

## Mediterranean Marine Science

Vol 17, No 1 (2016)

VOL 17, No 1 (2016)



### Reef building Mediterranean vermetid gastropods: disentangling the *Dendropoma petraeum* species complex

J. TEMPLADO, A. RICHTER, M. CALVO

doi: [10.12681/mms.1333](https://doi.org/10.12681/mms.1333)

#### To cite this article:

TEMPLADO, J., RICHTER, A., & CALVO, M. (2015). Reef building Mediterranean vermetid gastropods: disentangling the *Dendropoma petraeum* species complex. *Mediterranean Marine Science*, 17(1), 13–31.  
<https://doi.org/10.12681/mms.1333>

## Reef building Mediterranean vermetid gastropods: disentangling the *Dendropoma petraeum* species complex

J. TEMPLADO<sup>1</sup>, A. RICHTER<sup>2</sup> and M. CALVO<sup>1</sup>

<sup>1</sup> Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, 28006 Madrid, Spain

<sup>2</sup> Oviedo University, Faculty of Biology, Dep. Biology of Organisms and Systems (Zoology),  
Catedrático Rodrigo Uría s/n, 33071 Oviedo, Spain

Corresponding author: [richteralexandra@uniovi.es](mailto:richteralexandra@uniovi.es)

Handling Editor: Marco Oliverio

Received: 21 April 2014; Accepted: 3 July 2015; Published on line: 20 January 2016

### Abstract

A previous molecular study has revealed that the Mediterranean reef-building vermetid gastropod *Dendropoma petraeum* comprises a complex of at least four cryptic species with non-overlapping ranges. Once specific genetic differences were detected, ‘*a posteriori*’ searching for phenotypic characters has been undertaken to differentiate cryptic species and to formally describe and name them. The name *D. petraeum* (Monterosato, 1884) should be restricted to the species of this complex distributed around the central Mediterranean (type locality in Sicily). In the present work this taxon is redescribed under the oldest valid name *D. cristatum* (Biondi, 1857), and a new species belonging to this complex is described, distributed in the western Mediterranean. These descriptions are based on a comparative study focusing on the protoconch, teleoconch, and external and internal anatomy. Morphologically, the two species can be only distinguished on the basis of non-easily visible anatomical features, and by differences in protoconch size and sculpture. On the other hand, some differences between species are evident in features of the intracapsular larval development: the number and size of the egg capsules brooded per female at the same time, the number of egg/embryos per eggs capsule, egg diameter and type of intracapsular nutrition.

**Keywords:** *Dendropoma*, new species, cryptic species, taxonomy, Vermetidae, Mediterranean Sea.

### Introduction

Vermetids are a peculiar group of sessile, uncoiled, suspension-feeding, marine gastropods that include more than 160 living species, mainly found in shallow waters in warm temperate to tropical environments (Golding *et al.*, 2014). Members of this family attach their shells on hard substrata and may be solitary or live in aggregates sometimes exhibiting a colonial behaviour (Hughes, 1979). Taxonomy and systematics of Vermetidae is currently in a state of disarray and many species remain undescribed because of the difficulty in finding diagnostic phenotypic characters (Bieler & Petit, 2011; Golding *et al.*, 2014). Approximately ten vermetid species are present in the Mediterranean Sea (CLEMAM data base; Coll *et al.*, 2011), but no general taxonomic review has been carried out after Monterosato (1892), who concentrated on naming numerous nominal species and “varieties” based on teleoconch characters alone. Only in recent times some taxonomic notes on particular species have been published (Scuderi, 1995, 2000, 2012; Schiaparelli, 1996; Nardi & Scuderi, 2000).

The dominant reef-building vermetid species in the Mediterranean Sea has long been considered *Dendropoma petraeum* (Monterosato, 1892). This gregarious gastropod forms dense aggregations cemented by crustose

coralline algae (mainly *Neogoniolithon brassica-florida*) along the lower midlittoral fringe on rocky shores of the warmest areas of the Mediterranean. The upper surfaces of these aggregations often coincide with the actual mean sea level. These biogenic formations, commonly referred to by the French name of “trottoir”, can be considered a key intertidal habitat of the warmest areas of the Mediterranean Sea and play an important role in preventing or slowing down the rock erosive processes (Antonioli *et al.*, 1999). They can be especially found on rocks that can be easily eroded, and the abrasive processes favour the formation of conspicuous biogenic platforms on sub-horizontal surfaces (Laborel, 1987; Chemello, 2009). Thereby, these bioconstructions are modulators of coastal geomorphological processes (García Raso *et al.*, 1992; Naylor & Viles, 2002).

Furthermore, these vermetid bioconstructions are very intriguing from several points of view. They are paleoclimatic indicators (Silenzi *et al.*, 2004; González-Delgado *et al.*, 2005), and they are also indicators of sea-level and sea-surface temperature changes on a human timescale (Antonioli *et al.*, 1999; Silenzi *et al.*, 2004; Chemello & Silenzi, 2011). Likewise, Sisma-Ventura *et al.* (2009) pointed out that *D. petraeum* isotopic signatures are unique proxies for paleo-oceanographic environments, providing high-resolution records in the

Mediterranean region. Dead vermetid reefs, which can be easily dated by radiocarbon, have often proved very useful in reconstructing recent seismo-tectonic histories (e.g. Tzur & Safriel, 1978; Laborel & Laborel-Deguen, 1994; Pirazzoli *et al.*, 1996; Sivan *et al.*, 2010). Where these reefs are well developed, they act as biological engineers creating new habitats on the narrow Mediterranean intertidal fringe, thereby increasing its complexity and enhancing the associated biodiversity (Chemello *et al.*, 2000; Safriel & Ben-Eliahu, 1991; Pandolfo *et al.*, 1992; Colombo *et al.*, 2013). On the other hand, it has been noted that these vermetid reefs are now decimated or entirely extinct in some areas of the eastern Mediterranean (Galil, 2013), and along the Israeli coast it has become rare and is ecologically extinct (Rilov, 2013). For all these reasons *Dendropoma petraeum* was included in the Appendix II (Strictly Protected Fauna species) of the Bern convention, and in Annex II (List of Endangered or Threatened Species) to the Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean of the Barcelona Convention (1996). Besides, the reefs formed by this vermetid have been listed among the threatened habitats in the Mediterranean Red Data Book of threatened marine vegetation (UNEP/IUCN/GIS Posidonie, 1990).

The bioconstructions of *D. petraeum* were first described along the coasts of Isola delle Femmine, near Palermo (northern Sicily, central Mediterranean) by the French naturalist Henry de Quadrefages in 1854. Nearly one century later, Molinier & Picard (1953) gave a detailed description of the same biotope and Pérès & Picard (1952) described similar bioconstructions along the Algerian coast, using the name *Vermetus cristatus* Biondi, 1859. Subsequently, a series of papers have been published describing these bioconstructions in different areas of the Mediterranean, pointing out a discontinuous distribution along the coasts of Israel (Safriel, 1966, 1974, 1975; Galil, 2013), Lebanon (Dalongeville, 1977; Bitar & Bitar-Kouli, 1995), Syria (Dalongeville *et al.*, 1993; Al-Nimeh & Ellassafin, 1996), Turkey (Laborel, 1987; Bakır *et al.*, 2012), Cyprus (Ramos-Esplá *et al.*, 2007; Scaperrotta *et al.*, 2012), Crete (Kelletat, 1979; Laborel, 1987; Naylor & Viles, 2002), Malta (Azzopardi & Schembri, 1997), Sicily (Molinier & Picard, 1953; Chemello *et al.*, 2000), Gulf of Naples (Scuderi *et al.*, 1998), Sardinia (Schiaparelli *et al.*, 2003), Corsica (Molinier, 1960; Laborel, 1987), Algeria (Pérès & Picard, 1952) and Spain (Molinier & Picard, 1953; Molinier, 1954; Templado *et al.*, 1992).

Recent phylogenetic studies based on molecular data (Calvo *et al.*, 2009, 2015) have revealed that the Mediterranean reef-building gastropod *Dendropoma petraeum* comprises in fact a complex of at least four cryptic species with non-overlapping distributions. One species is distributed throughout the southwestern Mediterranean, from the neighbouring Atlantic coast to the Mediterranean coasts of Spain, Morocco, Algeria and Tunisia. A second

species is distributed in the Tyrrhenian Sea, around Sicily and Malta. The third species is known from Crete and Salentine Peninsula (SE Italy), and the fourth one in the Levantine basin (coasts of Syria, Lebanon and Israel). Hence, in agreement with taxonomic nomenclature rules, the species name *Dendropoma petraeum* (Monterosato, 1884) must be assigned to the species of this complex distributed in the central Mediterranean, because the type locality of *D. petraeum* (near Palermo, N Sicily, see below) falls within the range of distribution of this clade. On the other hand, the name *Dendropoma anguliferum* (Monterosato, 1878) should be assigned to the Levantine species, because the type locality of this taxon is Tripoli, Lebanon. The remaining two cryptic species from the other areas of the Mediterranean (the southwestern Mediterranean and Ionian-Aegean areas, respectively) are taxonomically new to science and therefore shall be named and described on the basis of diagnostic phenotypic characters. Particularly, reproductive and developmental characters shall be taken under consideration in the separation and description of the new species, since characters of larval development have been pointed out as particularly important in the taxonomy of vermetid gastropods (Calvo *et al.*, 2009). Furthermore, many species complexes of gastropods include species differing in reproductive and developmental traits (e.g. Moreno & Templado, 1994; Oliverio, 1994; Collin, 2005; Russo & Patti, 2005, among others).

The aim of the present paper is to carry out a thorough comparative study between the true *Dendropoma petraeum* from the central Mediterranean and the cryptic species of this complex distributed along the western Mediterranean (Fig. 1), firstly in order to find out phenotypic diagnostic characters that allow to separate species, and secondly to redescribe the true *D. petraeum*, here under its subjective senior synonym *Dendropoma cristatum* (Biondi, 1859), as suggested by Scuderi (1995).

## Material and Methods

Specimens from the following localities widespread all along the western and central Mediterranean have been studied:

Mohammedia (Atlantic Morocco, 33°42'37.03"N, 07°22'21.01"W), Sancti Petri (Atlantic coast of SW Spain, 36°23'13.02"N, 6°12'30.06"W), Punta Carnero (Strait of Gibraltar, 36°04'21.15"N, 5°25'44.18"W), Alboran Island (35°56'20"N, 3°02'06"W), Chafarinas Islands (Mediterranean coast of Morocco, 35°10'53.95"N, 2°25'38.18"W), Cape Bon (Tunisia, 37°03'31.25"N, 10°59'10.60"E), Cabo de Gata (SE Spain, 36°50'06.45"N, 2°01'28.83"W), El Calón (SE Spain, 37°21'28.52"N, 1°39'52.87"W), Cabo de Palos (SE Spain, 37°37'48.16"N, 0°42'07.33"W), Cabo Roig (SE Spain, 37°54'37.07"N, 0°43'19.67"W), Punta Prima (Alicante, SE Spain, 37°56'27.85"N, 0°42'33.00"W), Javea (E Spain, 38°44'53.96"N,





**Fig. 1:** Distribution ranges of *D. lebeche* sp. nov. (yellow lines) and *D. cristatum* (blue lines). Black dots: sampling sites.

0°13'30.41''W), Sierra de Irta (Castellón, E Spain, 49°19'56.07''N, 0°23'24.41''E), Punta Prima (Menorca, Balearic Islands, 39°48'24.26''N, 4°17'10.32''E), Lavezzi Islands (S Corsica, 41°20'15.09''N, 09°15'20.92''E), Capri Island (Gulf of Naples, W Italy, 40°33'28.33''N, 14°14'06.28''E), San Vito Lo Capo (NW Sicily, 38°09'19.09''N, 12°43'40.02''E), Isola delle Femmine (N Sicily, 38°11'51.05''N, 13°14'36.00''E), Capo Milazzo (NE Sicily, 38°16'08.03''N, 15°13'46.00''E), Acitrezza (Catania, E Sicily, 37°33'35.08''N, 15°09'29.01''E), Ognina di Siracusa (SE Sicily, 36°59'00.07''N, 15°15'45.00''E), Qawra (Malta, 35°57'31.38''N, 14°25'37.79''E).

Animals were collected mainly from the rocky intertidal level by removing pieces of the aggregates or isolated specimens with hammers and small chisels. Living specimens were examined from all localities mentioned above. Other specimens were preserved in diluted formalin or alcohol. Some tube shells were carefully broken to obtain the soft parts and encapsulated embryos, and their contents examined under a binocular microscope. Preserved animals were dissected under a stereo-microscope and drawings were made using a camera lucida. Protoconchs and radulae were cleaned with hydrogen peroxide or a concentrated water solution of NaOH, dehydrated in alcohol, air-dried and examined by scanning electron microscope (S.E.M.). Radulae, before being analyzed with S.E.M. at high vacuum, were sputter-coated with gold. Micrographs were acquired with an EVO 40 ZEISS and a FEI QUANTA 200. Several specimens destined for histological studies were fixed in Bouins or in a solution of 10% formalin and 0.9% NaCl and processed following standard histological techniques. Serial 5-7 µm thick histological sections were double-stained with haematoxylin-eosin and examined with an optic microscope.

## Abbreviations to collections

FMNH: Field Museum of Natural History, Chicago.  
MNHN: Muséum national d'Histoire Naturelle, Paris.  
MNCN: Museo Nacional de Ciencias Naturales, Madrid.  
USNM, Smithsonian Institution, National Museum of Natural History, Washington DC.

## Results

### Systematics

Family Vermetidae Rafinesque, 1815

Genus *Dendropoma* Mörch, 1861

Type species: *Siphonium* (*Dendropoma*) *lituella* Mörch, 1861 (by subsequent designation of Keen, 1961: 153) from California to La Paz, Baja California.

### Remarks:

*Dendropoma* is one of the traditionally recognized genera among the Vermetidae and includes a wide range of species characterized by a well-developed operculum. Recently Golding *et al.* (2014) have reviewed the taxonomy of *Dendropoma* s.l. (based on morphological, anatomical and molecular data). They describe 21 species, eight of which as new species, and recognize four robustly supported genera within *Dendropoma* s.l.: *Dendropoma* s.s., *Novastoa* Finlay, 1926 and two new genera named *Ceraesignum* and *Cupolaconcha*. In the phylogenetic analysis of Golding *et al.* (2014), the species of the *Dendropoma petraeum* complex resulted as belonging to *Dendropoma* s.s., a well-supported lineage in their molecular phylogeny, which was additionally supported by features of the operculum, reproductive traits and a novel mitochondrial gene order.



**Fig. 2:** *Dendropoma lebeche* sp. nov. A, holotype; B, adult shell attached to the substrate (13 x 10.5 mm); C, “*Petalconchus*-like” coiled adult shell; D, living specimen partially covered by crustose algae showing the operculum (22 mm x 10 mm) (all from type locality, Cabo de Palos SE Spain). Scale bars: A, C = 2 mm.

Golding *et al.* (2014) give also a complete diagnosis of the genus. Species of *Dendropoma* s.s. have a chitinous multispiral operculum that fills the aperture of the shell but does not have a raised, ruffled lamina on the exterior surface, as in *Novastoa*. Females bear primary and accessory seminal receptacles in the proximal region of the pallial oviduct and produce a variable number of unstalked egg capsules brooded inside the mantle cavity. Females and males lack a pallial slit. Males present an accessory gland of unknown function in the exhalant siphon near the anterior end of the pallial spermiduct. Larval development is typically intracapsular or with a short planktonic phase. The protoconch is globular with large increase in whorl size. Adults are solitary to gregarious or reef-building.

*Dendropoma lebeche* sp. nov.

<http://zoobank.org/EF8AC74D-EB29-45C5-80DC-0F55B715DB82>

*Vermetus cristatus* Biondi: Molinier (1954, 1955), Molinier & Picard (1956).

*Dendropoma petraeum* (Monterosato): García Raso *et al.* (1992), Templado *et al.* (2002, 2004, 2006), Calvo, Templado & Penchaszadeh (1998), Rawling *et al.* (2001); Calvo & Templado (2005), Moreno (2008).

*Dendropoma* cf. *petraeum* (Monterosato): Golding *et al.* (2014: 32-35, figs. 80-92).

Type locality: lowest mid-littoral, Cala Abellán, Cabo de Palos, Murcia province, SE Spain (37°37'48.16"N, 0°42'07.33"W).

Type material:

Holotype (Fig. 2A): one isolated specimen with dried soft parts (11 x 9 mm in extension over substrate, ap-

erture diameter: 2.1 mm), type locality, 12 April 2009 (MNCN 15.05/60163).

Paratypes (85 specimens): paratypes 1-7: seven isolated specimens with dried soft parts from the type locality, 12 April 2009 (MNCN 15.05/60164); paratype 8: adult shells with up to eleven juveniles specimens attached, from the type locality, 12 April 2009 (MNCN 15.05/60165); paratype 9: cluster of dried shells embedded by the coralline alga *Neogoniolithon brassica-florida*, from the type locality, 12 April 2009 (MNCN 15.05/60166); paratype 10: small cluster of empty shells embedded by the coralline alga *Neogoniolithon brassica-florida*, from the type locality, 12 April 2009 (MNCN 15.05/60167); paratypes 11-13: three pieces of clusters of empty shells embedded by crustose coralline algae, from the type locality, 3 January 2004 (MNCN 15.05/60168); paratypes 14-15: soft parts of two specimens preserved in 70% ethanol from type locality, 24 June 1995 (MNCN 15.05/60169); paratypes 16-25: 10 isolated specimens preserved in alcohol 70%, from the type locality, 19 March 2002 (USNM 1231360); paratypes 26-34: soft parts of 9 specimens preserved in alcohol 70%, from the type locality, 15 June 1996 (USNM 1231361); paratypes 35-39: soft parts of 5 males fixed in formalin 5% and preserved in alcohol 70%, from the type locality, 19 March 2002 (USNM 1231362); paratypes 40-43: soft parts of 4 specimens fixed in Bouin and preserved in alcohol 70%, from the type locality, 23 June 1996 (USNM 1231363); paratype 44: dried small piece of an aggregate, from type locality, 20 March 2002 (USNM 1231364); paratype 45: piece of an aggregate of dead shells, from type locality, 3 January 2004 (USNM 1231365); paratypes 46-68: twenty three isolated specimens with dried soft parts, from the type locality, 21 June 1993 (FMNH 337406); paratype 69: dried piece of a cluster of shells embedded by crustose coralline, from the type locality, 12 April 2009 (FMNH 337405); paratype 70: soft parts of a female, from type locality, 1 May 1996 (FMNH 337407); paratype 71: small cluster with soft parts fixed in 70% ethanol, from the type locality, 2 March 1996 (FMNH 337408); paratypes 72-76: five specimens from Cabo de Gata, Almería province (36°50'06.45"N, 2°01'28.83"W), 3 February 1995 (FMNH 286238); paratypes 77-82: six isolated shells with dried soft parts inside, from the type locality, 12 April 2009 (MNHN IM-2000-30469); paratype 83: dried piece of a cluster of shells embedded by crustose coralline, from the type locality, 12 April 2009 (MNHN IM-2000-30470); paratypes 84-85: soft parts of two specimens, from the type locality, 30 September 1995 (MNHN IM-2000-30471).

Other material examined: some pieces of bioconstructions collected down to 6 m deep in the type locality; some isolated specimens and pieces of the bioconstructions from the following localities: Mohammedia (Atlantic Morocco), Conil and Sancti Petri (Atlantic coast of SW Spain), Punta Carnero (Strait of Gibraltar), Alboran



Island, Chafarinas Islands (Mediterranean coast of Morocco), Cape Bon (Tunisia), El Calon, Cabo de Palos, Cabo Roig and Punta Prima (SE Spain), Javea and Sierra de Irta (E Spain), Punta Prima (Menorca, Balearic Islands). All this additional material is deposited in the research collection of the first author in MNCN.

For the study of developmental features the intracap-sular development was examined in live specimens from SE Spain, Atlantic coast of Morocco, Chafarinas Islands (N Africa) and Menorca (Balearic Islands).

GenBank accession numbers: EU495050-EU495058 (COI), EU495078-EU495086 16S rRNA), EU495022-EU495030 (ITS) (Calvo *et al.* 2009).

## Description

### Shell

Teleoconch: maximum dimensions of individual adult shells ranging from 11 x 9 mm to 20 x 18 mm in regularly coiled and isolated specimens. Maximum outside whorl diameter up to 4 mm in isolated or loosely aggregated individuals, smaller in dense aggregations (normally ranging from 1.5 to 2.0 mm).

First whorls of the adult shell growing in a planispiral coil around the protoconch with its axis forming a right angle with the larval shell axis. Coiling rarely deviated from counter-clock wise direction in isolated specimens (Fig. 2B), to very loosely coiled or irregular morphs when gregarious. Some isolated specimens found in crevices can adopt a “*Petalocochnus*-like” coiling (Fig. 2C). Specimens do not produce erect feeding tubes. Aperture is circular and sharp-edged, generally not projecting above the substratum in isolated specimens. Sculpture of irregular longitudinal (spiral) ribs (coarser when more dorsal) crossed by very close conspicuous transverse lamellae that may occlude the longitudinal ribs. Internal lamellae or septa are absent. The external surface is speckled bluish-gray with the transverse lamellae somewhat paler. Pinkish, purple or brown hues may be often due to algal overgrowth. The inner shell surface is smooth and glossy, usually dark red-wine near the aperture. It is a typically gregarious and reef-building species, embedded by coralline algae.

Protoconch (Fig. 3A): globular, covered by a thin and smooth periostracum, with a little over 1 1/8 whorls. Surface with fine and irregular transversal growth lines. It ranges in size from 580 to 720 µm in length and 425 to 550 µm in diameter. The nucleus of the protoconch measures from 240 to 300 µm in diameter. The limit between the protoconch and the teleoconch is marked by a white protruding edge (Fig. 4); in living specimens, the latter contrasts sharply with the brown colour of the protoconch. The aperture of the shell in the crawling juvenile (just before hatching) has a prominent angle at its dorsal edge that creates two different planes in about 90°. The newly attached juveniles can be easily detected by

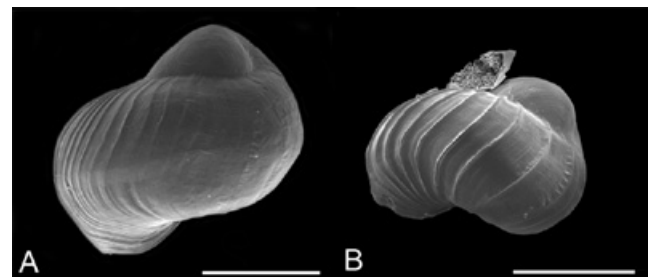
the distinctive dark brown colour of their shells over the whitish or pale pinkish calcareous algae on which they settle.

### External anatomy

Anaesthetized adult animals removed from the shell measure from 7 to 28 mm in length. The soft part (Fig. 5A) is clearly divided anatomically into three body regions, head-foot, mantle and a loosely coiled visceral mass, occupying at least half of the length and enclosing the long posterior lobe of the digestive gland and gonad.

### The head-foot

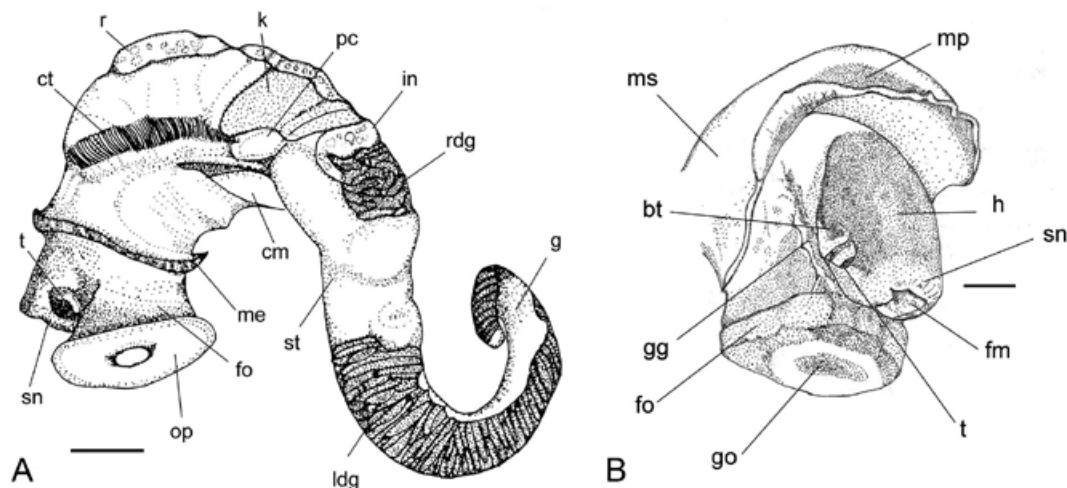
The large head (Fig. 5B) is wider than the rest of the body, and grossly pentagonal when viewed dorsally. It is predominantly black with two lateral grey longitudinal stripes flanking either side of the paired cephalic tentacles and dorsally there is a clearer central area where black flecks are spread over a greyish background. The black pigmentation of the head is interrupted mid-ventrally by a broad white longitudinal band. The paired cephalic tentacles are reduced and never exceed beyond the



**Fig. 3:** SEM micrographs of protoconchs. A, *Dendropoma lebeche* sp. nov. (from type locality, Cabo de Palos SE Spain); B, *Dendropoma cristatum* (San Vito Lo Capo, NW Sicily). Scale bars A = 300 µm; B = 400 µm.



**Fig. 4:** SEM photograph of a newly attached juvenile of *Dendropoma lebeche* sp. nov. from type locality. Scale bar = 500 µm.



**Fig. 5:** Soft parts of an individual of *Dendropoma lebeche* sp. nov. A, general view; B, lateral view from the head-foot region and mantle edge (bt, base of cephalic tentacle; cm, columellar muscle, ct, ctenidium; fo, foot; fm, false mouth; g, gonad; gg, glandular groove for the transport of spermatophores; go, metapodial groove where the opercular mammilla inserts; in, intestine; h, head; k, kidney; ldg, left digestive gland; me, mantle edge; mp, mantle pigmentation; ms, mantle skirt; op, operculum; pc, pericardium; r, rectum; rdg, right digestive gland; sn, snout; t, cephalic tentacle). Scale bars = 0.5 mm.

short squat greyish coloured snout. Each of them forms a short basal swelling protruding laterally from the head, which bears a minute rudimentary eye containing crystalline, and continues into a short dorso-ventrally compressed truncated tip, separated from the tentacle base by a circular groove with thickened border. The tentacle tips nest inside a lateral depression of the head and are grey dorsally and black ventrally. The snout opens through a false, not closable mouth through which the retracted radula is visible and leads to a short pre-buccal cavity. The false mouth has the form of a wide vertical slit with a dorsal bilateral and ventral transversal incision.

The foot is separated from the head by a transversal furrow and hardly projects beyond the snout. The foot sole (mesopodium) is strongly reduced, forming merely a fleshy grey rim dorsally bordering the black margin of the disc-shaped metapodium. Just below the snout and nested in the furrow separating head from foot, protrude the short, black, paired pedal tentacles of the propodium, which never project beyond the cephalic tentacles. They are more or less horn-shaped and transversely ridged. A deep transverse groove runs along the frontal edge of the foot to which opens the orifice of the pedal gland centrally just above the white mucous pad (a short, narrow, delicate slightly bilobed expansion of the ventral region of the pedal tentacles). By stripping off the operculum from the metapodium, a central hole in the middle (where the central protuberance of the operculum inserts) becomes exposed. The back of the foot is whitish, except close to the metapodium where it is densely black pigmented.

The pedal gland is quite developed and voluminous extending along the complete trunk as a milky white glandular mass filling more or less 3/4 of the trunk cav-

ity. It is composed of a bunch of densely packed tubules lined by a flat epithelium and surrounded by a sheet of subepithelial gland cells. The tubules confluence into a single main duct that emerges anteriorly from the glandular mass as a short straight tract, passes below the pedal ganglia and continues anteriorly to embed in the pedal musculature as a slightly spiralled duct until opening between the pedal tentacles above the mucous pad.

Ventrally, behind the mantle edge more or less at the middle of the ventral surface of the head-foot, the anterior tip of a broad and relative short columellar muscle inserts, whose posterior end reaches back to the anterior limit of the stomach. The section of the muscle extending from the posterior limit of the pallial cavity backwards is unattached to the body wall. The short columellar muscle, as well as the wide operculum, prevents deep withdrawal of the animal into the tube shell.

### Operculum

The well-developed operculum is flat to slightly domed, chitinous, flexicaudent (*sensu* Checa & Jiménez, 1998), multispiral, extending slightly beyond the rim of the metapodium and closing up completely the rounded aperture of the tubular shell (Fig. 2D). It is formed by concentric horny discs, dark red-wine in colour and decreasing in diameter from the innermost sheet to the outermost, with semitransparent margins. The inner surface in contact with the epithelium of the metapodium is slightly concave and smooth, and presents a conspicuous central button-like mamilla, which is inserted in a central hole of the metapodium.

### Mantle and mantle cavity

The mantle fold encloses a wide and deep pallial cavity encompassing more or less one third of the whole length of the extended animal. In females, it forms brood pouches in a zone covered by a villous epithelial skirt of highly prismatic cells extending between the roof of the rectum and the ctenidium. The floor of the mantle cavity is milky white and so the mantle fold, except a narrow black band right behind the reflected mantle rim. At the level of the mid-dorsal region, originating between the ctenidium and rectum, the black pigmentation of the mantle fold reaches farther back covering an area in the form of a half-moon. Dorsally, small black spots at the level of the ctenidium, osphradium and rectum are visible by transparency through the mantle fold. The mantle edge is entire in both sexes, without a slit.

The monopectinate ctenidium runs along the entire left side of the mantle cavity until its end, starting slightly behind the mantle edge (Fig. 6A). It is composed of narrowly triangular leaflets, taller than wide, with the base and height reducing gradually toward the posterior end of the ctenidium and abruptly towards its anterior tip, which bends ventrally in an open angle to the length axis of the ctenidium. The ventral edges of the gill leaflets are slightly thickened and accumulate black pigment at the level of the free tips.

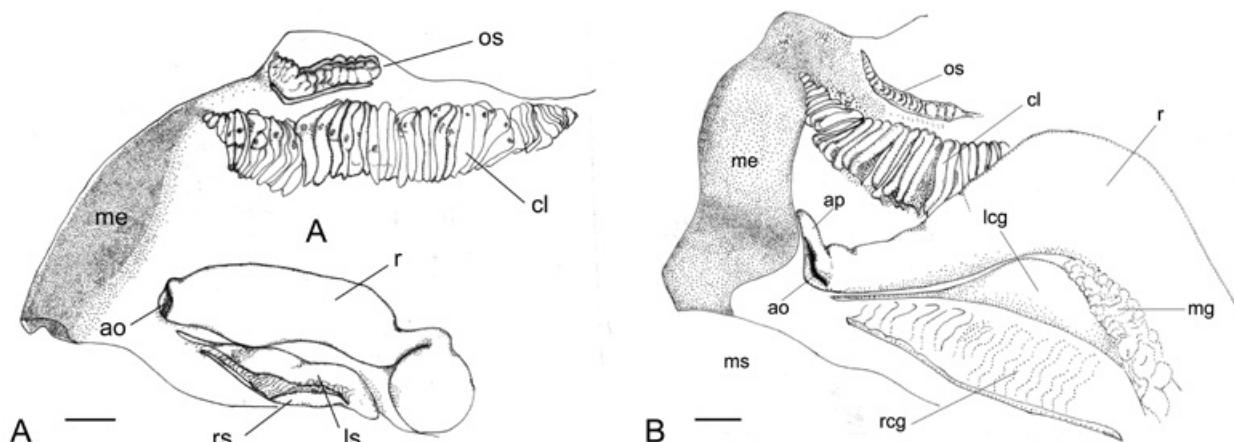
Ventral to the ctenidium, extending parallel alongside its base, is a relative narrow and reduced osphradium (Fig. 6A), between one fourth and one fifth as long as the ctenidium. Its anterior tip bends ventrally in a right angle to the length axis of the osphradium. It is formed by a relative thick longitudinal central crest with shallow transverse grooves, flanked on each side by a thinner and less high longitudinal fold with sensory epithelium.

The white rectum runs along the right side of the mantle cavity, covering approximately three quarters of the mantle length. It is voluminous, of uniform width,

and filled with golden brown faecal pellets. It opens to the mantle cavity through a wide terminal dorso-ventral slit far behind the mantle rim. The outer (left) lip of the anal orifice is slightly raised forming a more or less dorso-lateral triangular flap, whose height never exceeds the width and height of the anal orifice. The pallial gonoduct runs ventrally and to the left of the rectum, forming a deep glandular groove. An additional mucilaginous glandular strip, golden brown coloured in females, between the rectum and the left fold of the pallial gonoduct, extending in both sexes from the bottom of the pallial cavity reaching up to one third of the pallial gonoduct. In males, this strip is less developed than in females and produces a basophile secretion, while in females it is broader and thicker and produces a highly eosinophilic secretion. In both sexes, a raised thick accessory glandular groove (accessory gland) runs along the right side of the mantle floor, beginning slightly behind the anterior tip of the pallial gonoduct. This glandular groove continues along the right flank of the head-foot ventral to the head and ends up at the mesopodium. The glandular development of this accessory groove and of the pallial gonoduct may vary among specimens and seems to be related to the breeding season, reaching its maximum development when individuals have ripe gonads. This fold may carry spermatophores in females from the foot toward the female pallial gonoduct, and in males, from the spermatophoral gland to the foot.

### Reproductive system

*Dendropoma lebeche* is a gonochoristic species. The male reproductive system consists of a gonadic duct running mid-ventrally (forming a sinusoid turgid seminal vesicle during the breeding season), a renal section, a pallial spermiduct formed by an open glandular groove making up the prostate gland (encompassing four fifths of the pallial reproductive system), and a closed posterior



**Fig. 6.** General view of the mantle cavity of a male of *Dendropoma lebeche* sp. nov. (A) and a female of *D. cristatum* (B) opened along the baseline of the left side. Region extending from the rectal inflection backwards omitted (ao, anal orifice; ap, anal papilla; cl, ctenidial leaflet; lcg, left lobe of the capsule gland; ls, left lobe of the spermatophoral gland; me, pigmented mantle edge; mg, mucilaginous gland; ms, mantle skirt; os, osphradium; r, rectum; rs, right lobe of the spermatophoral gland). Scale bars = 0.2 mm.



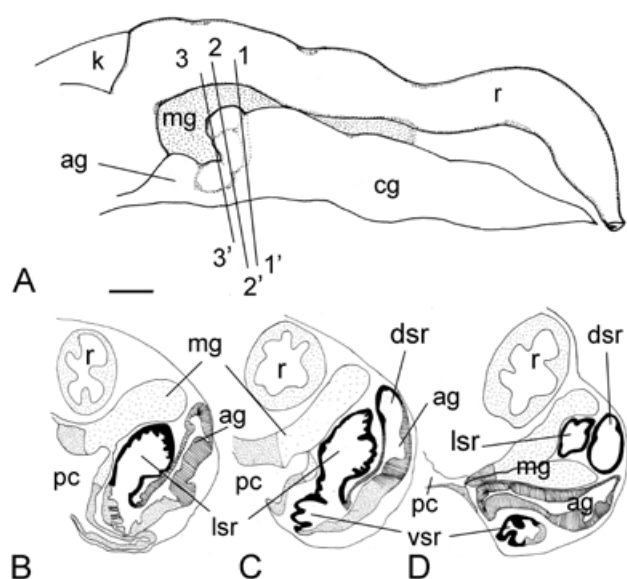
section. In this posterior section of the prostate gland the sperm is encapsulated in complex spermatophores. The spermatophores and spermatozoa of this species were described by Calvo & Templado (2005 as *D. petraeum*).

The female reproductive system is composed (from the proximal to distal region) of an ovary, a gonadic oviduct, a renal oviduct, and a glandular pallial oviduct. The ovary forms a mass of creamy yellow tubules to the right of the coiled visceral mass opposite to the greenish-brown left digestive gland and encompasses the region between the hind wall of the posterior gastric chamber and the tip of the visceral mass. The pallial section of the oviduct (Fig. 7A), extending along the entire rectum, is divided into a proximal closed albumen gland, making up the posterior fifth of the pallial oviduct, and a distal capsule gland. The capsule gland occupies four-fifths of the pallial gonoduct, forming a deep open groove flanked by a pair of lateral glandular folds, the right one attached to the mantle fold and the left one forming a flap hanging free from the mantle roof. The posterior portion of the albumen gland reaches back to the kidney region. Associated to the albumen gland are three seminal receptacles with orientated sperm. One of them forms a wide vertical blind sac extending dorso-ventrally to the left of the albumen gland closely attached to the free (left) lamina (Fig. 7B-C). Externally it is not visible, as it is embedded in the mucilaginous gland. The two additional seminal receptacles are visible externally and form two blind sacs which open anteriorly and extend backwards: a ventral

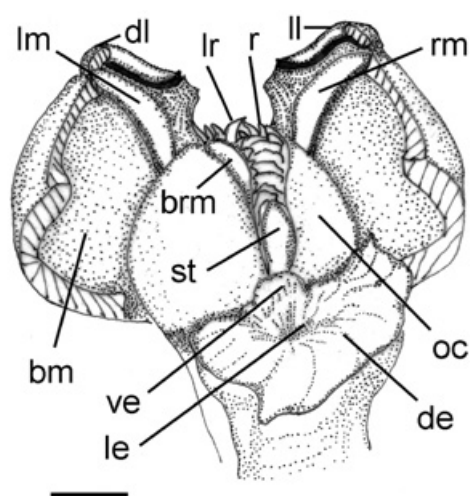
cylindrical blind sac running alongside the base of the right (attached) lamina reaching far back to the kidney region, and a small dorsal ovoid one (Fig. 7C-D). The latter extends mid-dorsally along the albumen gland, its lumen maintaining open connection with the glandular oviduct along almost its whole length except at its posterior blind end which hardly exceeds farther back the vertical blind sac and closes up from the glandular oviduct right behind it.

### Digestive system

A wide buccal mass (Fig. 8) occupies the entire head cavity and opens through a vertical slit-like mouth to a short pre-buccal cavity. A pair of hemispherical bilateral mandibles, with the curved mineralized frontal edge oriented dorso-ventrally and situated right behind the lips, lines the lateral walls of the buccal mass. A voluminous odontophore divided into two bilateral massive, more or less semicircular, halves fills the centre of the buccal mass. Its exposed surface is completely covered by the subradular membrane which bears a narrow taenioglossate radula (2+1+R+1+2) along its midline (Fig. 9A). The radular ribbon projects backwards into the radular sac, which borders externally the posterior edge of the odontophore. A white spongy tongue-like projection of the dorsal wall of the radular sac protrudes farther anteriorly from the mouth of the radular sac (Fig. 8), covering the hind rows of the exposed radular ribbon.



**Fig. 7.** Semi-diagrammatic representation of the female pallial oviduct of *Dendropoma lebeche* viewed from the right side (A), with semi-diagrammatic representations of histological transversal sections at different levels (B-D) (ag, albumen gland; cg, capsule gland; dsr, dorsal seminal receptacle; k, kidney; lsr, left seminal receptacle; mg, mucilaginous gland; pc, pallial cavity; r, rectum; vsr, ventral seminal receptacle). Scale bar = 0.3 mm.

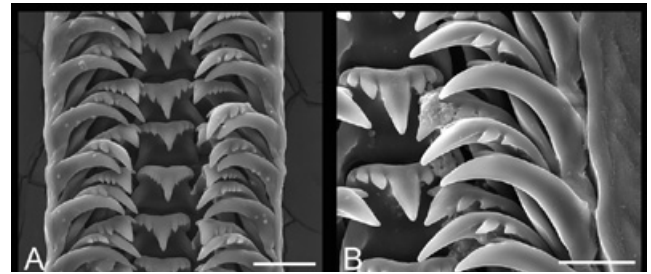


**Fig. 8.** Buccal mass of *Dendropoma lebeche* sp. nov. opened mid-dorsally (bm, wall of the buccal mass; brm, thickened border of the radular membrane; de, dorsal wall of anterior esophagus; dl, dorsal lip of the snout; le, lumen of esophagus; ll, lateral lip of the snout; lm, left mandible; lr, lateral radular tooth; oc, odontophoral cartilage; r, rachidian radular tooth; rm, right mandible; st, spongy tissue of the radular sac; ve, ventral wall of esophagus). Scale bar = 0.3 mm.

Right behind and dorsally to the odontophore the thin-walled anterior oesophagus opens to the buccal cavity, whose dorsal wall makes up the dorsal wall of the buccal cavity. The portion of the anterior oesophagus running along the trunk region presents longitudinal folds. After crossing the circum-oesophageal nerve ring, it loops from the right side to the left side since it is displaced by the voluminous pedal gland. A pair of yellowish-white bilateral tubular-acinous salivary glands are placed externally and dorso-laterally to the buccal mass. They are of unequal length; the blind end of the left one bends ventrally and does not exceed beyond the buccal mass. The right one, much longer than the left, extends farther posteriorly into the trunk region, crossing through the circum-oesophageal nerve ring and overlaying the portion of the anterior oesophagus that loops from the right to the left side. The posterior oesophagus presents longitudinal folds and opens into a voluminous stomach ventro-laterally, at its left side, shortly behind a large transversal fold separating the anterior gastric chamber (the style sac) from the posterior gastric chamber (containing the gastric shield). A crystalline style is present, sometimes filling the whole gastric chamber and sometimes only its anterior part. The style sac is large, making up more or less 3/4 of the stomach. It narrows anteriorly and continues into a short intestine, which bends at right angle to the right of the style sac, running first horizontally and then descending vertically at right angles and continuing as a short longitudinal ventral tract before leading to the rectum. The brownish-green digestive gland is composed of two lobes, a left lobe quite developed extending from the posterior end of the stomach to the tip of the visceral mass, and a right one reduced, nestled between the intestinal loop and the right flank of the style sac. Both lobes open independently into the stomach through their corresponding main digestive gland ducts. The orifice of the right digestive gland duct opens ventro-laterally to the left of the stomach, at the entrance of the style sac, shortly in front of the main transversal fold, dividing the two gastric chambers. The orifice of the left digestive gland duct opens immediately behind the entrance of the posterior oesophagus opposite to the anterior end of the gastric shield. There is a narrow sorting area, with short parallel folds at the right wall of the stomach spanning the main transversal fold and the posterior gastric chamber (gastric shield). At the left wall of the posterior gastric chamber, short parallel folds run posteriorly from the entrance of the oesophagus.

#### Radula (Fig. 9A)

The taenioglossate radula has a powerful central tooth flanked on either side by one lateral and two marginal teeth. The rachidian tooth is trapezoidal with its base broader than its cutting edge. The rachidian cutting edge has a prominent central lancet-shaped main cusp and lat-



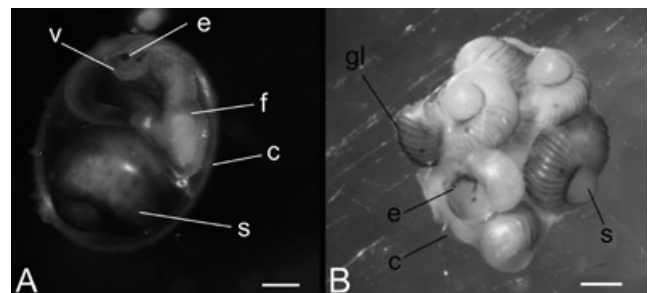
**Fig. 9:** Scanning electron microscopy of the radula of *Dendropoma lebeche* sp. nov. (A) and *D. cristatum* (B). Scale bars = 50  $\mu$ m.

erally a variable number of small denticles. The latter apparently tend to fuse in some teeth into three larger lateral cusps. The lateral tooth is rectangular, with a triangular cutting edge protruding as a central main cusp flanked on its internal margin by a subdistal lateral cusp and at its outer margin by up to four smaller lateral denticles, which may be partially eroded. The inner marginal tooth is somewhat slenderer than the lateral, hooked, with a prominent median slender cusp flanked at its inner margin by a subdistal lateral cusp and at its outer margin by two lateral cusps sometimes eroded in the used part of the radula. Outer marginal teeth hooked with a single subdistal cusp at their inner margins.

#### Embryonic and larval development

Calvo *et al.* (1998) detailed the reproductive biology of this species as *D. petraeum*. Up to 90 transparent, ovate-spheroid egg capsules are brooded free inside the mantle cavity of females (Table 1), but normally between 30 and 60 egg capsules are found in each brooding female. The size of the egg capsules varied from 575 to 1,260  $\mu$ m in maximum diameter, and each one contained a single embryo (Fig. 10A), rarely two.

The larval development is entirely intracapsular lecithotrophic without a pelagic larval phase. The single large egg within each egg capsule measures almost 500  $\mu$ m in diameter before cleavage. Nurse eggs were absent and the



**Fig. 10:** A, egg capsule of *Dendropoma lebeche* sp. nov. containing a single metamorphosed young snail; B, egg capsule of *Dendropoma cristatum* containing twelve metamorphosed young snails (c, capsule wall; e, eye; f, foot; gl, growth line; s, shell; v, velar lobe). Scale bars A = 0.1 mm; B = 250  $\mu$ m.

**Table 1.** Reproductive traits of Mediterranean cryptic species of the genus *Dendropoma* (data of *D. anguliferum* from Usvyatsov & Galil, 2012 as *D. petraeum*).

Trait	<i>D. lebeche</i> sp. nov. (W Mediterranean)	<i>D. cristatum</i> (Sicily)	<i>D. anguliferum</i> (Israel)
N° capsules/female	up to 90	up to 14	up to 27
Capsule diameter (mm)	0.58-1.26	1.60-2.20	0.96-1.62
N° eggs/capsule	1	9-30	5-14
Egg diameter (µm)	460-490	350-410	?
Protoconch length (µm)	580-720	740-830	?
Nurse eggs	no	yes	yes

yolk of the single embryo is likely to be the main source of intracapsular nutrition and is enough to complete development. Metamorphosis takes place within the egg capsule when the embryonic yolk supply is totally consumed. Hatching occurs at a crawling juvenile stage.

### Etymology

The epithet *lebeche* is a noun in apposition (the gender of *Dendropoma* is neuter) after the dominant southwest wind, called “Lebeche”, in the area of the type locality.

### Ecology

This gregarious vermetid forms compact bioconstructions cemented by encrusting coralline algae, mainly *Neogoniolithon brassica-florida*, but also *Lithophyllum incrustans* and *L. byssoides*. Both species (mollusc and alga) form concretions of different shapes and thicknesses in moderately exposed zones free of pollution and with low rates of sedimentation. These bioconstructions develop different morphologies (Fig. 11), from thin mono-layer encrustations over the rocky surfaces (Fig. 11A) to complex voluminous structures (Fig. 11C-D). They typically assume the aspect of a raised ridge up to 15-20 cm thick along the seaward edge of abrasion platforms at low intertidal levels. The raised rim is composed predominantly of dead vermetid shells cemented together by coralline algae, and only its surface is coated by living vermetids. These organic crusts also form irregular ridges and rounded cushion-like structures on horizontal rocky surfaces or ledges around rocks, becoming micro-atolls surrounding partially submerged rocks. The upper surface of these aggregations often coincides with the biological mean sea level, but some isolated and irregular aggregates of this vermetid can be found subtidally (Fig. 11B) down to 5-6 m deep in barren rocky surfaces which have occurred due to overgrazing by sea urchins.

Densities peak just bellow mean sea level, where this species forms continuous thick crusts together with the encrusting coralline algae. The population density in dense aggregates ranges normally between 400 and 600 individuals per dm<sup>2</sup>.

*Dendropoma lebeche*, in association with encrusting coralline algae, tends to monopolize the hard substrate, and both species (the gastropod and the coralline algae) may function as habitat engineers in the lower midlittoral fringe of the southwestern Mediterranean when growing together. Below this level, there is a dense belt of brown frondose algae mostly of the genus *Cystoseira*, which forms dense canopies and dominates the upper sublittoral in sites with high coastal water quality and hydrodynamic conditions which are high indirect to moderate (Montesanto & Panayotidis, 2001; JT pers. obs).

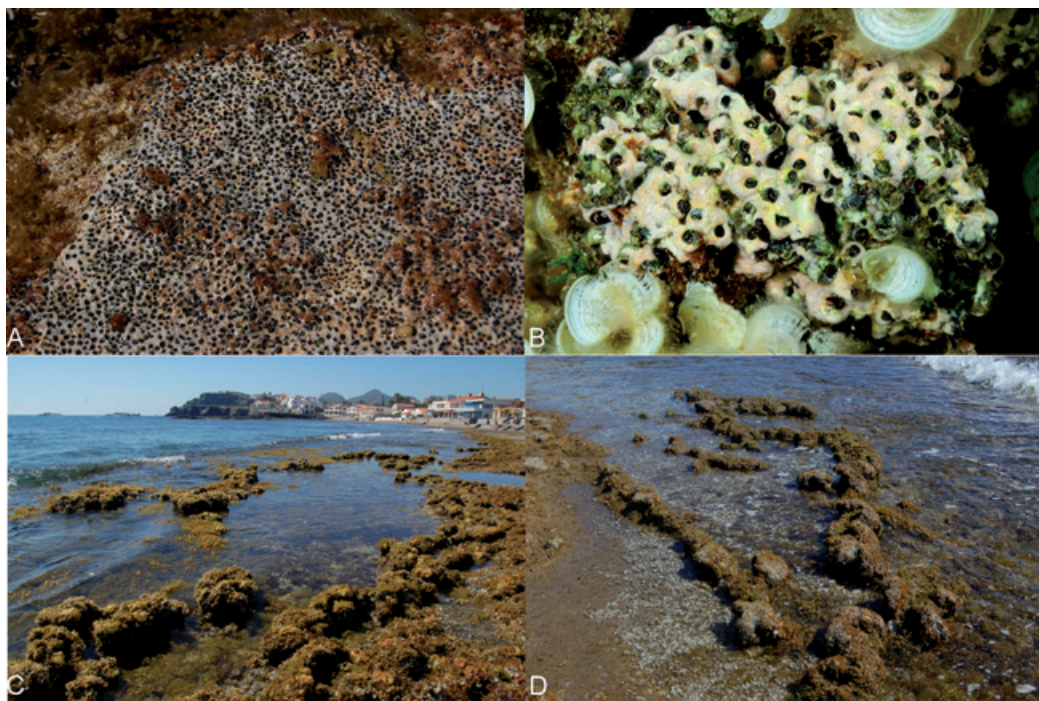
### Distribution (Fig. 1):

This new species is distributed in the southwestern Mediterranean and neighbouring Atlantic coasts. Its northwestern limits are located at Punta Prima (Menorca), in the Balearic Islands, and in Ebro Delta (Tarragona) in the Mediterranean coast of the Iberian Peninsula. On the African Mediterranean coast its known easternmost limit is located in Cape Bon, Tunisia. It presents discontinuous distribution on all the low rocky coasts of the Algerian coast (particularly in the Cherrchell-Hadjaret Ennous sector, Sidi Ghiles and the Sefah cove, particularly between Sidi Ghiles and Hadjaret Ennous) (UNEP/MAP, 2012). Its westernmost limit in the European Atlantic coast is placed in Conil (36.285533° N, 6.09086111° W), Cádiz, near the Strait of Gibraltar, and the known westernmost limit in the south is located in the area of Casablanca (33.71028611° N, 07.37250278° W), Morocco. Some shell aggregations related to the last interglacial deposit (aged as approximately 130 ka) in the eastern Canary Islands (Lanzarote and Fuerteventura, studied by González-Delgado *et al.* (2005) could be attributed to this species. The limited bathymetric range of this species results in an effectively one-dimensional coastal distribution.

### Remarks

The reef-building vermetid gastropods in the Mediterranean-Atlantic region are restricted to the Mediterranean basin and neighbouring Atlantic coasts of south Spain and northwestern Morocco. At present they are





**Fig. 11:** Bioconstructions formed by *Dendropoma lebeche* sp. nov. and coralline algae (all from the type locality). A, Monolayer encrustation, B, detail of a sublittoral aggregate, C-D, reefs partially covered by brown algae.

absent south until Senegal (JT pers. obs.), probably due to the cold Canary current and Saharan upwelling, which may act as a thermal barrier to the Mediterranean species with tropical affinities as noted by Vermeij (2012) for other molluscs. The new species of *Dendropoma* described differs from the other morphological similar species mainly by genetic divergence (about 14% divergence in COI sequences and 9-10% in 16S). Furthermore, *D. lebeche* differs from the other Mediterranean species of the complex by the large numbers of egg capsules incubated simultaneously by females (up to 90), each containing a single egg. In other species, females incubate fewer egg capsules, each containing a variable number of eggs.

On the tropical coasts of west Africa there are several gregarious species of *Dendropoma* (most of them undescribed) which form bioconstructions with calcareous algae (JT pers. obs.). Keen & Morton (1960) described two of these species (*D. marchadi* from Senegal, and *D. ghanaense* from Ghana), both being larger than *D. lebeche* and forming more tightly clustered colonial forms.

The most similar gregarious species in the Caribbean area is *D. corrodens* (D'Orbigny, 1842), which incubates up to eight egg capsules containing a variable number of embryos (Miloslavich & Penchaszadeh, 1992) and presents a high genetic divergence from the Mediterranean species of this genus (Calvo *et al.*, 2009; Golding *et al.* 2014).

A gregarious species that forms compact aggregations with coralline algae occurs in the Gulf of Sinai, considered a sister species of *D. meroclistum* Hadfield &

Kay, 1972 by Safriel & Hadfield (1988). This species has been recently named and formally described as *Cupola-concha sinaiensis* by Golding *et al.* (2014), and clearly differs from *D. lebeche* in its calcareous operculum, stalked egg capsules, and planktotrophic larval development with a high number of embryos per egg capsule.

#### *Dendropoma cristatum* (Biondi, 1859)

*Vermetus glomeratus* Bivona Bernardi, 1832: 7, pl. 2, fig. 5. Type locality: Isole delle Femmine, near Palermo, N Sicily [non *Serpula glomerata* Linnaeus, 1758].

*Vermetus cristatus* Biondi, 1859: 120, pl. (unnumbered), Fig. 5. Type locality: not specified but surely Acitrezza, Catania, E Sicily - Molinier (1960).

*Bivonia petraea* Monterosato, 1884: 81, 1884b: 61 [nomen novum for *Vermetus glomeratus* Bivona Bernardi, 1832]

*Spiroglyphus glomeratus* (Bivona Bernardi): Clessin, 1912: 112, 113, pl. 8 [1901], figs. 1, 2.

*Dendropoma* (*Novastoa*) *petraeum* (Monterosato): Keen (1961: 200), Vitturi *et al.* (1997:127-139).

*Bivonia cristata* (Biondi): Parenzan (1970: 96-97).

*Dendropoma petraeum* (Monterosato): Badalamenti *et al.* (1992a, 1992b), Pandolfo *et al.* (1992), Azzopardi & Schembri (1997), Antonioli *et al.* (1999), Dieli *et al.* (2001), D'Ancona *et al.* (2002), Schiaparelli *et al.* (2003, 2006), Silenzi *et al.* (2004), Vizzini *et al.* (2012), Milazzo *et al.* (2014).

*Dendropoma* (*Novastoa*) *cristatum* (Biondi): Scuderi (1995: 5), Scuderi *et al.* (1998).

*Dendropoma cristatum* (Biondi): Terlizzi *et al.* (2005).

*Dendropoma anguliferum* (Monterosato): Scaperrotta *et al.* (2012: 70).

#### Material examined:

Small pieces of aggregates from Lavezzi Islands (S Corsica); Capri Island (Gulf of Naples); San Vito Lo Capo, Isola delle Femmine, Capo Milazzo, Acitrezza, Ognina di Siracusa (Sicily); Bahar ic Caq and Qawra (Malta).

For the study of developmental features intracapsular development in live specimens from Lavezzi Islands (S Corsica) and Isola delle Femmine (N Sicily) were examined.

GenBank accession numbers EU495059- EU495067 (COI), EU495087-EU495095 (16S rRNA), EU495031-EU495039 (ITS) (Calvo *et al.*, 2009).

#### Remarks

*Bivonia petraea* was described by Monterosato (1884) from Isola delle Femmine near Palermo (Sicily) as a replacement name for *Vermetus glomeratus* Bivona, 1832 [secondary junior homonym of *Serpula glomerata* Linnaeus, 1758]. Nevertheless, Parenzan (1970) and Scuderi (1995) pointed out that *Vermetus cristatus* (Biondi, 1859) was a senior synonym of *D. petraeum*, and Parenzan (1970) accordingly used the name *Bivonia cristata* to designate the species in his book on the marine gastropods of the Mediterranean Sea. Indeed, Monterosato (1884) commented the original description of Biondi (1859) and pointed out that “Se questa identificazione sarà accertata il nome dato dal Prof. Biondi, dovrà prevalere al mio”. Later, Monterosato (1892) included *Bivonia petraea* among the synonyms of *Vermetus cristatus* in his monograph on the Mediterranean vermetids. Furthermore, *Vermetus cristatus* was the name used by the French School for this species (i.e. Pérès & Picard, 1952, Picard, 1954, Molinier, 1955, 1960). Nevertheless, the junior name *Dendropoma petraeum* is still being used in several legal lists of threatened species, such as in Appendix II of the ASPIM protocol and in Appendix 2 of the Bern Convention (Relini, 1999).

Since the name *D. petraeum* has been used to designate at least four different cryptic species (Calvo *et al.*, 2009), we propose (according to Scuderi, 1995) to consider the name *Dendropoma cristatum* (Biondi, 1859) as the valid name for the species of this complex from the central Mediterranean (Sicily as the type locality). As shown by Scuderi (1995), this is, in a strict application of ICZN rules, the oldest available name for the species currently known as *Dendropoma petraeum* (Monterosato, 1884) and has priority. Additionally, the name *Dendropoma cristatum* has been used recently by Terlizzi *et al.* (2005).

#### Description

Original description of *Vermetus cristatus* Biondi, 1859: “Questo vermeto è speciale perché il più grande non giunge a quattordici millimetri nel suo maggior diametro misurato in massa: avvolgimenti costantemente tre, distinti, ingrandendosi di molto l’ultimo. Il suo principale carattere è l’aver una cresta lungo il dorso, e d’essere molto rugoso con rughe lamelliformi avvicinate ed imbricate, prodotte dall’accrescimento della conchiglia: lo che fa vedere, che la sua forma costante è una specie d’imbuto, che il mollusco come man mano va crescendo, così sovrappone l’uno su l’altro”. [This vermetid is special because the largest one reaches up to fourteen millimeters in its maximum diameter. The whorls are always three in number, distinct, the last one increasing abruptly. Its most outstanding character is the presence of a crest along the dorsal side and a very rugose surface due to the densely imbricate lamellar folds that are produced during shell growth. It seems that this invariable shell form is a kind of funnel and that the mollusc extends each over the previous one while growing].

Teleoconch: the shell is very variable, as in *D. lebeche*, and virtually does not differ from that of the latter except in its size, which is somewhat larger: up to 4-5 mm in maximum outside whorl diameter, although shell aperture diameter in specimens from Malta is smaller and normally range between 3 and 4 mm (Azzopardi & Schembri, 1997).

Protoconch (Fig. 3B): globose, pale brown, about 800 µm in length and 680 µm in diameter. Surface initially smooth and then with axial ribs (approx. 9-12) regularly spaced. The protoconch of this species was illustrated by Scuderi *et al.* (1998: 286, fig. 2b), Scaperrotta *et al.* (2012: 70, as *D. anguliferum*), and Milazzo *et al.* (2014: 4, fig. 3). The operculum has been illustrated by Scaperrotta *et al.* (2012: 70, as *D. anguliferum*).

Soft parts: adult specimens measure approximately 2 cm in length (a colour photograph can be seen in D’Ancona *et al.*, 2002: 778, fig. 1). Soft parts are closely similar to those of *D. lebeche*, therefore, only the most striking differences with the former species will be detailed.

Mantle and mantle cavity: the anal orifice, like in *D. lebeche*, is a terminal dorso-ventral slit; however, in contrast, the outer (left) lip of the anal orifice forms dorsally a long finger-like appendix which protrudes anteriorly from the anal orifice exceeding the width and height of the anal orifice (Fig. 6B).

Male reproductive system: the male gonad lies near the digestive gland on the right side of the visceral mass, where it is enclosed by connective tissues. It is yellowish in colour, formed by tubular follicles which converge into a seminal vesicle running mid-ventrally along the visceral mass.

Female reproductive system: the ovary, found in



the same position as the testes, is creamy in colour and structurally compact (Vitturi *et al.*, 1997, and pers. obs.). The female reproductive system is grossly like in the preceding species; however, in contrast to *D. lebeche*, the blind portion of the dorsal seminal receptacle is relatively longer and forms a long bean-shaped sac which extends detached from the albumen gland farther back from the ventral seminal receptacle (Fig. 12). There is also an additional seminal receptacle associated to the right lobe of the albumen gland forming a longitudinally oriented extension.

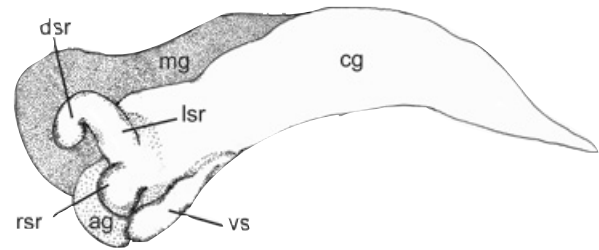
**Digestive system:** like in the preceding species, but in *D. cristatum* the right salivary gland is divided into two lobes of different sizes, the smallest one forming a small branching mass above the buccal mass, the longest one with externally a vesicular surface extending posteriorly, crossing the nerve ring and overlaying the loop of the anterior oesophagus of the trunk region. The intestine is relatively longer, and posteriorly it borders the kidney, running for a short tract backwards parallel to the style sac before turning at a right angle to the right. The pedal gland, like in *D. lebeche*, is voluminous filling roughly two-thirds of the body cavity at the level of the trunk region.

**Radula:** the radula is quite similar to that described in *D. lebeche* with a powerful trapezoidal central tooth with a strong median cusp flanked on either side by one lateral and two marginal teeth (Fig. 9B). The main differences between the two species is that in *D. cristatum*, the cutting edge of the rachidian within the same individual is uniform (not polymorphic) and bears two or three strong secondary cusps on either side of the central cusp. This differs from that in *D. lebeche*, whose rachidian has the cutting edge minutely serrated on either side of the central cusp or with a variable number of lateral denticles that tend to fuse into two to three secondary cusps. Additionally, the lateral and inner marginal teeth have a smaller number of secondary cusps, maximally three and two cusps in *D. cristatum*.

#### Reproductive biology

According to Vitturi *et al.* (1997) and D'Ancona *et al.* (2002), *D. cristatum* is a gonochoristic species with no obvious sexual dimorphism, either sex being recognizable only through examination of the gonad. Sexually mature testes were found from November-December to May-June, while ovaries appeared at the beginning of summer. Embryos at different stages of development occurred in females from June to October.

Larval development in the populations examined was lecithotrophic, entirely intracapsular without a pelagic larval stage. Females from south Corsica and around Sicily were found brooding up to 14 egg-capsules (measuring 1.60-2.20 mm in maximum diameter), each one containing up to 30 eggs (about 350-410  $\mu$ m in diameter)



**Fig. 12:** Semi-diagrammatic representations of the female palial oviduct of *Dendropoma cristatum* viewed from the right side (ag, albumen gland; cg, capsule gland; dsr, dorsal seminal receptacle; lsr, left seminal receptacle; mg, mucilaginous gland; rsr, right seminal receptacle; vsr, ventral seminal receptacle). Scale bar = 0.45 mm.

(Table 1). Some of the embryos acted as nurse eggs and were consumed by the developing embryos.

#### Kariology

According to Vitturi *et al.* (1997), the modal diploid number of chromosomes of *D. cristatum* (as *D. petraeum*) was found to be  $2n = 34$ ; whatever the sex of specimens examined none possess differentiated sex chromosomes.

#### Ecology

According to Antonioli *et al.* (1999) the bioconstructions of *Dendropoma cristatum* can develop into several morphologies: encrustations, ledges, platforms or “true reefs”, “mushroom-like” structures, and microatolls. Ledges and encrustations are common in coastal areas which are still subjected to vermetid colonisation or which are partially hindered by the unfavourable morphology of high energy coasts. *Dendropoma cristatum* reefs commonly colonise abrasion platforms generated through the action of high tide surf. Chemello (2009) described the distribution and structure of vermetid platforms and pointed out that the main reefs of *D. cristatum* (as *D. petraeum*) are located on the northwestern coast of Sicily. The overall features of the intertidal *Dendropoma* platforms in this area were outlined by Badalamenti *et al.* (1992 a, b) and Dieli *et al.* (2001). Some information on the populations of the eastern coast of Sicily and observations on the shell morphology related to population density are reported by Scuderi *et al.* (1998). Azzopardi & Schembri (1997) pointed out that the vermetid crusts in Malta are much less developed than those described in Sicily.

Schiaparelli *et al.* (2006) pointed out a certain degree of variability, over a geographical scale, in the feeding strategies of *D. cristatum*, according to the depth at which the bioconstructions were formed. These authors used the relationship linking the ctenidium surface area and the body weight to infer the feeding mode (i.e., ciliary or mucus-net filter feeding). They stated that in the



populations of this species studied, those at the upper limit of the infralittoral zone (in Sardinia and Sicily) were composed of true ciliary filter-feeders, while those at 4 m depth (in the Naples area) shifted to mucus-net feeding. In fact, the populations of the Gulf of Naples exhibit a remarkable genetic divergence with the other population studied by Calvo *et al.* (2009). Vizzini *et al.* (2012) studied the contribution of planktonic and benthic food sources to the diet of this species, and their results revealed a flexibility in the exploitation of food resources and diet shift at a small spatial scale: in sheltered sites, the snails fed predominantly on benthic food resources (epilithic), while in exposed sites, they mostly exploit suspended organic matter supplied by the waves.

#### Distribution (Fig. 1)

Corsica: reported in Cap Corse in the north, where it is considered extinct (Antonioli *et al.*, 1999) and needs further confirmation through direct observation (Chemello, 2009; Chemello & Silenzi, 2011), present in Lavezzi Islands in the south. Sardinia: northeast coast (Schiaparelli *et al.* 2003). Scattered along the mainland coast of Italy and nearby islands: Licosia (Campania), Campomarino (Apulia), Capo Rizzuto (Calabria) and Ischia, in the Gulf of Naples (Scuderi *et al.*, 1998; Chemello, 2009; Chemello & Silenzi, 2011). Sicily: irregularly distributed along the northwest coast between Egadi islands, Trapani and Cefalù, province of Palermo, and on the east coast between Capo Milazzo, Tyrrhenian coast of Messina and Capo Murro di Porco, Siracusa; it is absent in other places along the Sicilian coast, such as the Eolian islands, probably due to unsuitable environmental conditions (Scuderi *et al.*, 1998; Chemello *et al.*, 2000; Chemello, 2009). Further south from Sicily, it is also present in the Pelagie Islands, Lampedusa and Linosa in the Siculo-Tunisian Strait (Agrigento) (Chemello *et al.*, 1990; 2000, Scuderi *et al.*, 1998). Malta: mainly on its northeast coast (Azzopardi & Schembri, 1997).

#### Discussion

A cryptic species complex was documented by Calvo *et al.* (2009) under the name *D. petraeum*, composed of at least four genetically divergent clades in the Mediterranean Sea. Morphological stasis has been maintained in these reef-building vermetid gastropods despite major genetic divergence among lineages (Calvo *et al.*, 2009). The species of this complex share the same morphological characteristics in such way that they are hard to distinguish if their place of origin is not known. All of them inhabit similar habitats and play the same ecological role. Therefore, they can be considered as ecologically equivalent. The four genetic lineages of Mediterranean *Dendropoma* (as revealed by Calvo *et al.*, 2009), here considered as different species, showed a clearly delimit-

ed geographic distribution in a west-east direction. The lineage of the western Mediterranean has been described here as a new species and named *Dendropoma lebeche*. The Tyrrhenian-Sicilian lineage is considered as the true *D. petraeum*, whose valid name should be *Dendropoma cristatum* according to Scuderi (1995). The lineage extending along the Ionian-Aegean coasts needs a new name, since there is none available in the literature. Finally, we propose the available name *Dendropoma anguliferum* (Monterosato, 1878) for the Levantine clade, since its type locality is Tripoli (north coast of Lebanon). Neither the original description nor the type material of this taxon (stored in the Museo Civico di Zoologia in Rome), studied by D. Scuderi (pers. comm.), allow it to be distinguished from *D. cristatum* as the shell characters are not sufficient, but genetic studies on specimens collected near the type locality (Calvo *et al.*, 2009) proved that they belong to a different species.

A recent phylogenetic analysis by Golding *et al.* (2014) using morphological, anatomical, and molecular data concludes that the genus *Dendropoma* s.l. is not monophyletic and composed of at least by four robustly supported genera. According to these authors, all the species from the Mediterranean Sea belong to the genus *Dendropoma* s.s..

Although the two species here studied (*D. cristatum* and *D. lebeche*) cannot be clearly distinguished on the basis of adult shell morphology or easily visible anatomical features, previous molecular studies (based on sequence analyses of COI and 16S mitochondrial markers) showed high levels of mitochondrial genetic divergences (Calvo *et al.*, 2009, 2015). Such high genetic differences are enough to consider that they are two different species, despite the almost identical morphological characters. Both species are geographically separated, presumably suggesting an allopatric origin with no habitat diversification. In the present paper, phenotypic characters are provided that allow differentiation of both species, thus reinforcing their taxonomic and biological distinctions. Differences lie mainly in the intracapsular larval development, in the protoconch and teleoconch sizes, and in the soft parts. Females of *Dendropoma lebeche* brood up to 90 egg capsules, each one containing a single large egg, while females of *D. cristatum* brood up to 14 larger egg capsules, each containing up to approximately 30 smaller eggs, some of which are used as nurse eggs. Hence, differences between the two species consist in the number and size of the egg capsules simultaneously brooded by females, the number and size of eggs/embryos contained within each capsule, and the presence/absence of nurse eggs. In *D. anguliferum* from Israel, females brood up to 27 capsules containing up to 14 eggs, most of them probably used as nurse eggs, and normally only one developing embryo (Usvyatsov & Galil, 2011 as *D. petraeum*).

Differences are appreciated in the protoconch with irregular growth lines in *D. lebeche* and raised, regularly

concentric ribs in *D. cristatum*, in the size of the adult which are somewhat larger in *D. cristatum*, and in some details of the radula (fewer and larger lateral cusps in the cutting edge of the rachidian and lateral teeth). The internal anatomy is also very similar in both species: only slight differences have been noted in the dorsal seminal receptacle (longer and bean shaped in *D. cristatum*), in the right salivary gland (bilobed in *D. cristatum*), in the relative length and winding of the intestine (longer in *D. cristatum*, describing a loop running posteriorly parallel to the style sac), and in the lip of the anal orifice (forming dorsally a long finger-like appendix in *D. cristatum*, absent in *D. lebeche*).

Within marine gastropods, vermetids form a problematic group in which species boundaries are often difficult to assess because of the small number of diagnostic characters and the extreme plasticity of their irregular tube shells. Cryptic speciation within the genus *Dendropoma* was previously detected by Safriel & Hadfield (1988), who described the existence of apparent sibling species under the name *Dendropoma meroclista* Hadfield & Kay, 1972 in the Indo-Pacific. These authors distinguished two morphologically similar species on the basis of developmental characters. Therefore, once species boundaries were delimited by genetic or developmental data in this difficult group of gastropods, diagnostic morphological characters for each species should be searched for in order to allow a formal description and to facilitate identification, although the International Code of Zoological Nomenclature allows describing and naming species based on molecular data only. The detection of cryptic species by molecular methods increases our knowledge of the true diversity in the world oceans, but it is not enough by itself, since formal taxonomic descriptions should accompany the new species to ensure the usefulness of their discovery (Schlick-Steiner, 2007; Blanquer & Uriz, 2008) and to allow the use of the correct names. Within the genus *Dendropoma*, genetic and developmental features appear to diverge more rapidly than morphological characters. Such patterns of high genetic variation coupled with discrete morphological differentiation is most likely associated with recent speciation processes (Schluter, 2000) and cryptic species complexes, which are more frequent than expected in many marine species (Knowlton, 1993).

This study exemplifies the difficulty in finding phenotypic and biological characters that allow separating sibling species even when highly genetically divergent, especially in those groups with a shortage of discrete characters, such as rotifers (Fontaneto *et al.*, 2009), or species with a high phenotypic plasticity in key taxonomical traits such as sponges (Blanquer & Uriz, 2008), but also in some gastropods such as limpets (Ridgway *et al.*, 1998), calyptraeids (Véliz *et al.*, 2003; Collin, 2005), mesopsammic sea slugs (Jörger & Schrödl, 2013), or in *Dendropoma* species (present study). However, morpho-

logical and biological differences become evident when the species are carefully studied from living specimens collected at different localities along their entire range of distribution.

On the other hand, the identification and description of cryptic species have important implications for conservation and natural resource protection and management. In fact, molecular evidence has revealed that several endangered species are formed by a mosaic of cryptic species, making them a collection of even more critically endangered species with fewer populations and smaller distribution areas (Bickford *et al.*, 2007) than previously thought. Therefore, the contribution of cryptic species to current figures of biodiversity at regional and global scales should be carefully evaluated and taken into account in conservation planning. Research on cryptic species following an integrative approach combining molecular analysis with studies on the ecology and life history strategies of species complexes can also provide valuable insights into the evolutionary and ecological processes leading to genetic divergence and reproductive isolation in the absence of morphological differentiation.

*Dendropoma petraeum* is included in Annex II (Endangered or Threatened Species) of the Protocol for Specially Protected Areas and Biodiversity in the Mediterranean (Barcelona Convention), and its reefs have been listed as threatened biostructures in the Mediterranean Red Data Book (UNEP/IUCN/GIS Posidonie, 1990). Whereas the cryptic *Dendropoma* species complex had a broad geographical range along all Mediterranean Sea coasts, true biological species in this complex have more limited distributions in different sub-basins within this sea, making each more prone to extinction. Indeed Galil (2013) and Rilov (2013) have both drawn attention to the fact that populations along the Israeli coast have been decimated, if not made entirely extinct; therefore, all the species comprising the so-called *Dendropoma petraeum* species complex should be included in Annex II of Endangered or Threatened Species of the Barcelona Convention and in the national red lists of the countries where they inhabit.

## Acknowledgements

We are grateful to the following colleagues and organizations for providing support or samples: P. J. Schembri, J. Guallart, O. Ocaña, DK Kersting, D. Scuderi, C. Megina, J. Zapata, and A. Machordom, the staff of the Biological Station of the Chafarinas Islands, Organismo Autónomo de Parques Nacionales (Spanish Ministry of Environment) and the “Dirección General de Conservación de la Naturaleza”. We would like to thank also D. Scuderi, R. Bieler and E. Strong for the revision of a first version of this article and for their constructive suggestions and input. Marco Oliverio, Renato Chemello and

Stefano Schiaparelli provided some comments and suggestions as editor and reviewers respectively that greatly improved the paper. N. Yonow corrected the English. This study was supported by BBVA Foundation and by the projects CGL2011-23306 (from the Spanish Ministry of Science and Innovation), and COCONET (“Towards COast to COast NETworks of marine protected areas, coupled with sea-based wind energy potential”) from the VII FP of the European Commission. Part of the research was also supported by an ES-TAF-3701 Synthesis grant to the second author, who acknowledges Museo Nacional de Ciencias Naturales for allowing access and use of the research infrastructure. We also thank the “Dirección General de Conservación de la Naturaleza” of the Spanish Ministry of Environment.

## References

- Al-Nimeh, M., Ellassafin, I., 1996. Vermetid reefs (Gastropoda: Vermetidae) on the coast of Syria. *Zoology in the Middle East*, 13, 89-92.
- Antonioli, F., Chemello, R., Improta, S., Riggio, S., 1999. *Dendropoma* intertidal reef formations and their paleoclimatological significance, NW Sicily. *Marine Geology*, 161, 155-170.
- Azzopardi, L., Schembri, P.J., 1997. Vermetid crusts from the Maltese Islands (Central Mediterranean). *Marine Life*, 7 (1-2), 7-16.
- Badalamenti, F.R., Chemello, R., Cristina, M., Riggio, S., Toccacelli, M., 1992a. Caratterizzazione delle piattaforme a Molluschi Vermetidi nella costa della Riserva Naturale dello Zingaro (TP). *Oebalia*, suppl., 17, 543-545.
- Badalamenti, F.R., Chemello, R., Cristina, M., Riggio, S., Toccacelli, M., 1992b. Caratterizzazione delle piattaforme a Molluschi Vermetidi nella costa fra Capo Gallo ed Isola delle Femine (PA): area proposta come riserva naturale marine. *Oebalia* suppl., 17, 547-549.
- Bakır, B.B., Öztürk B., Doğan, A., Önen, M., 2012. Mollusc Fauna of Iskenderun Bay with a Checklist of the Region. *Turkish Journal of Fisheries and Aquatic Sciences*, 12, 171-184.
- Bieler R., Petit, R.E., 2011. Catalogue of Recent and fossil “worm-snail” taxa of the families Vermetidae, Siliquariidae, and Turritellidae (Mollusca: Caenogastropoda). *Zootaxa*, 2948, 1-103.
- Bickford, D., Lohman D., Sodhi, N.S., Ng, P.K.L., Meier, R. et al., 2007. Cryptic species as window on diversity and conservation. *Trends in Ecology and Evolution*, 22 (3), 148-155.
- Biondi, S., 1859. Descrizione di alcune specie malacologiche nuove che vivono nel nostro litorale. *Atti dell'Accademia Gioenia di Scienze Naturali, Catania, Sezione 2* (14), 114-124.
- Bitar, G., Bitar-Kouli, S., 1995. Aperçu de bionomie benthique et repartition des différents faciès de la roche littorale à Hannouch (Liban, Méditerranée orientale). *Commission Internationale pour l'Exploration Scientifique de la Méditerranée*, 34: 19.
- Bivona Bernardi Ant. 1832. Caratteri dei vermeti desunti da cinque specie che abitano nel mare di Palermo. *Effemeridi Scientifiche e Letterarie per la Sicilia*, 1, 59-62.
- Blanquer, A., Uriz, M.J., 2008. ‘A posteriori’ searching for phenotypic characters to describe new cryptic species of sponges revealed by molecular markers (Dyctyonellidae: Scopalina). *Invertebrate Systematics*, 22, 489-302.
- Calvo, M., Alda, F., Oliverio, M., Templado, J., Machordom, A., 2015. Surviving the Messinian Salinity Crisis? Divergence patterns in the genus *Dendropoma* (Gastropoda: Vermetidae) in the Mediterranean Sea. *Molecular Phylogenetic and Evolution*, 91, 17-26.
- Calvo, M., Templado, J., 2005. Spermatophores of three Mediterranean species of vermetid gastropods (Caenogastropoda). *Journal of Molluscan Studies*, 71, 301-303.
- Calvo, M., Templado, J., Oliverio, M., Machordom, A., 2009. Hidden Mediterranean biodiversity: molecular evidence for a cryptic species complex within the reef-building gastropod *Dendropoma petraeum* (Mollusca: Caenogastropoda). *Biological Journal of the Linnean Society*, 96 (4), 898-912.
- Calvo, M., Templado, J., Penchaszadeh, P., 1998. Reproductive biology of the gregarious mediterranean vermetid gastropod *Dendropoma petraeum*. *Journal of the Marine Biological Association of UK*, 78, 525-549.
- Checa, A.G., Jiménez, A., 1998. Constructional morphology, origin, and evolution of the gastropod operculum. *Paleobiology*, 24 (1), 109-132.
- Chemello, R., 2009. Le bioconstruzioni marine in Mediterraneo. Lo stato delle conoscenze sui reef a vermeti. *Biologia Marina Mediterranea*, 16 (1), 2-18.
- Chemello, R., Dieli, T., Antonioli, F., 2000. Il ruolo dei “reef” a molluschi vermetidi nella valutazione della biodiversità. 105-118. In: *Mare e cambiamenti globali*. Quaderni ICRAM, Roma.
- Chemello, R., Pandolfo, A., Riggio, S., 1990. Le bioconstruzioni a Molluschi Vermetidi nella Sicilia Nord-Occidentale. *Atti 53° Congresso UZI*, Palermo, 60.
- Chemello R., Silenzi, S., 2011. Vermetid reefs in the Mediterranean Sea as archives of sea-level and surface temperature changes. *Chemistry and Ecology*, 27 (2), 121-127.
- CLEAM. Check List of European Marine Mollusca. <http://www.somali.asso.fr/clemam/index.clemam.html> (accessed 21 April 2015).
- Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F. et al., 2010. Biodiversity of the Mediterranean Sea: status, patterns and threats. *PloS ONE*, 5 (8), e11842. doi:10.1371.
- Collin, R., 2005. Development, phylogeny, and taxonomy of *Bostrycapulus* (Caenogastropoda: Calyptraeidae), an ancient cryptic radiation. *Zoological Journal of the Linnean Society*, 144, 75-101.
- Colombo, F., Costa, V., Dubois, S.F., Gianguzza, P., Mazzola, A. et al., 2013. Trophic structure of vermetid reef community: High trophic diversity at small spatial scales. *Journal of Sea Research*, 77, 93-99.
- D’Ancona Lunetta, G., Damiani, F., 2002. Spermiogenesis in the vermetid gastropod *Dendropoma petraeum* (Gastropoda, Prosobranchia). *Eur. Journal of Histochemistry*, 46, 75-86.
- Dalongeville, R., 1977. Formes littorales de corrosion dans les roches carbonatées du Liban: étude morphologique. *Méditerranée*, 3, 21-33.
- Dalongeville R., Laborel, J., Pirazzoli, P., Sanlaville, P., Ar-



- nold, M. *et al.*, 1993. Les variations recentes de la ligne de rivage sur le littoral Syrien. *Quaternaire*, 4 (1), 45-53.
- De Quadrefages A., 1854. *Souvenirs d'un Naturaliste*, 1. Paris, 521 pp.
- Dieli, T., Chemello, R., Riggio, S., 2001. Eterogeneità strutturale delle formazioni a vermeti (Mollusca: Caenogastropoda) in Sicilia. *Biologia Marina Mediterranea*, 8 (1), 223-228.
- Fontaneto, D., Kaya, M., Herniou, E. A., Barraclough, T.G., 2009. Extreme levels of hidden diversity in microscopic animals (Rotifera) revealed by DNA taxonomy. *Molecular Phylogenetics and Evolution*, 53, 182-189.
- Galil, B.S., 2013. Going going gone: the loss of a reef-building gastropod (Mollusca: Gastropoda: Vermetidae) in the Mediterranean Sea. *Zoology in the Middle East*, 59 (2), 179-182.
- García Raso, J.E., Luque, A.A., Templado, J., Salas, C., Heragueta, E. *et al.*, 1992. *Fauna y flora marinas del Parque Natural de Cabo de Gata Níjar*. Madrid, 288 pp.
- Golding, R.E., Bieler, R., Rawlings, T.A., Collins, T.M., 2014. Deconstructing *Dendropoma*: a systematic revision of a world-wide worm-snail group with description of new genera (Caenogastropoda: Vermetidae). *Malacologia*, 57 (1), 1-97.
- González-Delgado, J.A., Zazo, C., Goy, J.L., Civis, J., Templado, J. *et al.*, 2005. Paleoenvironmental significance of C and O isotopic signal in last interglacial gastropod *Dendropoma* shell concentrations from Canary (Spain) and Sal (Cape Verde) Islands. *Revista de la Sociedad Geológica de España*, 18 (3-4), 207-211.
- Hughes, R.N., 1979. Colonialism in Vermetidae. In: *Biology and Systematics of Colonial Organisms*. Systematics Association, Special Volume, 11. 243-253. Larwood G., Rosen, B.R. (Eds.). Academic Press, London
- Jörger, K.M., Schrödl, M., 2013. How to describe a cryptic species? Practical challenges of molecular taxonomy. *Frontiers in Zoology*, 10 (1): 59, 27 pp. doi: 10.1186/1742-9994-10-59.
- Keen, A.M., 1961. A proposed reclassification of the gastropod family Vermetidae. *Bulletin of the British Museum of Natural History (Zoology)*, 7 (3), 181-213.
- Keen, A.M., Morton, J.E., 1960. Some new African species of *Dendropoma* (Vermetidae: Mesogastropoda). *Proceedings of the Malacological Society of London*, 34, 36-51.
- Kelletat, D., 1979. Geomorphologische Studien an den Küsten Kretas. *Abhandlungen der Akademie der Wissenschaften in Göttingen. Mathematisch-Physikalische Klasse*, 32, 1-105.
- Knowlton, N., 1993. Sibling species in the sea. *Annual Review of Ecology and Systematics*, 24, 189-216.
- Laborel, J., 1987. Marine biogenic constructions in the Mediterranean. *Scientific Reports Port-Cros National Park*, 13, 97-126.
- Laborel, J., Laborel-Deguen, F., 1994. Biological indicators of relative sea-level variations and of co-seismic displacements in the Mediterranean region. *Journal of Coastal Research*, 10 (2), 395-415.
- Milazzo, M., Rodolfo-Metalpa, R., Chan, B.S., Fine, M., Alessi, C. *et al.*, 2014. Ocean acidification impairs vermetid reef recruitment. *Scientific Reports*, 4, 4189, DOI: 10.1038/srep04189.
- Miloslavich, P.A., Penchaszadeh, P.E., 1992. Reproductive biology of *Vermetus* sp. and *Dendropoma corrodens* (Orbigny, 1842): two vermetid gastropods from the southern Caribbean. *The Veliger*, 35 (1), 78-88.
- Molinier, R., 1954. Première contribution à l'étude des peuplements superficiels des îles Pithyuses (Balears). *Vie et Milieu*, 5 (2), 226-242.
- Molinier, R., 1955. Les plates-formes et corniches récifales de Vermets (*Vermetus cristatus* Biondi) en Méditerranée occidentale. *Comptes Rendus de l'Académie des Sciences, Paris*, 240, 2-166.
- Molinier, R., 1960. Etude des biocénoses marines du Cap Corse. *Vegetatio*, 9, 121-312.
- Molinier, R., Picard, J., 1953. Notes biologiques a propos d'un voyage d'étude sur les cotes de Sicile. *Annales de l'Institut Océanographique*, 28 (4), 163-188.
- Molinier, R., Picard, J., 1956. Aperçu bionomique sur les peuplements marins littoraux des côtes rocheuses méditerranéennes de l'Espagne. *Bulletin des travaux publiés par la Station d'Aquiculture et de Pêche de Castiglione*, nouvelle série, 8, 1-17.
- Monterosato, T.A., (di), 1884. *Nomenclatura generica e specifica di alcune conchiglie mediterranee*. Naturalista Siciliano, Palermo, 152 pp.
- Monterosato, T.A. (di), 1892. Monographia dei Vermeti del Mediterraneo. *Bulletino della Società Malacologica Italiana*, 17, 7-48, pls. 1-7.
- Moreno, D., 2008. *Dendropoma petraeum* (Monterosato, 1884). pp. 323-329. In: *Libro rojo de los invertebrados de Andalucía*. Barea-Azcón J.M., Ballesteros-Duperón, E., Moreno, D. (Eds.). Consejería de medio Ambiente, Junta de Andalucía, Sevilla.
- Moreno, D., Templado, J., 1994. El complejo de especies "*Nassarius cuvierii*-*N. unifasciatus*" (Gastropoda, Nassariidae) en el SE de España. *Iberus*, 12 (2), 33-47.
- Nardi, G., Scuderi, D., 1999 (2000). Inquadramento sistematico e distribuzione geografica di *Vermetus* (*Vermetus*) *rugulosus* (Monterosato, 1878) (Mollusca: Gastropoda): ritrovamento e nuova iconografia. *La Conchiglia*, 31 (293), 47-49.
- Naylor, L.A., Viles, H.A., 2002. A new technique for evaluating short-term rates of coastal bioerosion and bioprotection. *Geomorphology*, 47, 31-44.
- Oliverio, M., 1994. Development vs genetic variation in two Mediterranean rissoid gastropod complexes. *Journal of Molluscan Studies*, 60, 461-465.
- Pandolfo, A., Chemello, R., Riggio, S., 1992. Notes sur la signification écologique de la faune d'un "Trottoir à vermetes" le long de la côte de Palerme (Sicile). *Oebalia*, supplement 17, 379-382.
- Parenzan, P., 1970. *Carta d'indentità delle conchiglie del Mediterraneo. Vol I. Gasteropodi*. Bios Taras (Eds.). Taranto, Italy, 283 pp.
- Pérès, J.M., Picard, J., 1952. Les corniches calcaires d'origine biologique en Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume*, 4, 2-23.
- Picard, J., 1954. Les formations organogènes benthiques méditerranéennes et leur importance géomorphologique. *Recueil des Travaux de la Station Marine d'Endoume*, 13, 55-76.
- Pirazzoli, P., Laborel, J., Stiros, S.C., 1996. Coastal indicators of rapid uplift and subsidence: Exemples from Crete and other Eastern Mediterranean sites. *Zeitschrift für Geomorphologie, suppl.* 102, 21-35.
- Ramos-Esplá, A., Cebrián, D., Demetropoulos, A., 2007. *Inte-*

- grated Coastal Area Management in Cyprus. UNEP-MAP RAC/SPA, Tunis, 69 pp.
- Rawlings, T.A., Bieler, R., Collins, T.M., 2001. Sessility, suspension-feeding, and uncoiling: exploring the evolutionary radiation of vermetid gastropods. pp. 283. In: *Abstracts, World Congress of Malacology 2001*. Salvini-Plawen, L., Voltzow, J., Sattmann, H., Steiner, G. (Eds.) Unitas Malacologica, Vienna
- Relini, G., 1999. L'Italia e la protezione della biodiversità in Mediterraneo. *Biologia Marina Mediterranea*, 6 (1), 151-171.
- Ridgway, T.M., Stewart, B.A., Branch, G.M., Hodgson, A.N., 1998. Morphological and genetic differentiation of *Patella granularis* (Gastropoda: Patellidae): recognition of two sibling species along the coast of southern Africa. *Journal of Zoology*, 245 (3), 317-333.
- Rilov, G., 2013. Regional extinctions and invaders' domination: an ecosystem phase-shift of Levant reefs. *Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, 40, 782-783.
- Russo, G.F., Patti, F. P., 2005. Early life history of two closely related gastropods, *Rissoa auriscalpium* and *Rissoa italiensis* (Caenogastropoda: Rissoiidae). *Marine Biology*, 147, 429-437.
- Safriel, U.N., 1966. Recent vermetid formation on the Mediterranean coast of Israel. *Proceedings of the Malacological Society of London*, 37, 27-34.
- Safriel, U.N., 1974. Vermetid gastropods and intertidal reefs in Israel and Bermuda. *Science*, 186, 1113-1115.
- Safriel, U.N., 1975. The role of vermetid gastropods in the formation of Mediterranean and Atlantic reefs. *Oecologia*, 20, 85-101.
- Safriel, U.N., Ben-Eliahu, M.N., 1991. The influence of habitat structure and environmental stability on the species diversity of Polychaete communities in vermetid reefs. pp. 349-369. In: *Habitat Structure: The Physical Arrangement of Objects in Space*. Bell, S. S., McCoy, E. D., Mushinsky, H. R., (Eds.). Chapman & Hall, Ltd. London.
- Safriel, U.N., Hadfield, M.G., 1988. Sibling speciation by life-history divergence in *Dendropoma* (Gastropoda; Vermetidae). *Biological Journal of the Linnean Society*, 35 (1), 1-13.
- Scaperrota, M., Bartolini, S., Bogi, C., 2012. *Accrescimenti. Stadi di accrescimento dei molluschi marini del Mediterraneo*. Vol IV. L'Informatore Piceno. Ancona, Italy, 184 pp.
- Schiaparelli, S., 1996. Contribution to the knowledge of Vermetidae (Mollusca: Gastropoda) from Ligurian sea. *Bollettino Malacologico*, 31, 267-276.
- Schiaparelli, S., Albertelli, G., Cattaneo-Vietti, R., 2006. Phenotypic plasticity of Vermetidae suspension feeding: a potential bias in their use as biological sea-level indicators. *Marine Ecology*, 27, 44-53.
- Schiaparelli, S., Guidetti, P., Cattaneo-Vietti, R., 2003. Can mineralogical features affect the distribution patterns of sessile gastropods? The Vermetidae case in the Mediterranean Sea. *Journal of the Marine Biological Association of the UK*, 83, 1267-1268.
- Schlick-Steiner, B.C., Seifert, B., Stauffer, C., Christian, E., Crozier, R.H. et al., 2007. Without morphology, cryptic species stay in taxonomic crypsis following discovery. *Trends in Ecology and Evolution*, 22 (8), 391-392.
- Schluter, D., 2000. *The Ecology of Adaptive Radiation*. Oxford University Press. Oxford. 300 pp.
- Scuderi, D., 1995. Il genere *Dendropoma* (Gastropoda: Vermetidae) nel Mediterraneo. *Bollettino Malacologico*, 31(1-4), 1-6.
- Scuderi, D., 2000. Contributo alla conoscenza dei vermetidae mediterranei: *Vermetus (Thylaeodus) granulatus* (Gravenhorst, 1831) e suoi principali morfotipi. *Bollettino Malacologico*, 35 (1-4), 45-48.
- Scuderi, D., 2012. A new species of *Petalococonchus* Lea, 1843 from the Mediterranean Sea (Mollusca, Gastropoda, Vermetidae). *Biodiversity Journal*, 3 (2), 123-128.
- Scuderi, D., Terlizzi, A., Faimali, M., 1998. Osservazioni su alcuni tratti della biologia riproduttiva di vermeti biocostruttori e loro ruolo nella edificazione dei "trottoir". *Biologia Marina Mediterranea*, 5 (1), 284-289.
- Silenzi, S., Antonioli, F., Chemello, R., 2004. A new marker for sea surface temperature trend during the last centuries in the temperate areas: Vermetid reef. *Global and Planetary Change*, 40, 105-114.
- Sisma-Ventura, G., Guzner, B., Yam, R., Fine, M., Shemesh, A., 2009. The reef-building gastropod *Dendropoma petraeum* – A proxy of short- and long-term climatic events in the eastern Mediterranean. *Geochimica et Cosmochimica Acta*, 73, 4376-4383.
- Sivan, D., Schattner, U., Morhange, C., Boaretto, E., 2010. What can a sessile mollusk tell about neotectonics? *Earth and Planetary Science Letters*, 296, 451-458.
- Templado, J., Templado, D., Calvo, M., 1992. The formations of the vermetid gastropod *Dendropoma petraeum* (Monterosato, 1884) on the coasts of the Iberian Peninsula (Western Mediterranean). pp. 514-515. In: *Abstracts of the 11th International Malacological Congress*. Giusti, F., Manganello, G. (Eds.). Siena.
- Templado, J., Calvo, M., García Carrascosa, A.M., Boisset, F., Jiménez, J., 2002. *Flora y Fauna de la Reserva Marina y Reserva de Pesca de la isla de Alborán*. Secretaría General de Pesca Marítima, Ministerio de Agricultura, Pesca y Alimentación. Madrid. 269 pp.
- Templado, J., Calvo, M., Luque, A.A., Garvía, A., Maldonado, M. et al., 2004. *Guía de los invertebrados y peces marinos españoles protegidos por la legislación nacional e internacional*. Ministerio de Medio Ambiente, Serie Técnica. Madrid, 214 pp.
- Templado, J., Calvo, M., Moreno, A., Flores, A., Conde, F. et al., 2006. *Flora y Fauna de la Reserva Marina de las islas Columbretes*. Secretaría General de Pesca Marítima, Ministerio de Agricultura, Pesca y Alimentación. Madrid, 263 pp.
- Terlizzi, A., Scuderi, D., Fraschetti, S., Anderson, M.J., 2005. Quantifying effects of pollution on biodiversity: a case study of highly diverse molluscan assemblages in the Mediterranean. *Marine Biology*, 148, 293-305.
- Tzur, Y., Safriel, V., 1978. Vermetid platforms as indicators of coastal movements. *Israel Journal of Earth-Science*, 27, 124-127.
- UNEP/IUCN/GIS Posidonie 1990. *Livre rouge 'Gérard Vuignier' des végétaux, peuplements et paysages marins menacés de Méditerranée*. MAP Technical Report Series 43. United Nations Environment Programme. Athens, 250 pp.
- UNEP/MAP (Mediterranean Action Plan). 2012. *Initial Assessment of the Mediterranean Sea: Fulfilling Step 3 of the ECAP Process*. UNEP/MAP. Athens, 254 pp.

- Usvyatsov, S., Galil, B., 2012. Comparison of reproductive characteristics among populations of *Dendropoma petraeum*-complex (Mollusca: Caenogastropoda), an endemic Mediterranean reef-building vermetid. *Journal of the Marine Biological Association of the UK*, 92, 163-170.
- Véliz, D., Winkler, F.M., Guisado, C., 2003. Development and genetic evidence for the existence of three morphological cryptic species of *Crepidula* in Northern Chile. *Marine Biology*, 143, 131-142.
- Vitturi, R., Pandolfo, A., Colomba, M., Damiani, F., Chemello, R., 1997. Characterization of mitotic and meiotic chromosomes of the vermetid Gastropod *Dendropoma (Novastoa) petraeum* Monterosato, 1884) (Mollusca, Caenogastropoda). *Ophelia*, 46 (2), 127-139.
- Vizzini, S., Colombo F., Costa V, Mazzola, A., 2012. Contribution of planktonic and benthic food sources to the diet of the reef-forming vermetid gastropod *Dendropoma petraeum* in the western Mediterranean. *Estuarine, Coastal and Shelf Science*, 96, 262-267.