Mediterranean Marine Science

Vol 23, No 1 (2022)

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doi: 10.12681/mms.27880

To cite this article:

CABALLERO-HERRERA, J. A., GOFAS, S., & RUEDA, J. L. (2022). Episcomitra angelesae (Mollusca: Gastropoda: Mitridae), a new species from an exceptional deep habitat in the Alboran Sea. *Mediterranean Marine Science*, *23*(1), 14–24. https://doi.org/10.12681/mms.27880

Research Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
DOI: http://doi.org/10.12681/mms.27880
www.hcmr.gr

Episcomitra angelesae (Mollusca: Gastropoda: Mitridae), a new species from an exceptional deep habitat in the Alboran Sea

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Contributing Editor: Vasilis GEROVASILEIOU

Received: 26 August 2021; Accepted: 4 January 2022; Published online: 19 January 2022

urn:lsid:zoobank.org:pub:3A8D849D-65EB-4EB2-86D5-490F21D9BA5C

Abstract

A new species of gastropod, *Episcomitra angelesae* (Neogastropoda: Mitridae), is described from specimens collected in the upper bathyal level of the Alboran Sea (Seco de los Olivos and Alboran Ridge). The new species is compared with other similar species known from the Atlanto-Mediterranean area, including *Episcomitra zonata* (Marryat, 1819) and *Isara turtoni* (Watson, 1890). The habitat of this new species, hard substrate with coral rubble patches at 250-320 m depth on submarine elevations, is very unusual in the Mediterranean Sea and is described based on Remotely Operated Vehicle video footage. The amount of coral rubble on the type locality is disproportionate to the very few live coral colonies found in the vicinity, and is assumed to be relict of former hydrological conditions.

Keywords: Mitridae; new taxon; Alboran Sea; coral rubble; Mediterranean cold-water corals.

Introduction

Miter shells (family Mitridae) are a group of mostly tropical and shallow water gastropods, which comprise about 400 species worldwide (WoRMS, 2021) but are represented by only three Recent species in European seas including the Mediterranean Sea. The group has recently been revised on the basis of DNA sequence data by Fedosov *et al.* (2018) who recognize 32 valid genera within the family. Details of life habits and diet are scarcely known for most species including the European ones, and the existing information suggests that some miter shells are specialized predators on sipunculids (Taylor, 1989; West, 1990).

This paper reports on a mitrid species which was known to us for many years by a single, enigmatic specimen collected in 1958 by R/V "Calypso" from 175-200 m, together with the cowry *Schilderia achatidea* (Gray, 1837) on the northern-east slope of the Alboran platform, and then tentatively identified as a juvenile and monochromatic specimen of *Episcomitra zonata* (Marryat, 1819). Recent multidisciplinary expeditions on a submarine elevation close to the Andalusian shore (Seco de los Olivos) have revealed abundant specimens of this so far elusive mitrid species, in a very restricted depth range between 250 and 320 m and brought conclusive evidence that it is distinct from all other species known from the Atlanto-Mediterranean area. The coral rubble habitat in which this species has been found is very unusual in the Mediterranean Sea and is here described based on Remotely Operated Vehicle (ROV) video footage.

Material and Methods

Study area

The Alboran Sea is the western-most part of the Mediterranean Sea with a very peculiar hydrological, physiographic and biogeographic setting. The influx of surface Atlantic Water (AW) forms two semi-permanent anticyclonic gyres, whereas in the deeper part of the basin, Levantine Intermediate Water (LIW) flows westwards along with Western Mediterranean Deep Water (WMDW) and eventually discharges into the Gulf of Cádiz through the Strait of Gibraltar (Heburn & La Violette, 1990; Vargas-Yáñez *et al.*, 2021). Those AW and LIW water masses mix at their interface, at a depth which varies according to the location in the basin and to temporal changes, but is situated at *ca* 200 m.

Physiographically, the seafloor of the Alboran basin has been shaped by a complex geological history (Vázquez *et al.*, 2021) and comprises a number of submarine elevations (Aguilar *et al.*, 2013; Palomino *et al.*, 2015). The Alboran Ridge is a large submarine elevation, oriented NE-SW, and situated in the middle of the Alboran Sea, culminating on the tiny Alboran Island and surrounded by depths of more than 1000 m on either flank (Gofas *et al.*, 2014). Seco de los Olivos, also known as Chella Bank, is a steep elevation located quite close to the continental shelf of Almeria province in SE Spain, culminating on a small platform *ca* 90 m deep but separated from the mainland shelf by depths of *ca* 400 m. A detailed description of Seco de los Olivos was provided by de la Torriente *et al.* (2014, 2018) to whom the reader is referred.

From the biogeographical point of view, the Alboran Sea is a crossroad between Atlantic and Mediterranean biota and therefore houses an exceptional diversity of fauna and flora, including many species which do not occur elsewhere in the Mediterranean Sea (Real *et al.*, 2021).

The exploration of the Alboran Sea was recently boosted by the move towards designating offshore marine protected areas in the EU Natura 2000 network (Marcos, 2005) starting in 2011-2012 with the EU funded LIFE+ INDEMARES project "Inventory and designation of marine Natura 2000 areas in the Spanish sea" (Gofas *et al.* 2014, de la Torriente *et al.* 2014). In 2016, Seco de los Olivos was visited by the ATLAS/MEDWAVES 0916 expedition, which aimed to study the influence of Mediterranean outflow water on the biodiversity and biogeography of cold-water corals and other key taxa (Orejas *et al.* 2017). In July-August 2021, the CIRCAESAL 0721 expedition was set out to visit or revisit several sites of the northern Alboran Sea, acquire underwater images of their habitats, and evaluate the environmental status of circalittoral and bathyal habitats under the Marine Strategy Framework Directive 2008/56/EC as well as to monitor possible changes in some of the sites since their designation in the Natura 2000 network.

Sample collecting and underwater imaging

Shells of this mitrid species were collected in the INDEMARES Alboran expedition on the Alboran Ridge using a rock dredge (80 x 20 cm frame) in 2012, and in the ATLAS/MEDWAVES 0916 expedition on the Seco de los Olivos with a Van Veen grab (30×20 cm) in 2016.

During the CIRCAESAL 0721 expedition, some living specimens, constituting the type material, were found on the seafloor of the Seco de los Olivos with the ROV LIROPUS 2000 (model Super Mohawk II) from the Instituto Español de Oceanografía but operated by three ROV pilots from the contractor ACSM <https://acsm-ships.com/>. Underwater imagery was obtained with a high-resolution camera and geo-referenced by means of a transponder (HiPAP 500) attached to the ROV that conveyed the positions of the ROV in relation to the research vessel. The vessel was equipped with a dynamic positioning system able to maintain a specified position, and the ROV was settled on the seafloor when acquiring high magnification images or taking samples.

Shells were photographed using a Nikon DXM camera mounted on a stereomicroscope, taking a series of views focused on distinct planes which were assembled using CombineZ software (Hadley, 2006). The type material will be deposited at the MNCN, Madrid.

Comparative material examined

Material of the new species consists of five live-taken specimens and 17 shells and is detailed in the following section. In addition, the following specimens were examined for the purpose of comparison:

Episcomitra zonata (Marryat, 1819) • 1 lv, Spain, off Malaga, 36.6283°N, -04.3313°W to 36.6325°N, -04.3275°W, 97-98 m depth, 28 May 2019, R/V "Isla de Alborán" leg. Gofas • 1 dd, Spain, off Caleta de Vélez, Málaga province, from fishing nets • 1 dd, Spain, Alboran platform, 35.9937°N, -02.8680°W to 35.9946°N, -02.8778°W, 102-112 m depth, 21 Jul. 2012, INDEMARES Alborán expedition, R/V "Isla de Alborán", sta. BV41, beam trawl on bioclastic gravel.

Isara turtoni (E.A. Smith, 1890) • 1 dd (holotype of *Mitra exilima* Locard, 1897), Western Sahara, 26.283°N, -14.850°W, 355 m, 08 Jul. 1883, R/V "Talisman" sta. 64 (MNHN IM-2000-30220) • 2 dd, Senegal, off Gorée Is., 35-42 m, leg. Marche-Marchad (MNHN) • 2 lv, Cape Verde Islands, Boavista, 16.017°N, -23.000°W, 45 m, R/V "Calypso"1959 sta. 75 • 2 dd, Angola, off Ilha de Luanda, -08.733°S, 13.200°E, 40-60 m depth, leg. Gofas.

Ziba gambiana (Dohrn, 1861) • 1 lv, Mauritania, 18.667°N, -19.5167°W, 96 m, R/V "Léon Coursin" sta. 8 (MNHN) • 2 dd, Senegal, off Gorée Is., 30-40 m, leg. Marche-Marchad (MNHN) • 1 dd, Mauritania (no more details), leg. Talavera (MNHN-IM-2012-18259; specimen wrongly stated as paratype of *Mitra cabrerai* Talavera, 1978 in Cernohorsky, 1991: 51, fig. 42.7, 42.8; that species was described on a single specimen).

Ziba ogoouensis Biraghi, 1984 • 1 lv, Côte d'Ivoire, Abidjan area, continental shelf, leg. Le Loeuff (MNHN).

Abbreviations

MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN:** Muséum National d'Histoire Naturelle, Paris, France; **lv:** live taken specimen; dd: dead shell; **H:** maximum shell height, from apex to siphonal canal; **D_** maximum shell diameter, measured perpendicular to coiling axis; **sta:** sampling station; **ROV:** Remotely Operated Vehicle.

Results

Systematic part

Episcomitra angelesae n. sp. (Fig. 1-2)
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Type material:

Holotype, lv (20.4 × 7.0 mm), 36.5420°N, -02.8196°W, 313 m depth, 12 Aug. 2021, CIRCAESAL 0721 expedition, R/V "Angeles Alvariño", ROV 25, ROV suction sample on coral rubble, MNCN 15.05/200151H.

Paratypes: 4 lv (19.5 × 6.7 mm to 21.6 × 8.5 mm) and 6 dd (12.7 × 4.5 mm to 21 × 7.4 mm), same data as for the holotype, MNCN 15.05/200151P.

Other material examined:

Alboran ridge, -1 dd (21.0 × 7.7 mm), 36.030°N, -02.850°W, 175-200 m depth, 4 Sep. 1958, R/V "Calypso" sta. 1305, volcanic rock with gorgonians, *Dendrophyllia* and large brachiopods, MNHN. • 1 dd (17.3 × 6.3 mm), 35.9012°N. -03.0268°W to 35.8968°N, -03.0235°W, 240-243 m, 22 Sep. 2011, INDEMARES Alborán expedition, R/V "Isla de Alborán", sta. BV11, beam trawl on muddy bioclastic gravel • 7 dd (old shells; 17.0 × 6.7 to 22.0 × 8.0 mm), 35.7953°N, -03.2998°W, 135-152 m, 22 Jul. 2012, INDEMARES Alborán expedition, R/V "Isla de Alborán", sta. DR44, rock dredge on bioclastic gravel.

Seco de los Olivos. – 1 dd. (17.4 × 6.1 mm), 36.3758°N, -02.8193°W, 321 m, 24 Oct. 2016, ATLAS/MEDWAVES 0916 expedition, R/V "Sarmiento de Gamboa", sta. VV37, grab sample, hemipelagic sand with abundant coral remains (*Madrepora*, *Lophelia*, *Caryophyllia*). • 1 dd. (22.0 × 7.6 mm), 36.5366°N, -02.8203°W, 250 m, 24 Oct. 2016, ATLAS/MEDWAVES 0916 expedition, R/V "Sarmiento de Gamboa", sta. VV39, grab sample, mud and gravels with coral rubble (*Madrepora*).

Type locality: NE of Seco de los Olivos, 36.5420°N, -02.8196°W, 313 m.

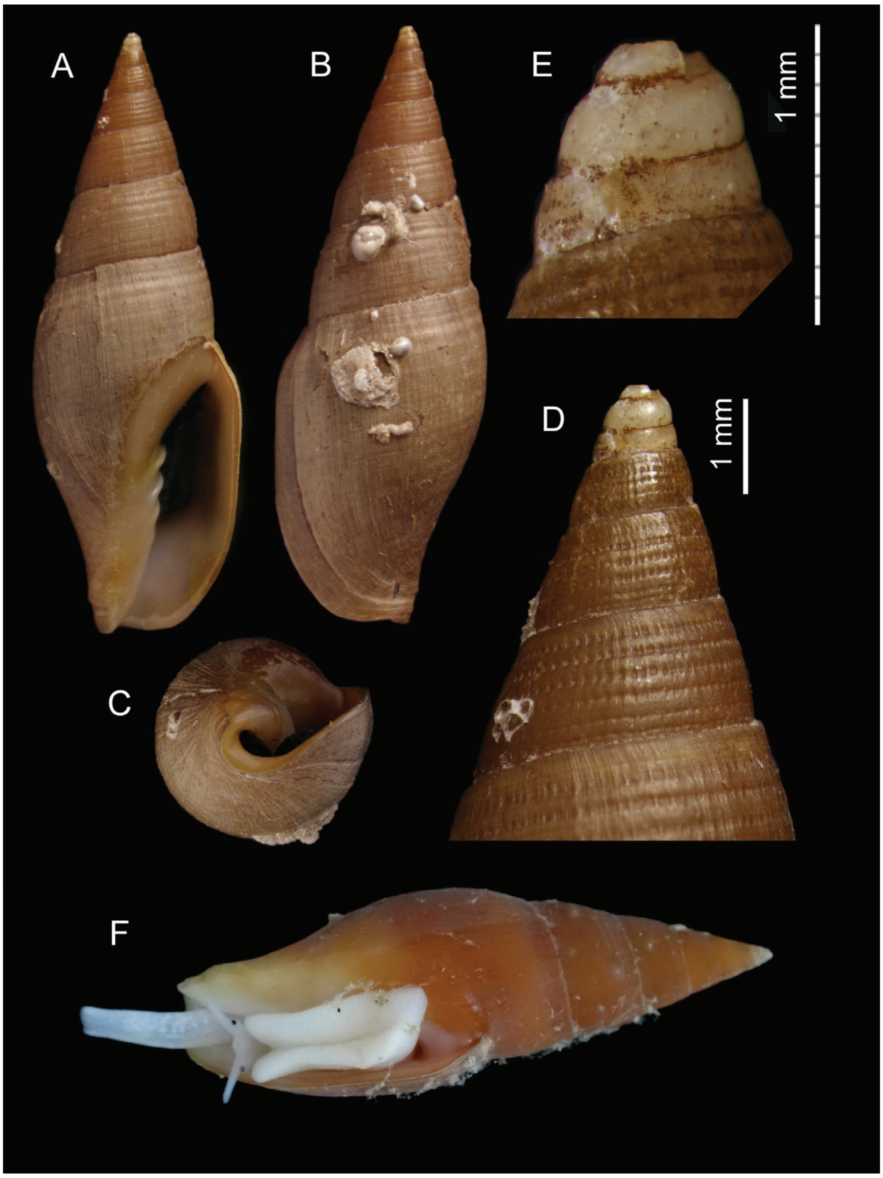

Fig. 1: *Episcomitra angelesae* n. sp., holotype (H=20.4 mm) from Seco de los Olivos (36.5420°N, -02.8196°W, 313 m depth), collected during CIRCAESAL 0721 expedition on board R/V Ángeles Alvariño. A-B: Apertural and abapertural views; C: Basal view showing siphonal canal; D: Detail of early whorls showing the protoconch and four teleoconch whorls with punctured spiral grooves; E: Detail of the protoconch; F: Photograph of the living animal taken during the expedition.

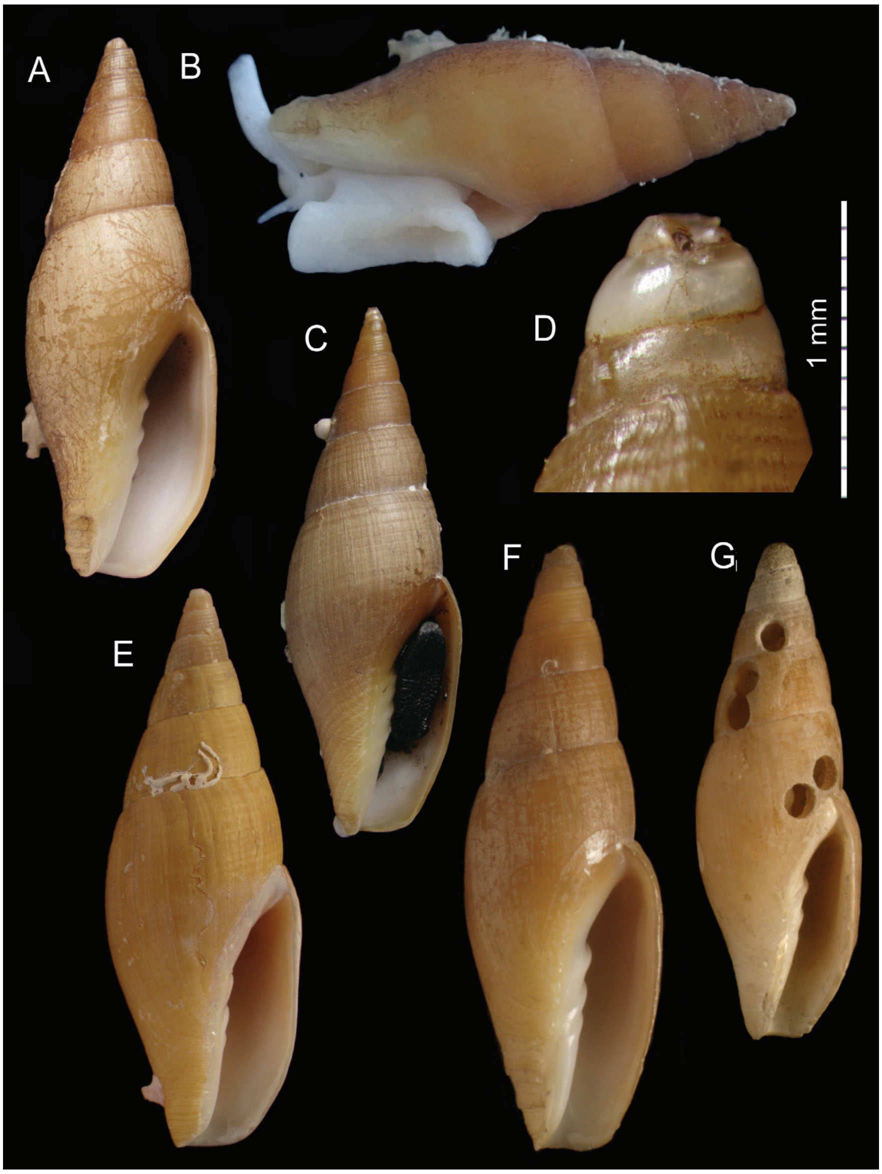

Fig. 2: *Episcomitra angelesae* n. sp. A: Paratype (H=20.4 mm); B: Photograph of the living animal taken during CIRCAESAL 0721 expedition, paratype; C: Paratype (H=19.5 mm); D: Protoconch of the same paratype displayed in C; E. Shell from Alboran platform, R/V "Calypso" sta. 1305, 175-200 m (H=21 mm); F: Shell from Seco de los Olivos, ATLAS/MEDWAVES 0916 sta. VV39, 250 m depth (H=22 mm); G: Shell from Seco de los Olivos, ATLAS/MEDWAVES 0916 sta. VV37, 321 m depth (H=17.4 mm) severely drilled, probably by an octopus.

Etymology: the species is dedicated to R/V "Angeles Alvariño", the captain and crew of this research vessel as well as the scientific party of the CIRCAESAL 0721 expedition, with a particular mention for the ROV pilots who made possible the collection of the living specimens (see Acknowledgements section).

Description of the holotype: Shell medium sized (20.4 mm), fusiform with last whorl 63% of total height in apertural view. Protoconch multispiral, with a little more than 3 smooth, slightly convex whorls, with a diameter of 0.8 mm at contact with teleoconch; whitish in colour. Teleoconch of nearly 6 whorls. Spire whorls slightly convex, with a deeply incised suture; early spire whorls incised by narrow spiral grooves (6 on second teleoconch whorl, 8 less distinct on fourth, *ca* 10 very slight on penultimate whorl above the insertion of outer lip). Spiral grooves with regularly spaced punctures along the grooves until the 4th whorl, becoming less conspicuous on the two last whorls, indistinct on the last whorl. No axial sculpture except for growth lines. Last whorl with maximum convexity above mid-whorl, with nearly straight or slightly concave profile towards the abapical part; no definite fasciole around siphonal canal. Aperture elongate, with outer lip definitely bent at its insertion on the preceding whorl, then with very slightly convex profile in apertural view; adapical sinus indistinct. Parietal and columellar callus thin, continuous, sharply delimited, appressed. Columella with three definite, oblique columellar folds, blunt, the abapical one weaker, and a hardly visible fourth fold abapically to these. Outer lip not thickened but with a rounded edge. Siphonal canal moderately short, moderately wide, straight with incised siphonal notch. Colour of teleoconch uniformly tawny. Living animal with a pure white head-foot and some opaque white blotches over the siphon.

Remark

When preserved in ethanol the body turns black, thereby staining the fixative as also noted by Harasewych (2009).

Variability

The largest specimen (live collected, Fig. 2A) is 22 mm in shell height. The shells have up to 6 ¾ teleoconch whorls, of which the last whorl represents 63 to 68% of the total height. The ratio of shell height to maximum diameter varies from 2.73 (the "Calypso" specimen) to 2.91 (holotype). The intensity of the spiral sculpture is variable. Most specimens (holotype, Fig 1A, paratypes, Fig. 2C) and shells have spiral striae until the last whorl but those are faint and always lack the punctures (Fig. 1D) seen on the early whorls. Some specimens (Fig. 2A) or shells (Fig. 2 E, F) have a nearly smooth last whorl.

Habitat

The live collected specimens were found on small patches of sand mixed with coral rubble, always bordering rocky outcrops at the depth interval where specimens of the large hexactinellid sponge *Asconema setubalense* Kent, 1870 were also found (Fig. 3). In the coral rubble, fragments of *Madrepora oculata* Linnaeus, 1758 and, in a lesser proportion, of *Desmophyllum pertusum* (Linnaeus, 1758) (formerly in genus *Lophelia*) formed an interlocking matrix over the sediment. Granulometric data cannot be obtained from the suction samples, but the mud content is inferred to be low, judging from the rapid clearing of the water when the ROV settles for imaging or sampling. The associated fauna included one living specimen (and one shell) of *Mitrella templadoi* Gofas, Luque & Urra, 2019, recently reported from the same site (Gofas *et al.,* 2019).

Where living animals were collected, a rocky bottom was always outcropping nearby, and the layer of sand was always found to be thin (*ca* 1 cm) over the underlying bedrock which became exposed after action of the suction pump.

Discussion

Species comparisons

Episcomitra zonata (Fig. 4 A-C), the type species of the genus, occurs sympatrically with *E. angelesae* n. sp. in the Alboran Sea. The former is a rare species and most

Fig. 3: Habitat near the type locality of *Episcomitra angelesae* n. sp. (36.5415°N, -02.8201°W, 298 m) on a coral rubble bottom intermixed with rocky outcrops at Seco de los Olivos (Alboran Sea). A: general view of the habitat with two large hexactinellid sponges *Asconema setubalense* and a rock with unidentified sponge and crinoid in the background, and a patch of coral rubble (dark) at the lower right; the laser pointers are spaced 10 cm, the arrow points to the miter; B: Detail of *E. angelesae* n. sp. crawling on the seabed. Images obtained during the CIRCAESAL 0721 expedition; this specimen was not collected.

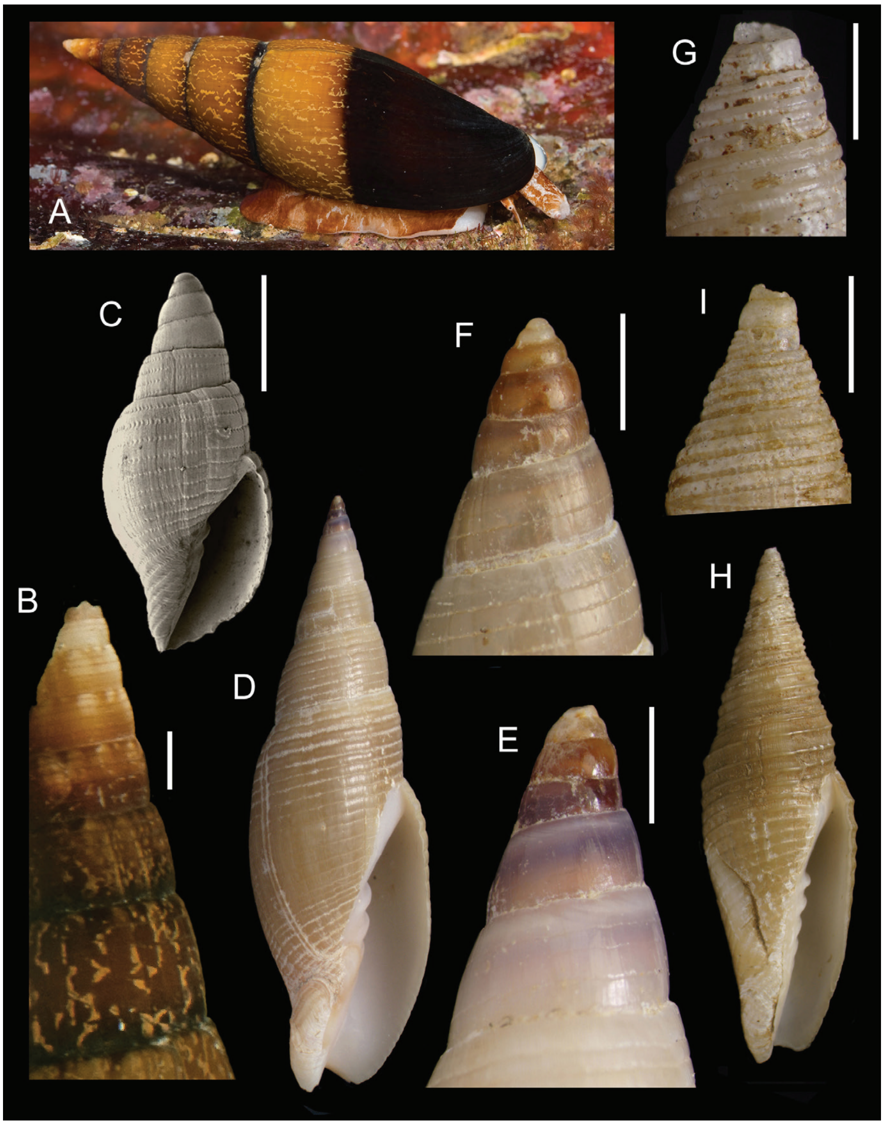

Fig. 4: A: *Episcomitra zonata* (Marryat, 1819), living specimen from Arrecife, Lanzarote, Canary Is. (photograph by L. Moro, reproduced from Bacallado *et al.* (2008) with permission; shell H=56 mm). B: Detail of the early spire whorls of the same specimen, showing the last protoconch whorl, the early teleoconch whorls with *ca* 4 incised spiral striae, and the onset of the abapical dark zone on the fifth teleoconch whorl (photograph by L. Moro). C: Scanning electron micrograph of a juvenile *E. zonata* from the Alboran platform (reproduced from Peñas *et al*. 2006: 103), showing the complete protoconch and two teleoconch whorls. D: *Isara turtoni* (E.A. Smith, 1890), specimen from Boavista, Cape Verde Islands, 45 m depth (H=32 mm). E: Early whorls of the same specimen, showing the protoconch and the first three teleoconch whorls, with onset of the spiral striae on the second one. F. *Isara turtoni*, early whorls of a specimen from off Gorée, Senegal. G. *Ziba gambiana* (Dohrn, 1861), shell from off Gorée, Senegal, detail of early whorls showing the last protoconch whorl and the strong spirals on the first teleoconch whorls. H. *Ziba ogoouensis* Biraghi, 1984, specimen from off Abidjan, Côte d'Ivoire (H=26.3 mm). I: Detail of early whorls of the same specimen. Scale bars are 1 mm.

specimens in collections are adults over 50 mm in size. Apart from juveniles in early teleoconch stage, the smallest *E. zonata* shell that could be found for the present study was 32 mm high and was not in good condition. Moreover, it is striking that Scaperrotta *et al.* (2013) could only find *E. zonata* shells either of millimetric size, or larger than 44 mm despite having access to a large array of Italian private collections. Compared to *E. angelesae*, *E. zonata* grows much larger (up to 100 mm instead of 22 mm - the maximum height of all *E. angelesae* specimen collected) and is diagnosed by a dark band above the suture, starting on the fourth or fifth teleoconch whorl and continued on the abapical part of the last whorl.

The assumption that the examined specimens of *E. angelesae* n. sp. are full-grown is supported by the configuration of the aperture. In shells of *ca* 20 mm height, there is a definite parietal callus and the adapical part of the outer lip is thick with a rounded edge and bends towards the preceding whorl to form an arch. In *E. zonata* even in larger specimens, that edge would be cutting and make an acute angle with the surface of the preceding whorl. *Episcomitra zonata*, like *E. angelesae* n. sp., has a planktotrophic larval development and is known to spawn egg capsules with numerous, tiny eggs (Gofas *et al.*, 2011: 311). Normally, the living animal of *E. zonata* has a brownish colour on the upper part of the head-foot and of the siphon (Fig. 4A, see also Mifsud, 1993: front page of journal), but occasionally, white specimens may be found (Gofas *et al.*, 2011: 311).

Adult *E. zonata* have a smooth shell surface but the early teleoconch whorls (up to fifth), prior to the onset of the colour banding, have a spiral sculpture of punctate striae (Figs. 4B, 4C; see also Scaperrotta *et al.*, 2013: 87), thereby these are very similar to the early teleoconch whorls of *E. angelesae* n. sp. In both species there are 4-5 spiral grooves at the start of the teleoconch but in *E. zonata*, the number of spiral grooves does not increase on the second to fourth teleoconch whorl, where they become widely separated; conversely in *E. angelesae* the number of spiral grooves increases to 6-8 towards the fourth teleoconch whorl. Therefore, we cannot rule out that the 10.5 mm specimen figured in Scaperrotta *et al.* (2013) could belong to *E. angelesae* n. sp. and not to *E. zonata*. A further difference is that adult specimens of *E. zonata* have a distinct fasciole surrounding the siphonal canal, unlike those of *E. angelesae* n. sp.

Apart from *E. zonata*, two other mitrids are reported from the Mediterranean Sea: *Episcomitra corniculum* (Linnaeus, 1758) and *Isara cornea* (Lamarck, 1811). The adult *E. corniculum* may also have a white head-foot but is readily distinguished from *E. angelesae* n. sp. by having a paucispiral protoconch (see Fedosov *et al.*, 2018: 38 and Scaperrotta *et al.*, 2010: 81, 160). *Isara cornea* superficially resembles *E. angelesae* n. sp. but lives in very shallow water, is much broader with the same height (H/D 2.1 to 2.6 instead of 2.7 to 2.9 in *E. angelesae*), lacks spiral sculpture, and the living animal has a very characteristic pattern of bright yellow lines bordering the foot (Rolán *et al.*, 1997, Gofas *et al.*, 2011: 311). Moreover, *I. cornea* generally lives in shallow water (Harasewych, 2009; Gofas *et al.,* 2011).

Isara turtoni, originally described from St Helena Island but later reported also from West Africa (Rolán, 2005), is the closest described species (Fig. 4 D-F). It is only slightly larger (32 mm) than *E. angelesae* n. sp. and also has punctate spiral grooves. However, it is more slender and with a much more marked spiral sculpture, particularly on the last whorl where flat, broad spiral cords are separated by grooves. Its protoconch (Fig. 4E-F) is also multispiral, similar in size to that of *E. angelesae* n. sp., but it has flatter whorls and is dark brown in colour except for the whitish apical whorl. Contrary to *Episcomitra* spp., the first teleoconch whorl of *I. turtoni* is smooth and the spiral grooves appear progressively on the second and third whorl. Moran *et al.* (1989) designated a lectotype (NHMUK 1889.1.10.2388), leaving the other 11 specimens of the type series as paralectotypes (NHMUK 188931.10.2389-2397). The lectotype designation by Cernohorsky (1991) is therefore invalid, and it is his figure 42.5 (labelled "paralectotype" with a wrong registration number) that represents the actual lectotype, also figured by Fedosov *et al.* (2018: 66). *Mitra exilima* Locard, 1897, described from bathyal bottoms (355 m depth) off Cape Bojador, Western Sahara, and *Mitra cabrerai* Talavera, 1975 are junior synonyms of *I. turtoni*, as correctly stated by Moran *et al.* (1989), and not synonyms of *Mitra gambiana* as asserted by Cernohorsky (1991).

The West African *Ziba gambiana* resembles *Isara turtoni* to the point that they were confounded by Cernohorsky (1991) and, previously, Moran *et al.* (1989) wrote that the species separation required confirmation. In the material examined for the present study, *Ziba gambiana*, as well as the similar *Z. ogoouensis* Biraghi, 1984 are easily and unambiguously distinguished from *I. turtoni* by the morphology of the early whorls. The last protoconch whorl is distinctly smaller (0.53 mm diameter at contact with teleoconch) than in *I. turtoni* (0.8-0.9 mm) and consequently the diameter of the first teleoconch whorl is also smaller (0.8 mm instead of over 1 mm) as also noted by Moran *et al.* (1989). The first teleoconch whorl of *Ziba* spp. has, from the start, a distinctive sculpture of 4-5 very strong spiral ridges separated by deep grooves that are nearly as broad as the ridges (Fig. 4 G,I), whereas in *I. turtoni* the first teleoconch whorl is nearly smooth and the spiral grooves appear progressively on the second and third whorl. The two species of *Ziba* are distinguished by the sculpture of the last whorl, with broad flat ribs separated by grooves in *Z. gambiana*, and with widely spaced ridges on the shoulder of the last whorl in *Z. ogoouensis*. Another West African species, *Domiporta hebes* (Reeve, 1845) (with its synonyms *Mitra pruinosa* Reeve, 1844*, M. asperulata* A. Adams, 1853 and *M. hamillei* Petit de la Saussaye, 1851), is even more different than the two *Ziba* species, because it has strong axial and spiral grooves delimiting squarish knobs and has a reduced abapical fold in the aperture.

The planktotrophic development inferred from the larval shell should not preclude that *E. angelesae* n. sp. could have an amphiatlantic distribution. The little known Western Atlantic *Isara straminea* (A. Adams, 1853), figured by Fedosov et al. (2018: 66) is extremely similar to, if not identical with, *I. turtoni*, and the same differences with respect to *E. angelesae* n. sp. apply as noted above. *Probata barbadensis* (Gmelin, 1791) is superficially similar to *E. angelesae* n. sp. but lives in shallow water, and its shell is much broader with the same height, has a stronger spiral sculpture and has up to five columellar folds in the aperture.

The fossil record features numerous species of *Episcomitra* and those of Miocene strata of the Paratethys have recently been revised by Harzhauser & Landau (2021). Although it is highly unlikely that a Paratethyan species could have Recent representatives in the bathyal level, we scrutinized those species and found none of them matching the punctured spiral grooves of the early spire whorls and shape of the aperture of *E. angelesae* n. sp.

Generic placement

The generic placement of the new species is equally plausible, and biogeographically consistent to both *Episcomitra* and *Isara*. An attempt to obtain a sequence from an ethanol-preserved tissue clip was unsuccessful and therefore the placement in *Episcomitra* rather than *Isara* is tentative. Our preference is essentially motivated by the strong resemblance of protoconchs (compared to *E. zonata*, Fig. 4 B-C) and of early whorls of *E. angelesae* n. sp. (Figs 1 D-E, 2 D) whereas those features are clearly different in *Isara turtoni* (Fig. 4 E-F). The early whorls of *E. corniculum* also show punctured spiral striae (see Scaperrotta *et al.*, 2010: 81) very similar to those of *E. zonata* and *E. angelesae* n. sp.

Larval development and distribution

The smooth and multispiral protoconch with a clearly marked limit with the teleoconch clearly indicates a planktotrophic development (Jablonski & Lutz, 1980). It is unexpected that a species with this kind of larval development could be endemic of the Alboran Sea, but the fact is that so far it has not been reported elsewhere. As discussed above, we are not aware of any Western Atlantic mitrid species which could be conspecific with *E. angelesae* n. sp. The large sampling effort directed to the NE Atlantic seamounts with the Seamount 1 and 2 cruises did not yield any mitrid specimen (SG, unpublished data) among thousands of shells sorted from the samples. Nevertheless, the columbellid *Mitrella templadoi*, which also has a planktotrophic larval development and lives in the type locality of *E. angelesae* n. sp., was represented on Hyères, Irving, Plato and Atlantis seamounts by abundant shells and some living specimens in a similar coral rubble habitat at 280-750 m depth (Gofas *et al.*, 2019). Other molluscs with planktotrophic larvae in the families Mathildidae and Architectonicidae are unusually abundant on Seco de los Olivos (JAC, unpublished results). The planktotrophic larval development should not be an advantageous trait for species with a restricted habitat and a small geographic range, because the bulk of larvae broadcasted in the plankton may fail to find again the right habitat at the time of metamorphosis. The case of the Alboran Sea, however, is different because of the presence of semi-permanent anticyclonic gyres (Vargas-Yáñez *et al.*, 2021). We hypothesize that those gyres enable the larvae to return repeatedly to their birthplace, therefore allowing self-sustaining populations to be maintained without an excessive loss of larvae. Notwithstanding, this species probably occurs somewhere else than in the Alboran Sea if the right habitat is found. Candidate areas include the Sicily Channel (and we do not exclude that the Maltese specimen identified as a juvenile *E. zonata* and figured by Mifsud (1993) could be *E. angelesae* n. sp.), but also the Lusitanian seamounts, still incompletely explored in the 250-500 m depth range, as well as the slopes of Canary and Madeira Islands.

Habitat

The new species is definitely an inhabitant of bathyal hard substrates, and the bottoms where the live-taken specimens were found were characterized by the presence of the hexactinellid sponge *Asconema setubalense*, which is typically attached to the bedrock even when some sedimentary deposits are present. The habitat in which *Episcomitra angelesae* n. sp. was found has not been distinguished in the classifications of Mediterranean habitats. Pérès & Picard (1964) and Bellan-Santini *et al.* (2002) only recognize shelf-edge rock (“Roche du Large”) and deep-sea corals (“Coraux Blancs”) as hard-bottom biocoenoses in the bathyal level. The coarse sedimentary substrates listed by these authors as shelf-edge detritic bottoms (“Détritique du Large”) and detritic sands with the brachiopod *Gryphus vitreus* (Born, 1778) do not involve the interlocking skeletal remains of *Madrepora*. The shelf-edge “detritic” (actually, bioclastic) bottoms occur shallower on the Alboran platform, below the lower limit of rhodoliths around 90 m (Gofas *et al.*, 2014), and are mostly made up of remnants of shells and other bioclasts deposited during low sea-level associated with glacial periods.

The EUNIS classification (Davies *et al.*, 2004) is not very detailed regarding the deep sea. There is a brief mention of categories “A6.11 Deep-sea bedrock” and “A6.22 Deep-sea biogenic gravels (shells, coral debris)” but the latter is used in the context of the mounds surrounding cold-water coral (CWC) habitats (e.g., Serrano *et al.*, 2017) in the Atlantic. Neither of these fully accounts for the type of habitat explored in the present study, basically a deep-sea hard bottom where the patches of bioclastic sediment provides a three-dimensional structure in which small invertebrates like *Episcomitra angelesae* n. sp. find shelter and resources. At a larger scale (macrohabitats in the sense of Greene *et al.*, 1999), the EUNIS classification recognizes a category “A6.72 Seamounts, knolls and banks” which fully matches the general context of the two sampled areas (Seco de los Olivos and Alboran Ridge), but features in this category are generally a mosaic of different substrates and habitats-benthic communities.

With increasing video footage of deep Mediterranean habitats becoming available, the need for the recognition of new habitats has been put forward and several proposals are being made. Several “new” habitats were proposed by de la Torriente *et al.* (2018) for their possible inclusion in the EUNIS classification, but their habitat definitions were based exclusively on large, conspicuous “habitat forming species” such as *Asconema setubalense* sponges, gorgonians or corals. Although they did recognize coral rubble as one of the substrate types, they did not distinguish it as a separate habitat because the characteristic species, such as encrusting sponges or the molluscs discussed here, are cryptic.

Coral rubble has been stressed as a major reservoir of diversity in shallow tropical reef environments (Meesters *et al*., 1991; Mumby & Harborne, 1999) where it provides an appropriate substrate for sipunculids (Taylor, 1989) among other invertebrates. Nevertheless, coral rubble must also be recognized ecologically important in deeper water because the lattice of coral fragments also provides shelter and complexity to some sessile and mobile invertebrates as well as a wide variety of food sources for different species. Indeed, some studies detected high species richness of particular groups (e.g., bryozoans, Ramalho *et al.*, 2020) in coral rubble bottoms when compared to other deep-sea habitats because of the higher availability of microhabitats, among other factors.

The Draft Classification of benthic marine habitat types for the Mediterranean region (UNEP – RAC/SPA, 2017; Montefalcone *et al.*, 2021) is also still not fully satisfactory for accommodating the habitat where *Episcomitra angelesae* n. sp. was discovered. This classification includes, among other new proposals, the habitat category ME1.51 "Upper bathyal rock invertebrate-dominated" (with ME1.512 "Facies with large and erect sponges"), and ME3.5 "Mediterranean upper bathyal coarse sediment" with one of the subordinate categories being "Bathyal *Madrepora* and/or *Lophelia* and/or *Dendrophyllia* rubble" but, like in the case of EUNIS, neither of these fully accounts for a habitat in which patches of sediment and coral rubble bring additional complexity to the bedrock substrate.

Living CWC (mostly *Madrepora oculata*) have been recorded on Seco de los Olivos (de la Torriente *et al.,* 2014, 2018 and observations made during ATLAS/MEDWAVES 0916 and CIRCAESAL 0721 expeditions), and on other submarine elevations of the Alboran Sea (Corbera *et al.*, 2019; Hebbeln, 2019 and references therein). However, the amount of coral rubble detected on the seafloor is far beyond what could be produced by the scattered contemporary colonies. Very high mound aggradation rates have been recorded during the last deglaciation and the Early Holocene (Fink *et al.*, 2013; Wienberg, 2019) and this suggests that existing coral rubble deposits are relicts of former and more favourable living conditions for CWC.

In any case, the habitat conformed by hard bottoms with patches of coral rubble where *Episcomitra angelesae* n. sp. dwells is very rare in the Mediterranean Sea, and this species is a textbook example for one of the forms of rarity described by Rabinowitz (1981) and discussed by Gaston (1994: 20): narrow habitat specificity, but locally abundant in that rare habitat.

Acknowledgements

Material from ATLAS/MEDWAVES 0916 expedition was collected by JLR and made available to JAC and SG, and commands the following statement: We thank the captain and crew of the R/V "Sarmiento de Gamboa", and the chief scientist of the MEDWAVES expedition of the ATLAS project. ATLAS has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 678760. This output reflects only the authors' view and the European Union cannot be held responsible for any use that may be made of the information contained therein.

The authors are particularly grateful to the shipboard party and crew of R/V "Angeles Alvariño", particularly to the ROV pilots Bernardo, Manu and Juan who showed infinite patience when we were chasing a semi-buried shell no larger than 2 cm. We consider the naming of the species as a tribute to all those who made possible this exceptional finding. The expedition CIRCAESAL 0721 was funded by the project 18-ESMARES2-CIRCA from the Instituto Español de Oceanografía (IEO), under the framework of the tasks ordered to the IEO by the Ministerio de Transición Ecológica y Reto Demográfico (MITERD) of the Spanish government for the application of the Marine Strategy Framework Directive (MSFD) in Spanish waters. We also appreciate the sampling permissions provided by the Subdirección General de Biodiversidad Terrestre y Marina from MITERD for conducting sampling and underwater images acquisition in the Site of Community Importance "Sur de Almería-Seco de los Olivos" during CIRCAESAL 0721.

We are extremely grateful to Leopoldo Moro Abad (Servicio de Biodiversidad del Gobierno de Canarias) for permission to use his pictures of a specimen of *Episcomitra zonata* with exceptionally well-preserved early whorls, and to Virginie Héros (Muséum National d'Histoire Naturelle, Paris) for the loan of the West African mitrid specimens.

Finally, we greatly appreciate the comments made by 3 reviewers and the English grammar corrections made by Terence W. Edwards on the manuscript.

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