along the Israeli Mediterranean coast (including the area of the present survey i.e., Habonim) and reported the extinction of *D. anguliferum* in all the sites. Rilov *et al.*, (2020) monitored the spatiotemporal community dynamics of vermetid reefs at 11 sites (two of which are within the boundaries of the present study) along the Israeli coast for a period of 8 years (2009-2017) and reported the extreme rarity of *D. anguliferum* throughout the study period with only some evidence for minor recovery in Achziv during 2013-4 and occasional sightings of several very small living *D. anguliferum* patches in Habonim and Shiqmona. Furthermore, Badreddine *et al* (2019) reported sharp declines in *D. anguliferum* populations along the Lebanese coastline with living individuals documented only at one site (Nakoura) out of five.

The causes for the local mass mortality of the *Dendropoma* population in Israel as well as other countries are not clear. This decline was hypothesized to be related to climate change (Rilov, 2016, Rilov *et al.*, 2020) and other anthropogenic factors such as coastal habitat degradation, increasing human activities (Badreddine *et al.*, 2019), pollution (Di Franco *et al.*, 2011), ocean acidification (Badreddine *et al.*, 2019) as well as to competition with invasive species as suggested by Milazzo *et al.* (2016). The rarity of live specimens of *D. anguliferum* alarmed the scientific community in Israel and a special consortium was convened to deal with the implications of this phenomenon, and to discuss its possible causes and optional ways to promote recovery (Brokovich *et al.*, 2015).

The aim of the present study was to collect new data on the presence/absence of *Dendropoma* sp. clusters in a pre-defined area (Carmel coast) along the Israeli Mediterranean coastline, an area which previously had served as a habitat for these vermetid snails.

Materials and Methods

Visual survey: The visual survey was the initiative of Israel's Nature and Parks Authority and was conducted in Habonim Nature reserve and 1 Km south and north from its borders (Carmel Coast area) during December 2020 and February 2021 (Fig. 1). The southern point of the survey was the detached platform across from the Nahsholim hotel (32.61421° N, 34.91537° E) and the northern point was the platform of Tel Nami (1 km south of Atlit, 32.66090° N, 34.92550° E). The outer rims of the abrasion platforms situated along the coastline (of the above-mentioned area) were inspected continuously for the presence of *Dendropoma* sp. clusters. The southern part of the surveyed area (indicated as "S" on Fig. 1) included a continuous transect of 3792 meters. The middle part of the surveyed area (indicated as "M" on Fig. 1) included a continuous transect of 1600 meters and the northern part of the surveyed area (indicated as "N" on Fig. 1) included a continuous transect of 728 meters. All the living clusters which were encountered, were photographed in scale (see Fig. S1). The clusters were documented, and were classified as 'living' after the detection of individuals in which the operculum was present (either on site or later in the inspection of the photographs). The total number of living clusters was recorded for each of the locations.

Sampling: Ten samples were collected for molecular analysis on the 9^{th} and 16^{th} of November 2021 using a hammer and chisel. A 2X2 cm piece of the *Dendropoma* spp. patch was scraped, and frozen at -20°C in marked vials. Sample names and locations are outlined in Table S1. Prior to DNA extraction, samples were thawed and the snail's tissue was carefully separated from the calcareous tubes with the aid of magnifying glass and tweezers.

DNA Extraction and sequencing

Total DNA was extracted from the tissue using the PowerSoil DNA Isolation Kit (QIAGEN, Germany), following the manufacturer's protocol. PCR amplification targeting 16S rRNA and cytochrome oxidase subunit I mitochondrial genes was performed using a Biometra Tone thermo-cycler PCR (Biometra, Göttingen, Germany). The PCR primers and conditions used were the same as those used by Calvo *et al.* (2009, 2015). The following primer set was used: 16sar-L-myt (Lydeard *et al.,*

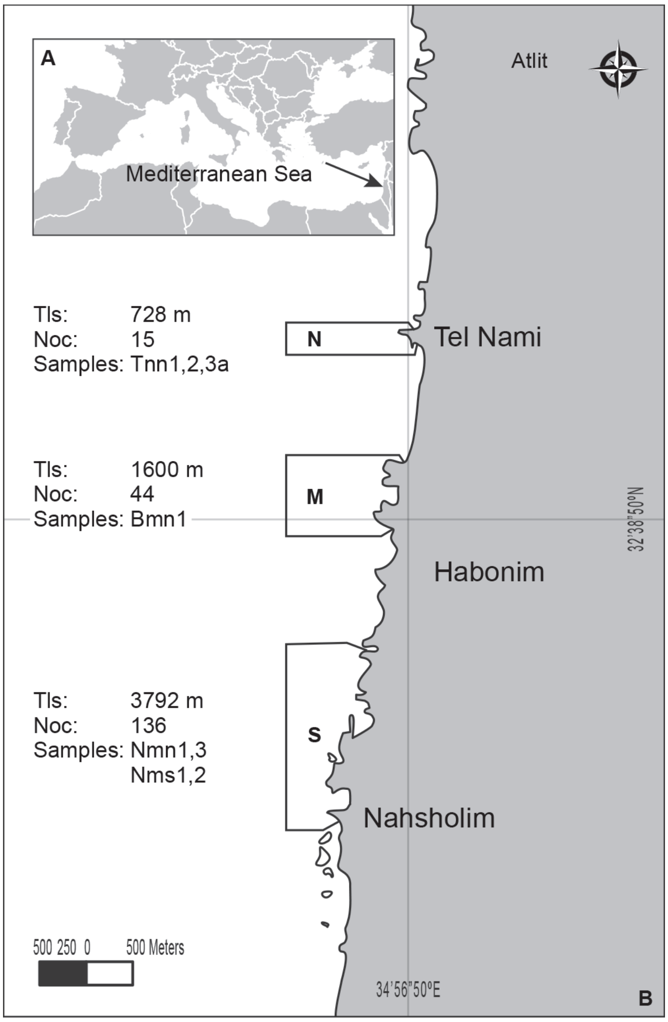

Fig. 1: (A). Location of the survey area in the eastern Mediterranean Sea. (B) Enlargement of the coastal area of the survey. Three sections of the survey are marked with the letters: S-Southern section, M-Middle section and N-Northern section. For each section the black rectangle indicates the southern and northern boundaries of the surveyed area. Tls = Total length surveyed. Noc = Number of clusters. The names of samples are given for each section.

1996), 16SBR (Palumbi *et al.*, 2002), LCO1490 (Folmer *et al.* 1994) and COI-H (Machordom *et al.,* 2003). PCR conditions were the same as those reported in Calvo *et al.* (2009). The PCR products were sequenced using the Sanger method on a Genetic Analyzer 3500 (Applied Biosystems/Hitachi). Sequences were deposited in GenBank and accession numbers are presented in Table S1.

Phylogenetic analysis

Sequences were aligned using the ClustelX algorithm, Maximum Likelihood analysis was performed in MEGA-X version 10.1.8 software (Kumar *et al.*, 2018) The phylogenetic trees were graphically constructed using iTOL version 6.6 (Ciccarelli *et al.,* 2006). The phylogenetic tree contains the current study sample sequences and related reference sequences obtained from NCBI GenBank that originate from Calvo *et al.* (2015).

Results and Discussion

DNA sequences from the present study (n=9, see Table S1 for 16S rRNA and COI gene sequence accession No.) show 96-100% identity to the Levantine-sea lineage of *D. petraeum* species complex (*D. anguliferum*) (Templado *et al.*, 2016). Figure 2 represents the phylogenetic trees of the 16S rRNA gene sequences. In the Levantine clade, the current sequences are closely related (99-100% identity) to the sequences from south Lebanon (Ras Al Bayada JQ672946). Phylogenetic trees of the partial sequences from mitochondrial cytochrome oxidase subunit I (COI) are presented in the supplementary Figure S2. The COI tree (based on 3 sequences from the present study) supports the findings from the 16S rRNA tree [The COI sequences are associated with the Levantine clade and are closely related (99% identity) to the sequences from south Lebanon (Ras Al Bayada EU495075)].

The visual survey revealed the presence of 195 living clusters of *D. anguliferum* along a cumulative rim-length of 6120 meters: 136 clusters in “S” area, 44 clusters in “M” area and 15 clusters in “N” area (Fig. 1). All the clusters were easily detected, as their immediate sur-

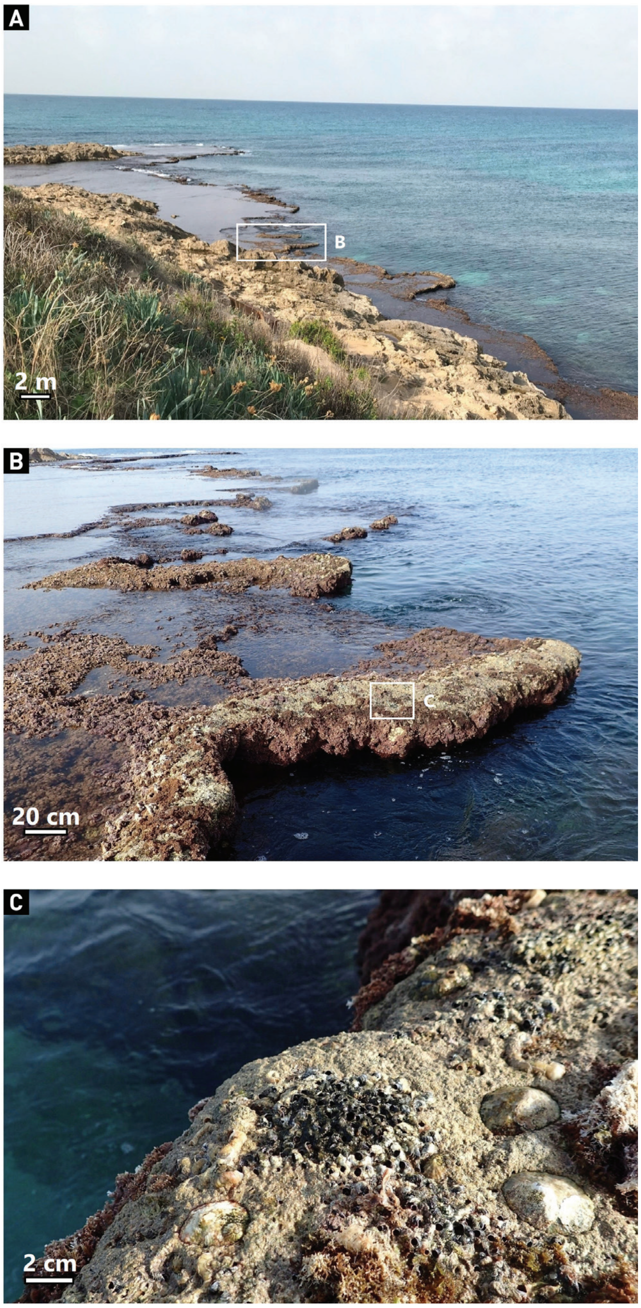

Fig. 2: Tel Nami abrasion platform: (A) General view of the northern facing platform. (B) the platform's rim showing several clusters of *D. anguliferum.* (C) a typical *D. anguliferum* cluster surrounded by exposed rock and limpets

roundings were devoid of algae and limpets were present (see Fig. 2). Most of the clusters which were encountered during the survey ranged in size between 5-20 cm in diameter with a mean size of 8.34±3.94 cm (n=116). The largest clusters were documented on the rims of the northern face of the abrasion platform in Tel Nami, an area where clusters occupied stretches of 40-70 cm (Fig. 3). Moreover, a mega-cluster of *D. anguliferum* which occupied a rectangular belt of 3900X50 cm was documented on the distal part of the abrasion platform and not on its rims (Fig. 4A, B, C). Although it should be noted that the abrasion platform was very narrow (1.5-3 meters between the outer and inner edges) at this location. In addition, recently settled *D. anguliferum* snails were documented on a rock in Tel Nami which was situated within 50 cm of the mega-cluster (Fig. 4D).

The results of the visual survey together with the molecular analysis conducted as part of the present study, clearly demonstrate the re-appearance of the gregarious gastropod *D. anguliferum* on abrasion platforms along the Carmel Coast area (from Nachsholim in the south to Tel Nami in the north) in Northern Israel Mediterranean-sea coastline. Reflecting back on the data regarding the spatial patterns of live *Dendropoma* clusters found on the Michmoret abrasion platforms (living patches of *Dendropoma* spp. constituted 3% of the raised rims areas), as reported by Lipkin & Safriel (1971), we suggest that our recent findings could be a sign for an ongoing recovery process of the *D. anguliferum* population in the surveyed area.

The new sequence similarities to the Levantine clade of *Dendropoma*, together with the current knowledge regarding reproductive traits and limited larval dispersion (Calvo *et al.*, 1998), suggests that the newly discovered clusters of *D. anguliferum* are the remnants of a more stable population that used to inhabit the abrasion platforms in Northern Israel and Lebanon and declined due to unknown reasons. It has been previously speculated that invasive species may be negatively affecting the *Dendropoma* populations in several locations (Franzitta *et al.*, 2022) including Israel (Milazzo *et al.*, 2016). One such invader may be the Red Sea mussel *Brachidontes pharaonis* (P. Fischer, 1878), one of the first Lessepsian migrants (sensu Por, 1978) to invade the Mediterranean Sea, first recorded by Fuchs at Port Said in Egypt just seven years after the opening of the Suez Canal in 1869 (Fuchs, 1878). Since then, it was found colonizing the eastern Mediterranean shores and over the last decades has become dominant in the rocky habitats of the Israeli Mediterranean coast displacing the indigenous mytilid *Mytilaster minimus* (Poli, 1795) (Rilov *et al.*, 2001). Extensive beds of this species were documented on the abrasion platforms along the Israeli coast (Rilov *et al.*, 2004) and in Habonim Nature Reserve (Yahel & Barneah, personal comm.). Milazzo *et al.* (2016) reported that most of the Israeli Abrasion platforms, formerly inhabited by living *Dendropoma* clusters were dominated by *B. pharaonis*. Milazzo *et al.* (2016) studying *Dendropoma cristatum* in a few locations near Palermo (Sicily), reported great detrimental effects of *B. pharaonis* on the density of *D. cristatum* and on the cover of the red algae *Neogoniolithon brassica-florida*. They suggested that the invasion of *B. pharaonis* represent a direct hazard to the vermetid reefs (Milazzo *et al.*, 2009). Thus, it is possible that the surprising summer collapse of the population of *B. pharaonis* along the Israeli coast in 2016 (Rilov, 2017; Rilov *et al.*, 2020; Yahel, Barneah and Tsadok personal observation) may have had an effect on the recovery of *D. anguliferum*. This recovery may have been driven by the recolonization of these snails from cryptic patches that had managed to survive and reproduce under the dense cover of bivalves. Thus, once the bivalves disappeared the *D. anguliferum* population could recover.

It should be emphasized that 195 live clusters of *D.*

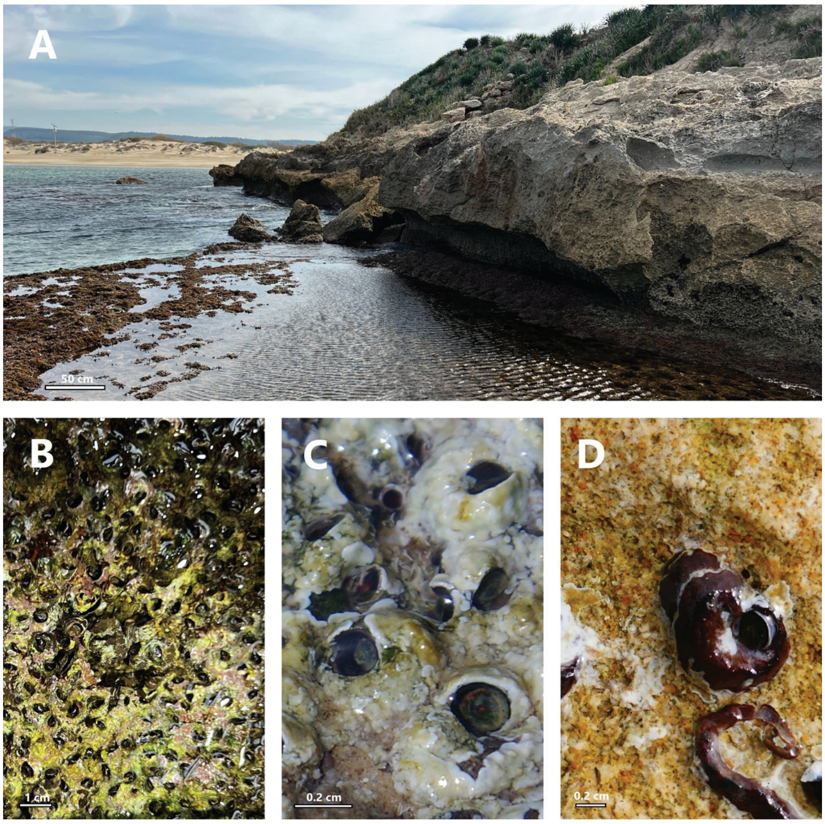

Fig. 3: The mega-cluster of *D. anguliferum* discovered on the distal part of the north face of the abrasion platform in Tel Nami: (A) General view of the location of the mega-cluster situated beneath the rocky ledge and stretching along 3.5 meters. (B) A closer view on a cluster of *D. anguliferum*. (C) A close view on shell openings with visible opercula. (D) Recently settled *D. anguliferum* specimens on a rock next to the mega-cluster

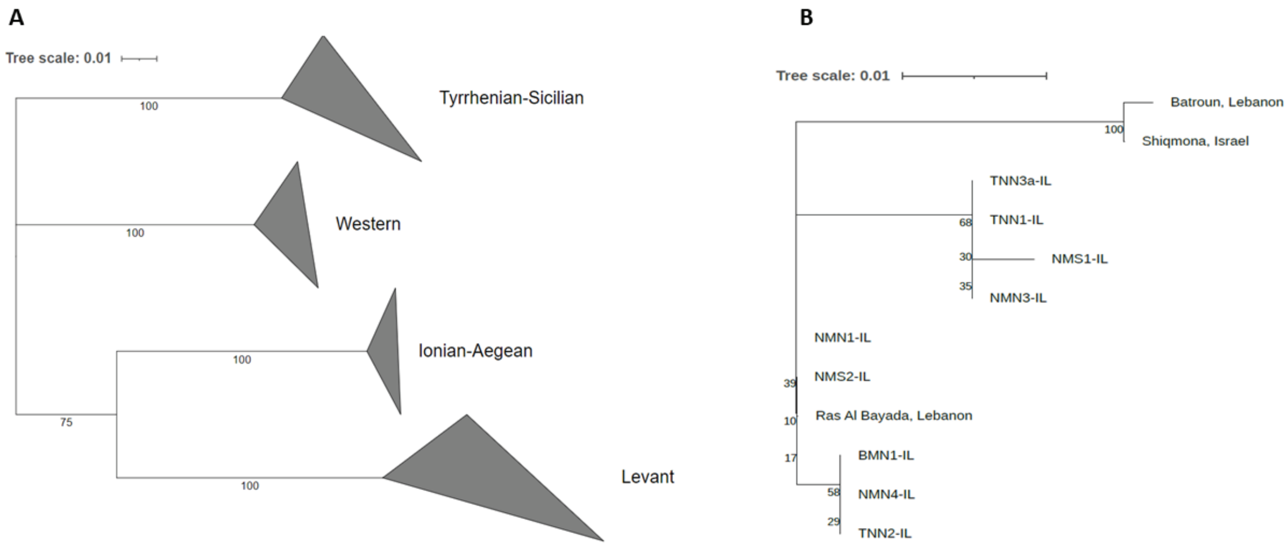

Fig. 4: Unrooted phylogenetic trees of the 16S rRNA gene sequences using maximum likelihood analysis. Numbers at the branch represent bootstrap values, indicating the statistical support for the branching pattern. (A) Phylogenetic tree of the samples from the current study and related reference sequences obtained from NCBI GenBank that originate from all Mediterranean Sea sample points obtained during the study of Calvo *et al.*, 2015. The triangles combine all the sequences of the same group within them. (B) Levantine sea lineage tree of the samples from the current study and reference sequences from Calvo *et al.*, 2015

anguliferum were documented in the present study, including a unique mega-cluster with unusually large dimensions. Although *Dendropoma* snails are considered valuable ecosystem engineers, the documentation and study of the population of these snails in Israel lacks consistency. Routine comprehensive surveys aimed at continuous monitoring of *D. anguliferum* have not been conducted in Israel in recent years. Moreover, the molecular data is still scarce and contains only limited (7) samples from Shiqmona (see Calvo *et al.*, 2009 and Calvo *et al.*,

2015) and 10 additional samples from the Carmel coast reported in the present study. The paucity of such data makes it difficult to draw solid conclusions from the results of our recent study, yet it emphasizes the need for the development of a thorough "national level" routine survey aimed at assessing and characterizing the population traits of *D. anguliferum.* This should be carried out along the entire area of vermetid reefs along the Israeli Mediterranean coast, as was formerly recommended by Galil (2013).

Acknowledgements

We thank The Israel Nature and Parks Authority (INPA) for the financial support of the survey and the permission to sample, the Avram and Stella Goldstein-Goren fund, BGU for partial support. We gratefully acknowledge Esti Kramarsky-Winter assistance with comments and scientific editing of the manuscript and would like to thank Eitan Maharam and Nili Bartov for valuable help in field work. In addition, we thank Asaf Tsionit (from INPA) for GIS work, Ruthie Vollweiler for valuable assistance with graphic design and Rei Diga and Ayelet Nir for important photographs.

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Supplementary Material

The following supplementary material is available for this article:

Table S1. 16S rRNA and COI gene sequence accession numbers.

Fig. S1: Nine clusters (out of 44) of *D. anguliferum* which were documented and photographed in "M" area (in Habonim nature reserve).

Fig. S2: Unrooted phylogenetic trees of the mitochondrial cytochrome oxidase subunit I (COI) gene sequences using maximum likelihood analysis. Numbers at the branch represent bootstrap values, indicating the statistical support for the branching pattern. (a) Phylogenetic tree of the samples from the current study and related reference sequences obtained from NCBI GenBank that originate from all Mediterranean Sea sample points obtained during the study of Calvo *et al.*, 2015. The triangles combine all the sequences of the same group within them. (b) Levantine sea lineage tree of the samples from the current study and reference sequences from NCBI GenBank that originate from Calvo *et al.*, 2015.