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The More You Search, the More You Find: A New Mediterranean Endemism of the Genus *Ocenebra* Gray, 1847 (Mollusca: Gastropoda: Muricidae) from a Submarine Cave of the Messina Strait Area (Italy)

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Abstract: Three hundred years of study on the Mediterranean molluscan fauna led the scientific community to consider it as the best ever known. However, the rate at which new taxa are discovered and described every year is still remarkably high, even in key predators such as Muricidae Rafinesque, 1815. Within this family, the genus *Ocenebra* Gray, 1847 comprises species widely distributed in the northeastern Atlantic and the Mediterranean Sea that were already the target of a decadal nomenclatural, morphological, and molecular combined research. Notwithstanding, we hereby describe an additional ocenebrid endemism from the Mediterranean Sea, whose distribution appears to be restricted to a circalittoral submarine cave of the Messina Strait area (Italy). The new species *Ocenebra vazzanai* is compared with the recent Atlanto-Mediterranean congeneric taxa on the basis of the known type materials, and a table summarizing the main diagnostic features of the species is offered to facilitate future identifications. The high biodiversity highlighted in the genus *Ocenebra* reveals a wide adaptive radiation and suggests the necessity of further studies aiming to tackle biodiversity issues even in popular groups, such as molluscs, and in widely studied biogeographic areas, such as Italy, and the Mediterranean basin in general.

Keywords: mussel drills; adaptive radiation; biodiversity; alpha taxonomy; *Ocenebra vazzanai* new species

1. Introduction

The Mediterranean Sea has a long history of scientific exploration and is commonly considered a biodiversity hotspot, hosting about 17,000 marine species [1,2]. The Mediterranean Mollusca, in particular, have been the subject of a plethora of studies over the last three centuries, with malacologists producing an extensive bibliography aiming to clarify taxonomical and nomenclatural issues and to discover, as much as possible, the real magnitude of the molluscan biodiversity in the Mediterranean Sea [3,4]. In fact, despite the general crisis of taxonomic studies in recent decades and the increasingly reduced recognition of the importance of taxonomy, which in turn resulted in diminished funding, lower interest from journals in publishing taxonomic research, and a reduced number of young scientists entering the field [5,6], Mollusca always remained a popular,

and thus frequently investigated group by both professional and amateur malacologists, with more than 2000 recent taxa recorded in or described from the Mediterranean Sea to date [1,4].

Among them, the family Muricidae Rafinesque, 1815 (oyster drills, mussel drills, and rock shells) includes predators of commercial interest because of their potential impact on marine resources. After centuries of taxonomic studies on muricids of the northeastern Atlantic and Mediterranean [7–24], the local species biodiversity was first summarised by Houart [25], who highlighted the need for a careful revision of several groups. Then, the taxonomy and the phylogenetic position of several species was reviewed by additional authors [26–32], who mostly investigated the subfamily Ocenebrinae Cossmann, 1903 and not only clarified the phylogenetic position of the species formerly ascribed to the genera *Ocenebra* Gray, 1847 and *Ocinebrina* Jousseaume, 1880 but also described several species new to science and synonymised other ones.

Notwithstanding twenty years of continuous work, the alpha taxonomy and the general biodiversity of the local muricids is still unclear and presumably underestimated. Some genera, including *Murexsul* Iredale, 1915 and *Muricopsis* Bucquoy & Dautzenberg, 1882, have never been investigated through an integrative approach (authors' data). Other genera or species still require additional work. As an example, recent molecular studies suggested that specimens previously ascribed to *Hexaplex trunculus trunculus* (Linnaeus, 1758) may comprise a complex of cryptic species [33,34], but the validity of its Levantine congeneric species *Hexaplex pecchiolianus* (d'Ancona, 1871) is still debated, and nobody has investigated the phylogenetic relationships between these two species to date (authors' data). Some muricid taxa are widespread and highly polymorphic, e.g., *Ocenebra erinaceus erinaceus* (Linnaeus, 1758), whose distributional range spans from the British Isles to Madeira and the Azores, including the entire Mediterranean Sea [25,35], whereas other taxa have a restricted distribution connected to peculiar habitats, e.g., *Ocenebra paddeui* (Bonomolo and Buzzurro, 2006), only known from northern Sardinia (western Mediterranean) and living in association with the red coral *Corallium rubrum* (Linnaeus, 1758) [26,36]. A review of the taxonomy of the shallow water taxa of the *Ocenebra edwardsii* (Payraudeau, 1826) complex revealed the possible presence of several cryptic lineages, some of which may account for undescribed species [30]. *Ocenebra* taxa, and especially deep-water species, seems to be rare to absent in the easternmost areas of the Mediterranean basin (i.e., the Levant Sea) [37–39], thus leaving as unknown whether the area is characterised by a paucity of species or this is the result of taxonomic impediments and a lack of field studies. Yet, even widely studied biogeographic areas may reveal the presence of possibly undescribed taxa. This is the case of a new *Ocenebra* species, described here, from the Messina Strait area (Italy) and only known to date from a circalittoral submarine cave.

2. Material and Methods

2.1. Field Work

The material examined in the present paper was collected by SCUBA diving by Angelo Vazzana (Associazione-Museo di Biologia Marina e Paleontologia di Reggio Calabria, MBMPRC; Italy) in a circalittoral submarine cave located at a depth of 50–52 m between "secondo dente di Scilla" and "terzo dente di Scilla" and known as "Grotta dei Gamberi" (38°15'25.05" N, 15°42'46.11" E) [40,41]. The biogenic sediment of the cave (52 m) was collected with a scoop. The internal surfaces of the cave (50–52 m) were scraped with a broom. The material obtained was subsequently placed in different nets (mesh size: ~0.2 mm) and subsequently transferred to the MBMPRC laboratory. The cave is generally characterised by the presence of benthic communities dominated by poriferans and mostly by the unicorn shrimp *Plesionika narval* (Fabricius, 1787) [40,41]. The nearby area is dominated by cnidarian taxa, among which a *Paramuricea clavata* (Risso, 1826) forest was widely investigated [40–43]. Preliminary results on the living molluscan communities and the local thanatocoenoses of the area were published by Vazzana [41].

2.2. Laboratory Work

The biogenic sediment was washed with fresh water and air dried for subsequent sorting under a Skymaster stereomicroscope. Fragments (including complete protoconchs) and shells were mounted on SEM stubs and gold-palladium coated in an SC7640 Sputter Coater for SEM examination with a Jeol JSM-6700 F microscope. Live material was sorted out in Petri dishes filled with sea water soon after sampling. Living molluscs were isolated, photographed with a lightstand and 1–5× macro lens mounted on a Canon EOS 5D, and soon fixed in 70% alcohol for radula extraction. The radula was extracted from the buccal mass after tissues had been partly dissolved in a 10% solution of sodium hydroxide (NaOH), then rinsed in distilled water, air dried on a bed of polyvinyl acetate glue, and gold coated. Photos were taken with a Hitachi s-4300 field emission instrument. Samples were measured with Vernier calipers to the nearest 0.1 mm. Sizes are reported in millimetres and given as total height (TH, from the protoconch to the end of the siphonal canal) × total width (TW, perpendicular from the height line). The analysed material is currently preserved either in private or institutional collections (explanation under individual records).

2.3. Nomenclature, Abbreviations, and Acronyms

The following abbreviations and acronyms were also used: AN (Andrea Nappo private collection, Pomezia, Italy); AR (Agatino Reitano private collection, Catania, Italy); FC (Fabio Crocetta private collection, Napoli, Italy); GB (Giuseppe Bonomolo private collection, Jesi, Italy); MBMPRC (Associazione-Museo di Biologia Marina e Paleontologia di Reggio Calabria, Italy); MCZR (Museo Civico di Zoologia, Roma, Italy); MMF (Marine Biology Station of Funchal, Portugal); MNHM (Museo Civico di Storia Naturale, Milano, Italy); MNHN (Muséum National d'Histoire Naturelle, Paris, France); NHMUK (The Natural History Museum, London, U.K.); RH (Roland Houart private collection, Landen, Belgium); SMF (Senckenberg Museum Frankfurt, Frankfurt/Main, Germany); SZN (Stazione Zoologica Anton Dohrn, Naples, Italy); sh, shell(s); lv, specimen(s); TH (total height); TW (total width).

Abbreviations used for spiral sculpture and internal denticles in Muricidae follow Merle [44,45]: IP (infrasutural primary cord); abis (abapical infrasutural secondary cord); P1–P6 (primary cords of the convex part of the teleoconch whorl); s1–s5 (secondary cords of the convex part of the teleoconch whorl); t (threads); ADP (adapical siphonal cord); D1–D5 (denticles within the apertural outer lip).

Updated species taxonomy and nomenclature follow MolluscaBase [46], unless differently stated.

3. Results

3.1. Systematics

Phylum Mollusca Cuvier, 1797
Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Neogastropoda Wenz, 1938
Superfamily Muricoidea Rafinesque, 1815
Family Muricidae Rafinesque, 1815
Subfamily Ocenebrinae Cossmann, 1903
Genus *Ocenebra* Gray, 1847
Ocenebra vazzanai sp. nov. (Figure 1A–G and Figure 4C)
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3.2. Material Examined

Type material. Holotype: one shell (SZN-MOL034—15.5 × 8.5). Paratypes: A-one shell (SZN-MOL035—14.9 × 8); B-one shell (SZN-MOL036—14 × 7); C-one shell (SZN-MOL037—15 × 8); D-one shell (SZN-MOL038—15.5 × 8); E-one shell (SZN-MOL039—16.1 × 8.2); F-one shell (SZN-MOL040—18.4 × 9.6); G-one damaged shell (broken apex) (SZN-MOL041—16.2 × 10); H-one

specimen (shell broken to analyse radular features) (SZN-MOL042—12.9 × 8.1); I-one juvenile specimen (SZN-MOL043—4.5 × 2.3). All specimens/shells listed here come from the type locality.

Additional material. One golden-coated stub, on which (among others) both the specimen used to represent juveniles and the selected protoconchs are mounted (SZN-MOL044); one shell (FC—16 × 7.8); one shell (GB—15 × 7.6); one shell (RH—15.1 × 7.5); four shells (MBMPRC—12.2 × 6.4; 11.3 × 6.1; 16.2 × 9.3; 12.1 × 7); 12 juvenile shells (MBMPRC); 40 fragments (MBMPRC). All shells listed here come from the type locality.

3.3. Type Locality

Grotta dei gamberi (Scilla, Reggio Calabria, Italy) (38°15'25.05"N, 15°42'46.11" E), 50–52 m depth.

3.4. Description

Species with solid and fusiform shell, slightly scalariform appearance. Medium-sized for the genus, TH up to 18.4 mm (paratype F) and TW up to 10 mm (paratype G) (15.5 × 8.5 mm in the holotype—Figure 4C). Paucispiral protoconch of 1.25–1.5 rounded whorls (holotype: 1.5) (Figure 1E), globose, apparently smooth, with micro-sculpture of several irregularly shaped granules, ca. 5 μm in diameter (Figure 1F–G). Teleoconch of 5.5–6 convex whorls at maturity (holotype: 5.5), elongated but rounded, broad in median zone, with last whorl consisting of ca. ⅔ of total height.

Protoconch amber, teleoconch pale brown, reddish, or orangish in colour, sometimes with whitish spiral band in median zone, and occasional second tiny whitish spiral band near siphonal canal (paratype C); dark spots on ribs, in proximity of spiral cords, often more expanded on P1 (Figure 1A and Figure 4C); edge of aperture white, pale brown within. Subsutural ramp slightly angled, fairly broad, with adpressed suture.

Spiral sculpture of convex part of whorl consisting of six nodose, rounded primary cords, higher and more spinose on last whorl, alternated by smaller secondary cords and smaller threads (holotype: present) (Figure 1A,C and Figure 4C). IP, P1, and P2 starting from first teleoconch whorl, soon followed by abis from second whorl, while s1 and s2 can start from second to third whorl (holotype: s1 from second whorl, s2 from third whorl, and abis from second whorl). P3 often visible from third whorl, but sometimes partially covered by subsequent whorl. Axial sculpture consisting of rounded and nodose ribs: 13 or 14 on first teleoconch whorl; 11–13 on second; 10 or 11 on third; nine or 10 on fourth; eight or nine on fifth and on last whorl (holotype: 12 on first whorl; 11 on second; 11 on third; 10 on fourth; nine on the last whorl: Figure 1A,B and Figure 4C). Ribs usually more prominent, high and spinose on last whorl or rarely on penultimate and last whorl, occasionally with one or two erratically placed varices, and one or two strong nodes on last whorl.

Aperture (Figure 1C) slightly narrow, elongate-ovate, outer apertural lip crenulate, erect, with five strong internal denticles: D1–D5 (one rarely split), ID absent. Labral varix slightly high and expanded, from nodose-rounded to spiny aspect. Columellar lip smooth, slightly expanded ventrally, erect abapically and adherent adapically. Labral tooth absent. Siphonal canal moderately long, ventrally sealed and dorsally spirally sculptured (Figure 1C).

Animal translucent with pale brown/whitish spots all over body, yellow spots at base of foot and at end of ocular tentacles, black eyes (Figure 1A). Radula typical of Ocenebrinae, with sickle-shaped lateral teeth with broad base, rachidian bearing short and thick central and lateral cups with short and thick inner lateral denticle on base. Marginal area with short denticles and thick marginal cusp (Figure 1B).

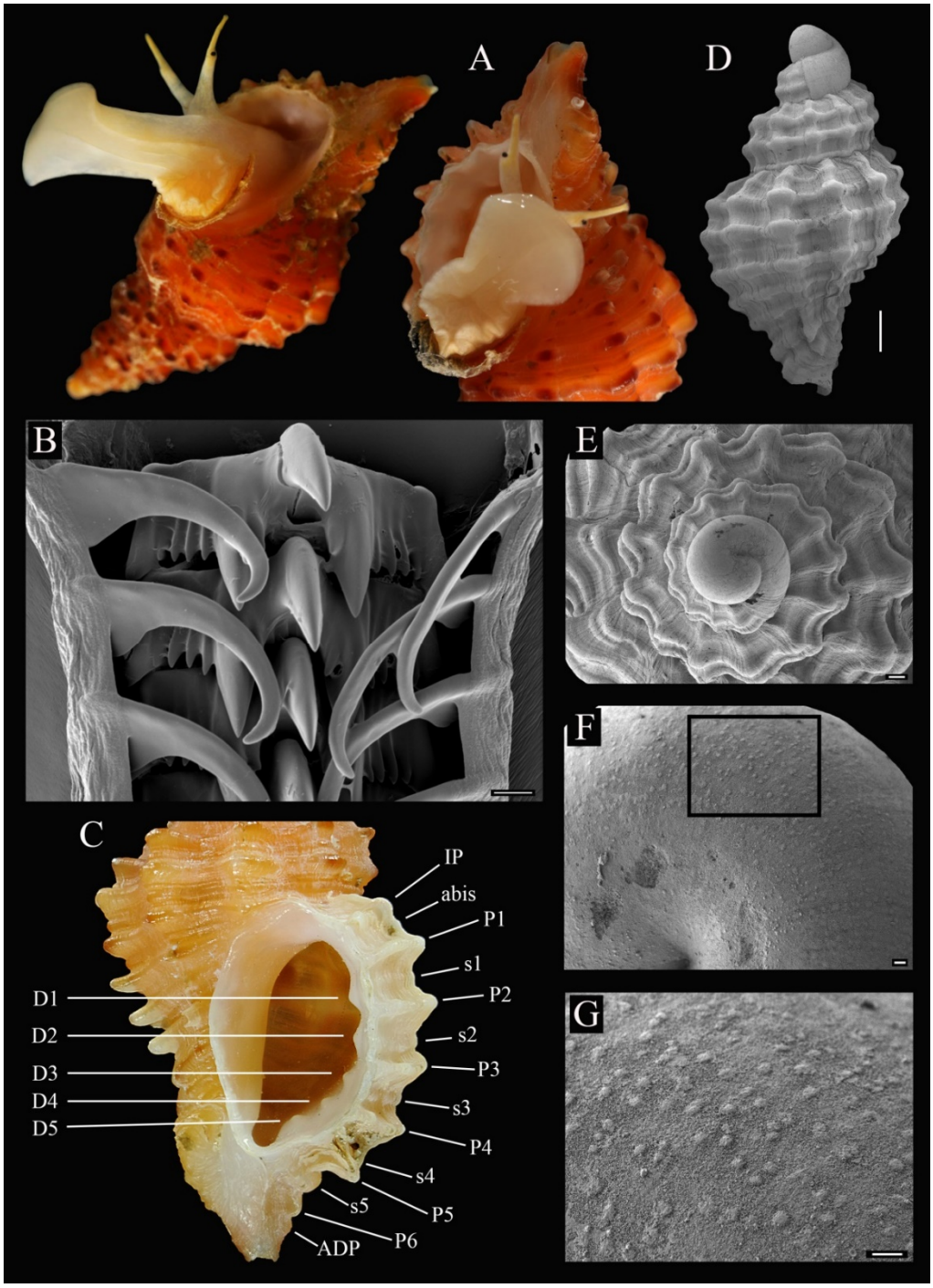

Figure 1. *Ocenebra vazzanai* sp. nov. (**A**,**B**) Paratype H (SZN-MOL042—12.9 × 8.1): details of the animal and its radula. (**B**) Scale bar: 10 µm. (**C**) Holotype (SZN-MOL034—15.5 × 8.5): spiral sculpture on the last whorl and internal denticles (for acronyms see "Abbreviations used"). (**D**) Juvenile specimen (SZN-MOL044): adapertural view and protoconch-teleoconch border. Scale bar: 200 µm. (**E**) Protoconch (SZN-MOL044): apical view. Scale bar: 100 µm. (**F**,**G**) Protoconch (SZN-MOL044): general microsculpture and higher magnification (Figure 2G corresponds to the black square in Figure 2F). (**F**,**G**) Scale bars: 10 µm.

3.5. Etymology

Named after Angelo Vazzana (male), scientific director of MBMPRC (Italy), who provided the material studied here.

3.6. Distribution

A species endemic to the Mediterranean Sea, to date restricted to its type locality.

3.7. Taxonomic Remarks

Ocenebra vazzanai sp. nov. is easily distinguishable from the other northeastern Atlantic and Mediterranean species of *Ocenebra* and *Ocinebrina* due to its unmistakable shell. In fact, the shell of *O. vazzanai* only partially resembles that of *Ocinebrina reinai* Bonomolo and Crocetta, 2012 due to the colour pattern with presence of dark spots on ribs and the spiral and axial sculpture of the teleoconch. However, *Ocinebrina* taxa are characterised by animals with reddish colour patterns, contrarily to the creamish pattern of the *Ocenebra* taxa. *Ocinebrina reinai* is also smaller than *O. vazzanai*, lacks the general spiny aspect of the last whorl, and has a different aperture, with the presence of ID and sometimes of a labral tooth. With regards the congeneric species, the *Ocenebra* taxa more similar to *O. vazzanai* are *O. helleri* (Brusina, 1865), *O. nicolai* Monterosato, 1884, and *O. paddeui* Bonomolo and Buzzurro, 2006 due to the general teleoconch aspect of their shells and the known depth range. However: i) *Ocenebra helleri* has a more scalariform appearance than *O. vazzanai*, its spiral sculpture is stronger and conspicuous all over the shell (in *O. vazzanai* it is mostly visible on the axial sculpture and varices), P3 is always visible from the third whorl, its general aspect is less spiny and more nodose, and the shell usually lacks dark spots on the ribs. In addition, *Ocenebra helleri* has five strong and conspicuous teeth, but often one, and sometimes two, are split, whilst *O. vazzanai* has always five strong teeth and rarely one is split; ii) *Ocenebra nicolai* is rounder than *O. vazzanai*, has larger whorls, and the general teleoconch aspect is quite different due to a stronger sculpture and the absence of spiny varices. Moreover, the teleoconch colour is usually lighter, with an absence of brown spots; iii) *Ocenebra paddeui* has a smooth protoconch with obvious growth lines, is slenderer than *O. vazzanai*, and lacks both its typical spiny and scalariform aspect. It also mostly differs in the lesser number of axial ribs and, as in *O. nicolai*, it always lacks dark spots on the ribs. No other fossil species of European Muricidae assigned to the genera *Ocenebra* or *Ocinebrina* is close enough to *O. vazzanai* to require further comparisons [47–53]. We here deepen the differences between *O. vazzanai* and the recent northeastern Atlantic and Mediterranean congeneric species in Table 1 and also offer an amended comparative plate of the small species of the genus so as to facilitate future identifications (Figures 2–4).

Table 1. Comparative table of the recent northeastern Atlantic and Mediterranean species of the genus *Ocenebra* Gray, 1847. Data amended from [21,25–28,30,35,36,54–57].

	***O.* [*erinaceus*] *erinaceus* (Linnaeus, 1758)**	***O.* [*erinaceus*] *brevirobusta* Houart, 2000**	***O. chavesi* Houart, 1996**	***O. edwardsii* (Payraudeau, 1826) complex**
Figures				2A–E
Shell TH (in mm)	up to 65	up to 42	up to 21.4	up to 26.82
Protoconch w: whorls m: microsculpture	w: 1.25–1.5 m: smooth	w: 1.5 m: smooth	w: 1.5 m: smooth	w: 1.25–1.5 m: smooth or with small granules
Teleoconch ga: general aspect w: whorls cp: colour pattern	ga: fusiform, rounded whorls w: up to 7 cp: whitish, light tan, pale brown, occasionally with darker spiral bands	ga: rounded w: up to 6 cp: pale or dark brown	ga: rounded, slightly scalariform w: up to 6 cp: light tan or pale brown	ga: rounded, scalariform w: up to 6.5 cp: various (from whitish to dark brown, usually light tan with brown blotches or whitish spiral bands)
Teleoconch sculpture of the convex part of the last whorl a: axial s: spiral t: threads	a: 3–11 low or high, rounded, occasionally strong varices s: 6 primary cords alternated by smaller secondary cords t: often present	a: 4–6 broad, large, rounded varices, occasionally very low s: 6 primary cords (with obsolete P2) alternated by smaller secondary cords t: occasionally present	a: 6–7 broad, high, squamous ribs s: 6 primary cords alternated by smaller secondary cords t: often present	a: from 7–9 low, rounded, nodose or occasionally spinose ribs, usually with 1–2 erratically placed varices s: 6 narrow and strong primary cords alternated by smaller secondary cords t: present, occasionally absent
Aperture ga: general aspect cl: columellar lip ol: outer lip d: denticles ID: infrasutural apertural denticle lt: labral tooth	ga: moderately large, elongate-ovate, whitish internal colour cl: narrow, smooth, adherent adapically ol: weakly crenulate d: from absent to 5 weak or strong, occasionally some could appear double ID: occasionally present lt: absent	ga: moderately large, broad, roundy-ovate, whitish internal colour cl: narrow, smooth, adherent adapically ol: crenulate d: 5 strong, occasionally some could appear double ID: occasionally present lt: absent	ga: moderately large, ovate, whitish internal colour cl: smooth, adherent adapically ol: crenulate d: 5 weak, sometimes one could appear double ID: occasionally present lt: absent	ga: large, ovate, white or pale brown internal colour, with occasionally whitish spiral bands cl: narrow, smooth, adherent ol: crenulate, erect. d: 5 weak, sometimes one could appear double ID: absent lt: absent
Radula rachidian cusps c: central l: lateral	c: elongate but quite thick l: elongate but quite thick	unknown	c: elongate but quite thick l: elongate but quite thick	c: elongate l: elongate
Animal general colour pattern	creamish	unknown	unknown	creamish
Depth range (in m)	0–130	littoral	10–22	0–70
Distribution	Atlantic-Mediterranean	Atlantic	Atlantic	Atlantic-Mediterranean
Notes	1	1		2

Table 1. *Cont.*

	O. helleri **(Brusina, 1865)**	***O. hybrida*** **(Aradas and Benoît, 1876)** **-** ***O. piantonii*** **(Cecalupo, Buzzurro, and Mariani, 2008)**	***O. inordinata*** **Houart and Abreu, 1994**	***O. miscowichae*** **(Pallary, 1920)**
Figures	2F	3A, possibly 3B, and 3C (see Notes)	3D	3E
Shell TH (in mm)	up to 23	up to 18.5	up to 21	up to 22
Protoconch w: whorls m: microsculpture	w: 1.5 m: smooth with small and dense granules, often with well visible dense growth lines on the last half whorl	w: 1.25–1.5 m: uncertain, presumably with small granules	w: 1.25–1.5 m: unknown	w: 1.25 m: unknown
Teleoconch ga: general aspect w: whorls cp: colour pattern	ga: slender, scalariform w: up to 6.5 cp: from pale orange to light tan, often with a whitish spiral band in median zone (sometimes two)	ga: rounded, scalariform w: up to 5 cp: various (uniformly light or dark brown, blackish or whitish, occasionally with one or two spiral bands in median zone)	ga: shouldered, strongly nodose w: up to 6 cp: light brown	ga: rounded, scalariform w: up to 5 cp: uniformly light tan or light tan with darker spiral bands
Teleoconch sculpture of the convex part of the last whorl a: axial s: spiral t: threads	a: 6–13 broad, rounded, nodose ribs, occasionally with an erratically placed varix s: 6 high and rounded primary cords alternated by smaller secondary cords t: absent	a: from 3–5 to 6–7 narrow, high, spinose varices, occasionally with weak nodose ribs s: 6 narrow and strong rounded primary cord alternated by smaller secondary cords t: present	a: 4–5 varices alternated by 1–2 high strong nodes s: 6 low shallow primary cords alternated by smaller secondary cords t: occasionally present	a: 7–9 low, weakly nodose ribs s: 6 strong and narrow primary cords alternated by smaller secondary cords t: occasionally present
Aperture ga: general aspect cl: columellar lip ol: outer lip d: denticles ID: infrasutural apertural denticle lt: labral tooth	ga: moderately large, ovate, brown internal colour cl: narrow, smooth, weakly erect abapically, adherent adapically ol: crenulate, erect d: 5 strong and well-marked, often one (or two) appear/s double ID: occasionally present lt: absent	ga: large, ovate, white or black internal colour cl: smooth, adherent, weakly erect abapically ol: crenulate d: 5 strong, sometimes one could appear double ID: absent lt: absent	ga: moderately large, ovate, white internal colour cl: smooth, margin partially weakly erect, adherent adapically ol: crenulate, erect d: 5 strong, sometimes one could appear double ID: absent lt: absent	ga: moderately large, ovate, white internal colour with brown spiral bands cl: narrow, smooth, adherent ol: crenulate, erect d: 5 weak, sometimes one could appear double ID: absent lt: absent
Radula rachidian cusps c: central l: lateral	unknown	c: elongate l: elongate	unknown	unknown
Animal general colour pattern	creamish	creamish	unknown	unknown
Depth range (in m)	20–80	0–8	14–86	infralittoral
Distribution	Mediterranean	Mediterranean	Atlantic	Atlantic
Notes		3		

Table 1. *Cont.*

	O. nicolai **(Monterosato, 1884)**	***O. paddeui*** **(Bonomolo and Buzzurro, 2006)**	***O. purpuroidea*** **(Pallary, 1920)**	***O. vazzanai*** **sp. nov.**
Figures	3F	4A	4B	1A–G and 4C
Shell TH (in mm)	up to 19.74	up to 15.03	up to 16	up to 18.4
Protoconch w: whorls m: microsculpture	w: unknown m: unknown	w: 1.15 m: smooth with growth lines	w: 1.25–1.5 m: unknown	w: 1.25–1.5 m: with small granules
Teleoconch ga: general aspect w: whorls cp: colour pattern	ga: rounded, slightly scalariform w: up to 6.5 cp: from uniformly whitish to light tan or pale brown with a whitish spiral band in median zone (sometimes two)	ga: slender, not scalariform w: up to 5.5 cp: pale brown with whitish spiral bands in median zone (always two but even more)	ga: broad, not scalariform w: up to 5 cp: light tan with brown blotches	ga: slender, slightly scalariform w: up to 6 cp: uniformly pale brown/reddish/orangish, often with a whitish spiral band in median zone (sometimes two), dark spots on ribs
Teleoconch sculpture of the convex part of the last whorl a: axial s: spiral t: threads	a: 7–9 rounded and nodose ribs, sometimes with 1–2 erratically placed varices s: 6 low and strong primary cords alternated by smaller secondary cords t: occasionally present	a: 6–7 low ribs, occasionally with an erratically placed varix s: 6 low and weak primary cords alternated by smaller secondary cords t: occasionally present	a: obsolete, with rarely broad, very low ribs s: 6 high and narrow primary cords and approximately similarly sized secondary cords t: occasionally present	a: 8–9 rounded and nodose/spinose ribs, sometimes with 1–2 erratically placed varices s: 6 nodose and rounded primary cords alternated by smaller secondary cords t: often present
Aperture ga: general aspect cl: columellar lip ol: outer lip d: denticles ID: infrasutural apertural denticle lt: labral tooth	ga: moderately large, ovate, pale brown internal colour cl: narrow, smooth, adherent ol: crenulate, erect d: 5 weak ID: absent lt: absent	ga: narrow and elongate, ovate, shiny white internal colour with brown spiral bands cl: smooth, weakly erect abapically, adherent adapically ol: crenulate, erect d: 5 weak ID: absent lt: absent	ga: large and broad, roundly-ovate, white internal colour with brown spiral bands cl: narrow, smooth, adherent ol: crenulate d: 5 weak pairs ID: absent lt: absent	ga: slightly narrow, elongate-ovate, pale brown internal colour cl: smooth, slightly expanded ventrally, erect abapically and adherent adapically ol: crenulate, erect d: 5 strong, rarely one could appear double ID: absent lt: absent
Radula rachidian cusps c: central l: lateral	unknown	unknown	unknown	c: short and thick l: short and thick
Animal general colour pattern	unknown	unknown	unknown	creamish
Depth range (in m)	circalittoral	80–120	infralittoral	50–52
Distribution	Mediterranean	Mediterranean	Atlantic	Mediterranean
Notes				

Notes: (1) Houart [25] considered *O. erinaceus* and *O. brevirobusta* as different species, whereas Berrou et al. [35] kept them as subspecies. We keep them separated based on MolluscaBase [41]; (2) Taxa previously ascribed to *O. edwardsii*, *O. hispidula*, *O. ingloria*, and *O. leukos* belong to an unsolved complex of species, that we keep here as "*Ocenebra edwardsii* (Payraudeau, 1826) complex" [30]. These taxa are figured below with *O. cyclopus* (Monterosato, 1884); (3) *Ocenebra hybrida* is morphologically indistinguishable from *O. piantonii*. Despite this, we still kept the two taxa separated [30], but our *O. hybrida* description includes *O. piantonii*. *Ocenebra hybrida* is also possibly conspecific with *O. baetica* (Reeve, 1845), figured below. If so, *O. hybrida* should be considered a junior synonym.

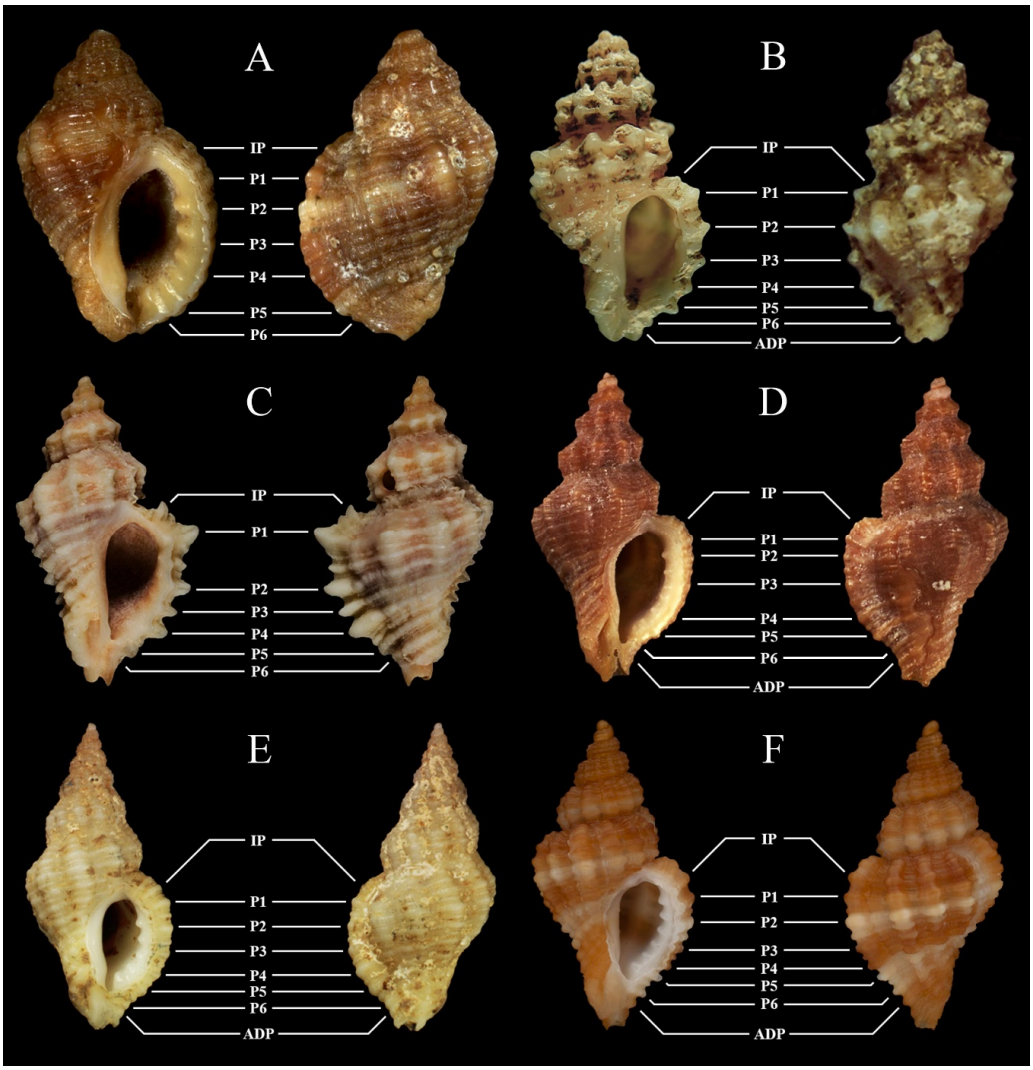

Figure 2. Recent northeastern Atlantic and Mediterranean small species of the genus *Ocenebra* Gray, 1847, with primary cords in the labral varix of the last whorl highlighted (when present): apertural and adapertural views (part 1). Specimens not to scale (sizes in mm as TH × TW). Abbreviations used for spiral sculpture as in Material and Methods. (**A**–**E**) *Ocenebra edwardsii* (Payraudeau, 1826) complex. (**A**) *Ocenebra edwardsii* (Payraudeau, 1826). Holotype of *Amyclina compacta* Nordsieck, 1968 (SMF 344006, 12.6 × 7.7). (**B**) *Ocinebrina cyclopus* Monterosato, 1884 (already a synonym of *O. edwardsii*, see Table 1). Syntype (MCZR-M-30033, 13 × 7.45), frontal view after Appolloni et al. [57]. (**C**) *Ocenebra hispidula* (Pallary, 1904). Syntype (MNHN 1001, 21.9 × 12). (**D**) *Ocenebra ingloria* (Crosse, 1865). Holotype (MNHN 0993, 18.2 × 8.6). (**E**) *Ocenebra leukos* (Houart, 2000). Holotype (MNHN 0966, 18.9 × 8.8). (**F**) *Ocenebra helleri* (Brusina, 1865). Specimen from the closest site to its original description (Mijet Island, Croatia, 60–90 m, 11 × 5.7) (AN private collection).

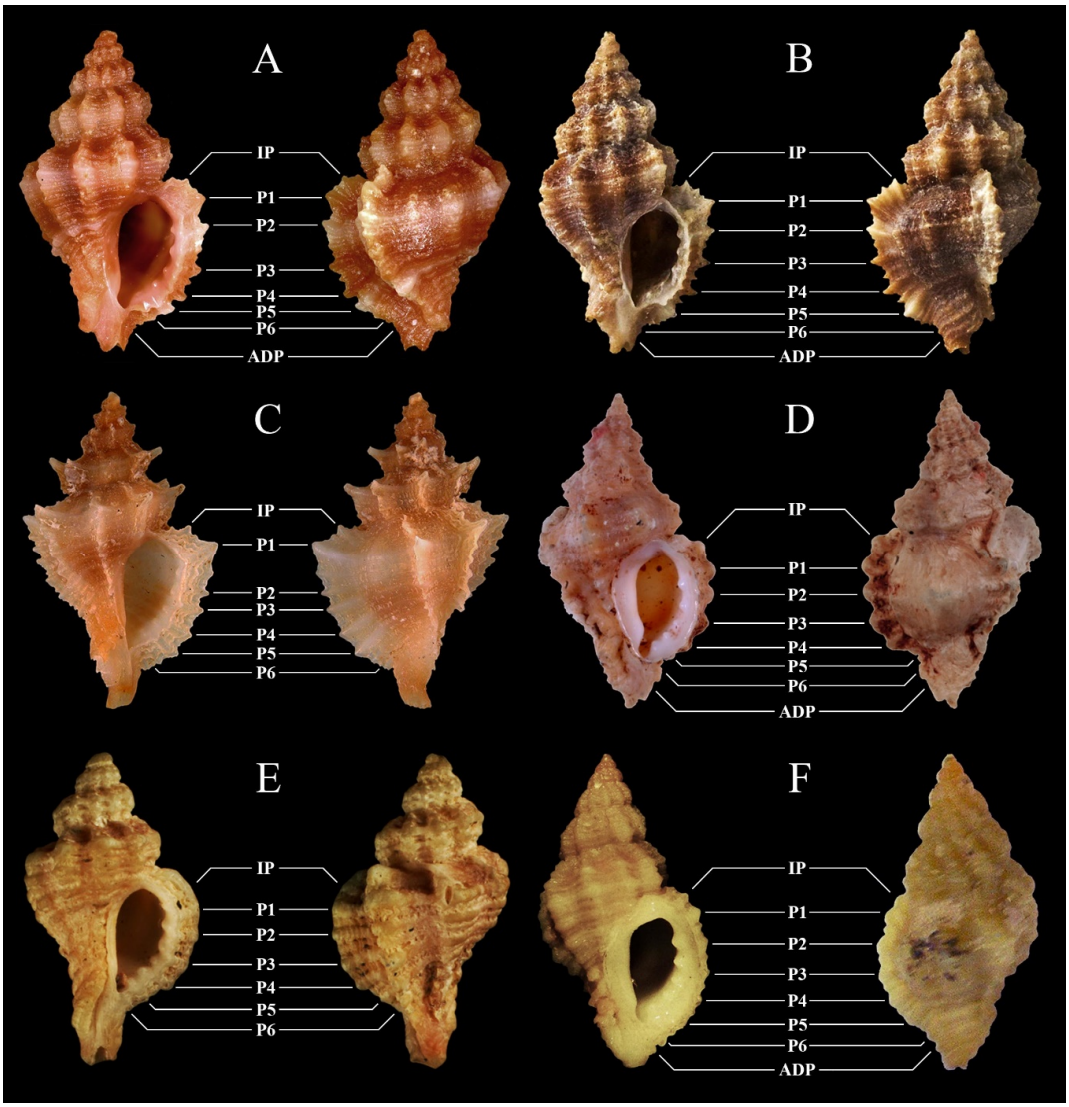

Figure 3. Recent northeastern Atlantic and Mediterranean small species of the genus *Ocenebra* Gray, 1847, with primary cords in the labral varix of the last whorl highlighted (when present): apertural and adapertural views (part 2). Specimens not to scale (sizes in mm as TH × TW). Abbreviations used for spiral sculpture as in Material and Methods. (**A**) *Ocenebra hybrida* (Aradas and Benoît, 1876). Specimen from the closest site to its original description (Isola delle Correnti, Italy, 2 m, 11.5 × 6.5) (AR private collection). (**B**) Syntype of *Murex baeticus* Reeve, 1845 (NHMUK 1972024, 15.8 × 8.5), a possible senior synonym of *O. hybrida*. (**C**) *Ocenebra piantonii* (Cecalupo, Buzzurro, and Mariani, 2008). Holotype (MNHM 33490, 10.3 × 6.5). (**D**) *Ocenebra inordinata* Houart and Abreu, 1994. Holotype (MMF 25429, 19.2 × 10.0). (**E**) *Ocenebra miscowichae* (Pallary, 1920). Syntype (MNHN 177, 12 × 6.3). (**F**) *Ocenebra nicolai* (Monterosato, 1884). Syntype (MCZR-M-30034, 19.7 × 11.3), frontal view after Appolloni et al. [57].

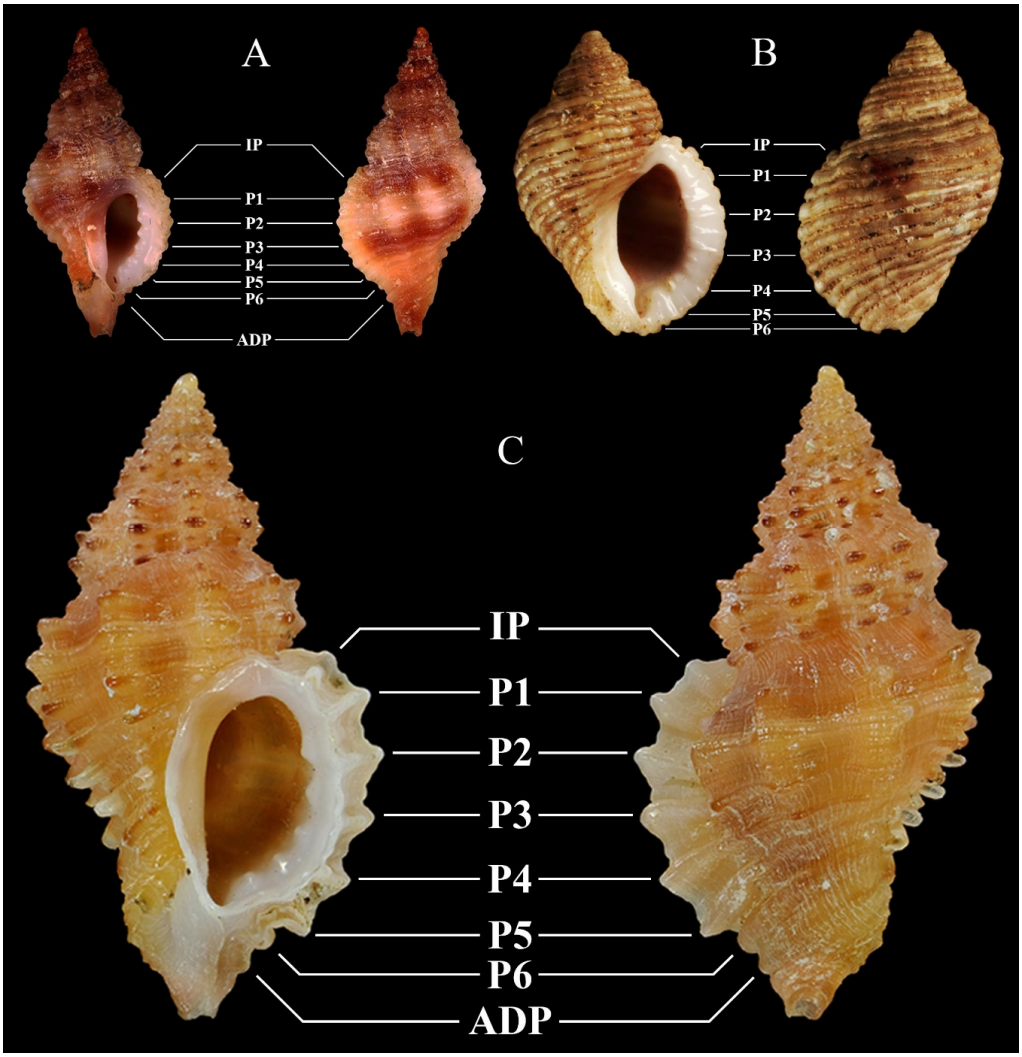

Figure 4. Recent northeastern Atlantic and Mediterranean small species of the genus *Ocenebra* Gray, 1847, with primary cords in the labral varix of the last whorl highlighted (when present): apertural and adapertural views (part 3). Specimens not to scale (sizes in mm as TH × TW). Abbreviations used for spiral sculpture as in Material and Methods. (**A**) *Ocenebra paddeui* (Bonomolo and Buzzurro, 2006). Holotype (MNHM 29909, 13.2 × 6). (**B**) *Ocenebra purpuroidea* (Pallary, 1920). Syntype (MNHN 0931, 14.8 × 9). (**C**) *Ocenebra vazzanai* sp. nov. Holotype (SZN-MOL034, 15.5 × 8.5).

4. Discussion

Muricidae in the northeastern Atlantic and Mediterranean have been always considered a relatively speciose family, with about 60 species (excluding the subfamily Coralliophilinae Chenu, 1859), of which 40 occur in the Mediterranean Sea, a number that also includes about 15 endemic taxa [25; authors' data]. Results from recent systematic studies further confirmed this perception [26–30,32,34], and the present paper additionally raises the biodiversity of the genus *Ocenebra* to at least 13 taxa (one of which is a complex, see Table 1). Such a wide adaptive radiation in the northeastern Atlantic–Mediterranean is not entirely unexpected per se, as *Ocenebra* taxa possess a paucispiral protoconch (up to 1.75 whorls) pointing toward an intracapsular development or a very short pelagic phase, which is usually related to low dispersal capability, high speciation rates, and the presence of endemisms [58]. This is also in agreement with recent studies investigating, among the others, the genera *Aplus* De Gregorio, 1885 and *Dendropoma* Mörch, 1861 in the Mediterranean Sea [59,60]. At the same time, it is also worth a mention that the rate of description of new taxa in the northeastern Atlantic and Mediterranean continues to be

remarkably high [28,32,61–65]. However, the majority of the taxa described as new in the last decades were minute shelled taxa (usually about or less than 5 mm) or sea slugs (and thus without shells that can be found even centuries after their death), or were discovered through a combined approach that involves molecular tools, being cryptic or pseudocryptic of common and widespread species. Contrarily to the examples listed above, *Ocenebra vazzanai* sp. nov. is a relatively large species, belongs to a well-studied taxonomic group, and comes from a widely studied biogeographic area such as Italy.

During the last decades, we (F.C., R.H., G.B.) analysed a wide number of muricids from the northeastern Atlantic and Mediterranean (about 20,000 shells and specimens), and found no samples similar to *O. vazzanai* from any other locality than the Messina Strait area. Despite the fact that we were not able to obtain here any molecular data due to the paucity of living samples and objective difficulties in sampling the type locality again, this new taxon has an unmistakable shell morphology which does not even slightly resemble any other known recent or fossil species, and thus, if widespread, it should not have passed unnoticed until now. Overall, this suggests that *O. vazzanai* is presumably a true endemism, or that it lives in a peculiar habitat connected to underwater caves or perhaps dark environments not easily sampled by professional and amateur malacologists. Marine caves are now widely acknowledged for their rich biodiversity, hosting a variety of sciaphilic communities, ranging from coralligenous to semi- and entirely-dark cave assemblages, and are known to host more than 2000 taxa in the Mediterranean Sea, among which there are ~250 molluscan species [66]. Among them, some Mollusca were described and are still known only from these peculiar environments, i.e., the gastropods *Skeneoides digeronimoi* La Perna, 1999 and *Hyalogyra zibrowii* Warén, 1997 and the bivalves *Neolepton discriminatum* Palazzi and Villari, 2001 and *Lucinoma spelaeum* Palazzi and Villari, 2001 [67–69]. Until further evidence, *O. vazzanai* should also be ascribed to this group of species.

In summary, the present paper adds another proof to the fact that even the northeastern Atlantic-Mediterranean is still an understudied biogeographic region prone to the discovery of new species and further highlights the necessity of taxonomic studies on the local biota, despite the long-lasting malacological and zoological tradition.

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