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A molecular framework for the systematics of the Mediterranean spindle-shells (Gastropoda, Neogastropoda, Fasciolariidae, Fusininae)

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Abstract

A remarkably high diversity of native small spindle-shells (Gastropoda, Fasciolariidae, Fusininae) has been recently inventoried in the Mediterranean Sea, with 23 species identified based on shell morphology. They have almost invariably been classified in the genus *Fusinus*, and a few of them recently moved to other genera (*Aptyxis* Troschel 1868, *Aegeofusinus* Russo, 2017 and *Gracilipurpura* Jousseaume, 1880), mostly based on the sole shell features. We have reconstructed a molecular phylogenetic framework for the Mediterranean Fusininae, focusing on native species representative of the genus-level taxa. Our results confirmed that *Fusinus* s.s. (type species *Murex colus* Linnaeus, 1758) should be restricted to a group of large-shelled species from the Indo-West Pacific and does not fit any of the small-shelled Mediterranean fusinines. We confirm that *Murex syracusanus* Linnaeus, 1758 represents a distinct lineage, and show that for all the remaining species the pattern is suggestive of a single monophyletic radiation of small Mediterranean fusinines, for which the name *Pseudofusus* Monterosato, 1884 must be used.

Keywords: Fasciolariidae; Molecular phylogeny; Systematics; *Aegeofusinus; Aptyxis; Fusinus; Gracilipurpura; Hadriania; Pseudofusus.*

Introduction

Spindle-shells, along with tulip shells and horse-conchs, belong to the neogastropod family Fasciolariidae Gray, 1853. This large lineage of predatory marine snails probably appeared during the Albian (Bandel, 1993), and includes over 500 extant species in *c*. 63 currently accepted extant genera worldwide (MolluscaBase, 2022). Fasciolariids feed on sedentary polychaetes, bivalves, cirripedes and other gastropods (Taylor *et al.*, 1980), and a large majority of species undergo a non-planktotrophic intracapsular development (Leal, 1991).

A recent molecular phylogenetic study (Couto *et al.*, 2016) provided support to recognize three major lineages within the family Fasciolariidae [excluding the unstably positioned *Dolicholatirus* Bellardi, 1884 and *Teralatirus* Coomans, 1965, which are now classified in the Dolicholatiridae (Kantor *et al.*, 2022a]:

1. the so-called *Fasciolaria tulipa* (Linnaeus, 1758) clade, including several genera and broadly corresponding to a revised concept of Fasciolariinae;
2. the *Peristernia nassatula* (Lamarck, 1822) clade, for which the subfamily name Peristerniinae Tryon, 1880 can be used, with species usually ascribed to *Peristernia* Mörch, 1852 and *Fusolatirus* Kuroda & Habe, 1971;
3. the *Fusinus colus* (Linnaeus, 1758) clade, including almost all taxa of Fusininae Wrigley, 1927.

Within the latter clade, five major lineages were recovered, broadly corresponding to five genera: *Fusinus* Rafinesque, 1815, *Amiantofusus* Fraussen, Kantor & Hadorn, 2007*, Granulifusus* Kuroda & Habe, 1954*, Chryseofusus* Hadorn & Fraussen, 2003 and *Angulofusus* Fedosov & Kantor, 2012, with species traditionally ascribed to *Pseudolatirus* Bellardi, 1884 (previously in Peristerniinae) split among *Granulifusus* and *Chryseofusus*.

Kantor *et al.* (2018) revised *Pseudolatirus* restricting its use to fossil species only. Adding new sequences, they provided a framework including the newly introduced genera *Okutanius* Kantor, Fedosov, Snyder & Bouchet, 2018 (preoccupied name, replaced by *Takashius* Kantor, Fedosov, Snyder & Bouchet, 2022, type species *Fusolatirus kuroseanus* Okutani, 1975) and *Vermeijius* Kantor, Fedosov, Snyder & Bouchet, 2018 (type species *Pseudolatirus pallidus* Kuroda & Habe, 1961).

Subsequently, Vermeij & Snyder (2018:71), in a morphology-based revision, proposed groupings of extant and fossil 'large' fusinines in genera largely but not completely in agreement with the molecular phylogenetic schemes of Couto *et al.* (2016) and Kantor *et al.* (2018).

The currently accepted fusinine systematics (MolluscaBase, 2022) is largely based on Vermeij & Snyder (2018) and recognises 46 genera, of which 15 exclusively fossil.

In the Mediterranean Sea, beside the recently immigrated alien species *Marmorofusus verrucosus* (Gmelin, 1791), a remarkably high diversity of native small spindle-shells has been inventoried, with 23 species identified based on shell morphology (Buzzurro & Russo, 2007; Prkić & Russo, 2008; Russo, 2013, 2017; Russo & Germanà, 2014; Russo & Angelidis, 2016; Russo & Calascibetta, 2018; Russo & Pagli, 2019). All those species have been almost invariably placed in *Fusinus*, until Russo (2015) proposed to resurrect the genus *Aptyxis* Troschel, 1868 for *Murex syracusanus* Linnaeus, 1758; then, Russo (2017) introduced the new genus *Aegeofusinus* Russo, 2017 to include some small species endemic to the Aegean Sea; and eventually, Vermeij & Snyder (2018) proposed to place *Murex rostratus* Olivi, 1792 in the genus *Gracilipurpura* Jousseaume, 1880 (Table 1), together with a group of related fossil species.

In this work, we aimed at drawing a molecular phylogenetic framework for the Mediterranean Fusininae, by expanding the molecular dataset of Couto *et al.* (2016) and Kantor *et al.* (2018) with the inclusion of additional samples representative of the native Mediterranean genus-level taxa. This work will provide a systematic scheme for a future revision of the diversity of the spindle-shells of the north-eastern Atlantic and the Mediterranean, in an integrative taxonomy framework.

Material and Methods

Specimen collection

We have used sequences derived from Couto *et al.* (2016) and Kantor *et al.* (2018) relative to 58 specimens. Additionally, DNA sequences were obtained from 10 specimens belonging to 5 Mediterranean species, currently classified as: *Gracilipurpura rostrata*, *Fusinus pulchellus*, *F. parvulus*, *Aegeofusinus rolani, A. eviae*.

Two buccinoidean species, corresponding to the vouchers MNHN-IM-2013-60325 (Buccinidae indet.) MNHN-IM- 2013-19891 (*Manaria* sp.; Eosiphonidae), were used as outgroups (sequences derived after Kantor *et al.*, 2022b). Voucher ID, collecting localities, sequence details and GenBank accession numbers are reported in Table 2.

Molecular analyses and sequence alignment

Specimens were either directly fixed in alcohol upon collection, or pre-treated with microwave to separate the animal from the shell (Galindo *et al.*, 2014). For each specimen, whole genomic DNA was extracted from a ~ 1 mm^3 clip of foot tissue by using a 'salting out' protocol (Aljanabi & Martinez, 1997), or a proteinase K/phenol–chloroform extraction protocol (Oliverio & Mariottini, 2001), with a final elution volume of 50 µL.

Four molecular markers were amplified: the 658-bp barcode region of the mitochondrial COI gene, using the primers LCO1490 and HCO2198 (Folmer *et al.* 1994); a *c*. 800-bp region of the mitochondrial 16S rDNA, with the primers 16SA (Palumbi, 1996) and CGLeuR (Hayashi, 2003); a *c*. 777-bp region of the nuclear 28S rDNA with the primers C1 and D2 (Jovelin & Justine, 2001); and a 328-bp region of the H3 nuclear gene, with the primers H3F and H3R (Colgan *et al.*, 2000).

PCR reactions were performed with 1 µL of undiluted DNA template in 25 µL reactions. Reaction volumes consisted of 2.5 µL of 10x NH4 Reaction Buffer, 2.5 µL of 50 mM MgCl2 Solution, 0.15 µL of BIOTAQ DNA Polymerase, 0.4 µL of each 25 pM primer solution, 1 µL of 10% BSA solution, 0.5 µL of 10 mM nucleotide mix solution. PCR conditions were as follows: initial denaturation (94 °C/5′); 35 cycles of denaturation (94 °C/30″), annealing (48°C for COI, 52°C for 16S, 56°C for 28S, 57°C for H3/40″), and extension (72 °C/1′); final extension (72 °C/10′). PCR products were purified using ExoSAP-IT (USB Corporation) and both strands were sequenced at Macrogen, Inc. COI and H3 sequences were aligned using the alignment algorithm of Geneious v. 11 [Biomatters, 2022. https://www.geneious.com (20 June 2022)] and checked for stop codons, while 16S rRNA and 28S rRNA sequences were aligned with the E-INS-i algorithm in MAFFT v. 7 (Katoh & Standley, 2013; Katoh *et al.*, 2019). Sequences were deposited in GenBank (accession numbers: COI, ON166814-ON166823; 16S, ON178680-ON178689; 28S, ON178690-ON178697; H3, ON214773-ON214782).

Phylogenetic analyses

In our phylogenetic analyses we used several distinct datasets.

Each single-gene dataset (COI; 16S rRNA; 28S rRNA; H3) was employed to derive single-gene trees that were used to check for phylogenetic consistency of the placement of each single sequence. Two concatenated datasets were also produced including only those specimens for which three out of four genes (G3) and all four genes

Table 1. Currently accepted species of Fusininae from the Mediterranean and the Ibero-Moroccan Gulf, with their classification (MolluscaBase, 2021) and known distribution (according to: Buzzurro & Russo, 2007; Prkić & Russo, 2008; Gofas, 2011; Russo, 2013, 2017; Russo & Germanà, 2014; Russo & Angelidis, 2016; Russo & Calascibetta, 2018; Russo & Pagli, 2019).

Genus	species	Distribution	Sequenced
***Aegeofusinus* Russo, 2017**			
	Aegeofusinus angeli (Russo & Angelidis, 2016)	Aegean Sea (Chalki Is.)	
	Aegeofusinus eviae (Buzzurro & Russo, 2007)	Aegean Sea (Astypalea Is.)	✓
	Aegeofusinus margaritae (Buzzurro & Russo, 2007)	Aegean Sea (Karpathos Is.)	
	Aegeofusinus patriciae (Russo & Olivieri, 2013)	Aegean Sea (Crete Is.)	
	Aegeofusinus profetai (Nofroni, 1982)	Aegean Sea (Karpathos Is.)	
	Aegeofusinus rolani (Buzzurro & Ovalis, 2005)	Aegean Sea (Saronikós Gulf; Cyclades)	✓
***Aptyxis* Troschel, 1868**			
	Aptyxis syracusana (Linnaeus, 1758)	Mediterranean Sea (excluding Alboran Sea)	✓
***Gracilipurpura* Jousseaume, 1880**			
	Gracilipurpura rostrata (Olivi, 1792)	Entire Mediterranean Sea and neighbouring Atlantic	✓
***Fusinus* Rafinesque, 1815**			
	Fusinus albacarinoides Hadorn, Afonso & Rolán, 2009	Ibero-Moroccan Gulf	
	Fusinus alternatus Buzzurro & Russo, 2007	Tyrrhenian Sea; Sicily Channel; Aegean Sea	
	Fusinus buzzurroi Prkić & Russo, 2008	Adriatic (Croatia)	
	Fusinus clarae Russo & Renda in Russo, 2013	Messina Strait and southern Sardinia	
	Fusinus corallinus Russo & Germanà, 2014	Jonian Sea (eastern Sicily)	
	Fusinus cretellai Buzzurro & Russo, 2008	Alboran Sea and Ibero-Moroccan Gulf	
	Fusinus dimassai Buzzurro & Russo, 2007	Messina Strait and Lampedusa Is.	
	Fusinus dimitrii Buzzurro & Ovalis in Buzzurro & Russo, 2007	Aegean Sea (Limnos Is.)	
	Fusinus fioritai Russo & Pagli, 2019	Jonian Sea	
	Fusinus insularis Russo & Calascibetta, 2018	Southern Tyrrhenian Sea (N Sicily)	
	Fusinus labronicus (Monterosato, 1884)	Central Mediterranean (N Tyrrhenian; Sardinia; southern France)	
	Fusinus parvulus (Monterosato, 1884)	Mediterranean Sea (excluding Alboran Sea)	✓
	Fusinus pulchellus (Philippi, 1840)	Entire Mediterranean Sea and neighbouring Atlantic	✓
	Fusinus raricostatus (Del Prete, 1883)	Southern Tyrrhenian Sea; Sicily Channel; Sardinia (Adriatic?)	
	Fusinus rusticulus (Monterosato, 1880)	Gulf of Gabès	
	Fusinus ventimigliai Russo & Renda in Russo, 2013	Messina Strait	
***Marmorofusus* Snyder & Lyons, 2014**			
	Marmorofusus verrucosus (Gmelin, 1791)	Alien from Western Indian Ocean: Levant basin	

Table 2. List of material used in this study along with voucher registration numbers, collection localities, GenBank accession numbers for sequences.

			GenBank accession numbers				
Taxon	**Voucher ID**	**Locality**	**COI**	**16S rRNA**	**28S**	**H3**	**References**
Raphitomidae							
Hemipolygona macgintyi	MZSP-36166	USA, Florida	KT754023	-	KT753792	KT754152	Couto *et al.* 2016
Peristernia marquesana	MNHN-IM-2013-15306	Papua New Guinea, Kranket I., 5°12′27″ S, 145°49′1″ E	KT753914	-	KT753681	KT754045	Couto *et al.* 2016
Fusolatirus pearsoni	MNHN-IM-2007-32495	Philippines, W Pamilacan I., 9°30′6″ N, 123°50′24″ E 100–138 m	KT753921	KT753814	KT753688	KT754052	Couto *et al.* 2016
Peristernia nassatula	MNHN-IM-2013-18061	Papua New Guinea, Tab I., 1–8 m	KT753957	KT753845	KT753724	KT754088	Couto *et al.* 2016
Fusolatirus rikae	MNHN-IM-2007-32498	Vanuatu, E Aoré I., 15°33′21″ S, 167°12′43″ E	KT753976	KT753864	KT753743	KT754106	Couto *et al.* 2016
Turrilatirus turritus	MNHN-IM-2013-17100	Papua New Guinea, Tab I., 5°10′6″ S, 145°50′15″ E, 1–4 m	KT753981	KT753869	KT753748	KT754111	Couto *et al.* 2016
Leucozonia nassa	MNHN-IM-2013-20181	Guadeloupe, Point of Saline, 16°12′10″ N, 61°26′41″ W	KT753902	KT753797	KT753668	KT754032	Couto *et al.* 2016
Lamellilatirus lamyi	MNHN-IM-2013-56511	French Guiana, 6°31′6″ N, 52°27′15″ W, 102–104 m	KT754007	KT753884	KT753775	KT754136	Couto *et al.* 2016
Benimakia lanceolata	MNHN-IM-2013-11873	Papua New Guinea, BilBil I., 5°17′54″ S, 145°46′44″ E	KT753959	KT753847	KT753726	KT754090	Couto *et al.* 2016
Hemipoligona armata	MNHN-IM-2013-42511	Senegal, sector of Dakar, 14°40′12″ N, 17°23′48″ W	KT753974	KT753862	KT753741	KT754104	Couto *et al.* 2016
Fasciolaria tulipa	MNHN-IM-2013-19559	Guadeloupe, 16°11′58″ N, 61°34′17″W	KT753954	KT753842	KT753721	KT754085	Couto *et al.* 2016
Pleuroploca trapezium	MNHN-IM-2007-32591	Vanuatu	KT753962	KT753850	KT753729	KT754093	Couto *et al.* 2016
Granulifusus williami	MNHN-IM-2007-39389	Society Islands, 16°43′ S, 151°26′ W, 350–360 m	MG838150	-	MG936641	MG838017	Kantor *et al.* 2018
Granulifusus williami	MNHN-IM-2009-15090	South Madagascar, 24°53′ S, 47°28′ E, 184–203 m	MG838148	-	MG936640	MG838016	Kantor *et al.* 2018
Granulifusus annae	MNHN-IM-2013-42520	New Caledonia, 21°55′24″ S, 166°55′24″ E, 246–255 m	KT753899	-	KT753664	KT754028	Couto *et al.* 2016
Granulifusus annae	MNHN-IM-2013-14709	Papua New Guinea, Rempi Area, 05°03′ S, 145°49′ E, 120 m	KT753937	KT753827	KT753704	KT754068	Couto *et al.* 2016

Continued

Table 2 continued

			GenBank accession numbers				
Taxon	**Voucher ID**	**Locality**	**COI**	**16S rRNA**	**28S**	**H3**	**References**
Granulifusus jeanpierrevezzaroi	MNHN-IM-2007-35083	New Caledonia, Grand Passage, 20°17′7″ S, 163°50′8″ E, 590–809 m	MG838127	-	MG936630	MG838006	Kantor *et al.* 2018
Granulifusus jeanpierrevezzaroi	MNHN-IM-2007-36886	New Caledonia, 22°1′52″ S, 167°6′22″ E, 320–380 m	MG838147	-	MG936639	MG838015	Kantor *et al.* 2018
Granulifusus norfolkensis	MNHN-IM-2013-68811	New Caledonia, N Ile des Pins, 22°28′ S, 167°29′ E, 404–405 m	MG838155	-	MG936643	MG838019	Kantor *et al.* 2018
Granulifusus staminatus	MNHN-IM-2007-32750	Philippines, W Pamilacan I., 9°29′18″ N, 123°51′30″ E, 95–128 m	KT753973	KT753861	KT753740	KT754103	Couto *et al.* 2016
Granulifusus aff. kiranus	MNHN-IM-2013-19037	Bismarck Sea, NE Sissano, 2°54′40″ S, 142°10′46″ E, 535–540 m	KT753966	KT753854	KT753733	KT754096	Couto *et al.* 2016
Granulifusus sp.	MNHN-IM-2009-6658	Solomon Islands	KT753927	KT753820	KT753694	KT754058	Couto *et al.* 2016
Granulifusus hayashii	MNHN-IM-2013-19210	Bismarck Sea, Dogreto Bay, 3°17′42″ S, 143°2′22″ E	KT753955	KT753843	KT753722	KT754086	Couto *et al.* 2016
Granulifusus discrepans	MNHN-IM-2007-34604	Philippines, 16°01′ N, 121°51′ E, 342–358 m	KT753928	KT753821	KT753695	KT754059	Couto *et al.* 2016
Takeshius kuroseanus	MNHN-IM-2013-59070	Papua New Guinea, New Ireland, 2°30′19″ S, 150°44′2″ E, 191–290 m	MG838142	-	MG936636	MG838012	Kantor *et al.* 2018
Takeshius ellenae	MNHN-IM-2013-68819	New Caledonia, S Ile des Pins, 22°53′ S, 167°35′ E, 376–390 m	MG838143	-	MG936637	MG838013	Kantor *et al.* 2018
Angulofusus nedae	MNHN-IM-2007-32574	Vanuatu, N Tutuba I., 15°32′28″ S, 167°16′51″ E, 100–105 m	KT753984	-	KT753751	KT754114	Couto *et al.* 2016
Vermeijius pallidus	MNHN-IM-2007-35093	New Caledonia, Grand Passage, 18°58′33″ S, 163°8′7″ E, 580–647 m	MG838126	-	MG936629	MG838005	Kantor *et al.* 2018
Vermeijius pallidus	MNHN-IM-2007-32537	Solomon Islands, Tetepare, 8°39′58″ S, 157°31′40″ E, 384–418 m	KT753910	KT753806	KT753677	KT754041	Kantor *et al.* 2018
Vermeijius virginiae	MNHN-IM-2009-15084	South Madagascar, SE Point Barrow, 25°3′9″ S, 43°58′28″ E, 400–402 m	MG838134	-	MG936632	MG838008	Kantor *et al.* 2018
Vermeijius sp.	MNHN-IM-2007-32913	Philippines, Bohol Sea, 9°36′12″ N, 123°43′48″ E, 382–434 m	KT753952	KT753841	KT753719	KT754083	Couto *et al.* 2016
Vermeijius sp.	MNHN-IM-2007-32510	New Caledonia	KT753931	KT753823	KT753698	KT754062	Couto *et al.* 2016
Vermeijius retiarius	MNHN-IM-2009-15087	South Madagascar, South Point Barrow, 25°35′28″ S, 44°15′25″ E, 821–910 m	MG838129	-	MG936631	MG838007	Kantor *et al.* 2018

Continued

Table 2 continued

			GenBank accession numbers				
Taxon	**Voucher ID**	**Locality**	**COI**	**16S rRNA**	**28S**	**H3**	**References**
Chryseofusus acherusius	MNHN-IM-2013-44302	China seas, off Taiping Island, 10°25′37″ N, 114°14′21″ E, 1707–1799 m	KT753956	KT753844	KT753723	KT754087	Couto *et al.* 2016
Chryseofusus bradneri	MNHN-IM-2007-32977	New Caledonia	KT753943	KT753833	KT753710	KT754074	Couto *et al.* 2016
Chryseofusus graciliformis	MNHN-IM-2013-19938	Solomon Sea, Dampier Strait, 5°36′18″ S, 148°12′38″ E, 500–640 m	KT753963	KT753851	KT753730	KT754094	Couto *et al.* 2016
Chryseofusus graciliformis	MNHN-IM-2007-32797	Solomon Islands	KT753948	KT753838	KT753715	KT754079	Couto *et al.* 2016
Amiantofusus sebalis	MNHN-IM-2013-44196	China seas, V bis (seamount), 15°5′22″ N, 116°29′40″ E	KT753958	KT753846	KT753725	KT754089	Couto *et al.* 2016
Amiantofusus candoris	MNHN-IM-2013-19759	Bismarck Sea	KT753912	KT753807	KT753679	KT754043	Couto *et al.* 2016
Amiantofusus pacificus	MNHN-IM-2013-44400	China seas, An-Da Chiao, 10°24′52″ N, 114°46′9″ E, 464–1076 m	KT753947	KT753837	KT753714	KT754078	Couto *et al.* 2016
Aptyxis syracusana	BAU_2384_1	Croatia, Sabunike	ON166818	ON178684	ON178693	ON214777	This work
'Cyrtulus' serotinus	MNHN-IM-2013-42532	Marquesas Islands, Eiao, 7°58′46″ S, 140°42′42″ W	KT753969	KT753857	KT753736	KT754099	Couto *et al.* 2016
'Cyrtulus' mauiensis	FMNH-413989	Hawaii	KT753987	KT753873	KT753754	KT754117	Couto *et al.* 2016
Fusinus forceps	MNHN-IM-2007-38235	Madagascar, between Majunga and Cap Saint-André, 15°29′44″ S, 46°5′31″ E, 22–27 m	KT753940	KT753830	KT753707	KT754071	Couto *et al.* 2016
Fusinus crassiplicatus	MNHN-IM-2007-34663	New Caledonia, Grand Passage, 19°7′3″ S, 163°28′26″ E, 199–215 m	KT753917	KT753811	KT753684	KT754048	Couto *et al.* 2016
Fusinus sp.	MNHN-IM-2007-36654	Madagascar	KT753944	KT753834	KT753711	KT754075	Couto *et al.* 2016
Fusinus sandvichensis	FMNH-414020	Hawaii	KT754009	KT753886	KT753777	KT754138	Couto *et al.* 2016
Fusinus similis	ANSP-A20012-411168	Japan, Wakayama Prefecture, Honshu, off Cape Kirime, 70 m	KT754016	KT753890	KT753785	KT754146	Couto *et al.* 2016
Fusinus colus	MNHN-IM-2007-32560	New Caledonia, N Banc Nova, 22°16′5″ S, 159°25′53″ E, 335–338 m	KT753901	KT753796	KT753666	KT754030	Couto *et al.* 2016
Fusinus salisbury	MNHN-IM-2007-32588	New Caledonia, Banc Kelso, 24°7′38″ S, 159°40′55″ E, 310–463 m	KT753975	KT753863	KT753742	KT754105	Couto *et al.* 2016
Fusinus brasiliensis	MZSP-108889	Southeast Brazil	KT754005	KT753882	KT753773	KT754134	Couto *et al.* 2016

Continued

Table 2 continued

Taxon	Voucher ID	Locality	GenBank accession numbers COI	16S rRNA	28S	H3	References
Fusinus brasiliensis	MZSP-117595	Southeast Brazil	KT753986	KT753872	KT753753	KT754116	Couto *et al.* 2016
Propefusus australis	MNHN-IM-2013-42512	Western Australia, Albany, 35°3′52″ S, 117°56′30″ E	KT753923	KT753816	KT753690	KT754054	Couto *et al.* 2016
Aristofusus excavatus	ANSP-A21957	Barbados	KT754000	KT753879	KT753767	KT754129	Couto *et al.* 2016
Pseudofusus rolani	BAU-3615.4	Greece, Attica, Anavyssos	ON166821	ON178687	-	ON214780	This work
Pseudofusus rolani	BAU-3615.5	Anavyssos Greece, Attica, Anavyssos	ON166822	ON178688	ON178696	ON214781	This work
Pseudofusus parvulus	BAU-3788.1	Italy, Marettimo Island, 37°58’03.1”N, 12°04’40.6”E, 35 m	ON166823	ON178689	ON178697	ON214782	This work
Pseudofusus eviae	BAU-3558.1	Grecce, Astypalea Island, 80 m	ON166820	ON178686	ON178695	ON214779	This work
Pseudofusus rostratus	BAU-2022.6	Italy, Venezia Lagoon	ON166814	ON178680	ON178690	ON214773	This work
Pseudofusus rostratus	BAU-2023.2	Italy, off Chioggia, 25–28 m	ON166815	ON178681	-	ON214774	This work
Pseudofusus pulchellus	BAU-2367.1	Italy, Capo Linaro, 45 m	ON166817	ON178683	ON178692	ON214776	This work
Pseudofusus pulchellus	BAU-2024.1	Italy, Sapri, 40 m	ON166816	ON178682	ON178691	ON214775	This work
Pseudofusus pulchellus	BAU-2475.1	Spain, Fuengirola	ON166819	ON178685	ON178694	ON214778	This work
Pseudofusus pulchellus	MCZ-378473	France, Banyuls sur Mer	KT753996	-	KT753763	KT754125	Couto *et al.* 2016
Buccinoidea							
Manaria sp.	MNHN-IM-2013-19891	Solomon Islands, Huon Golf	MW077004	MW067253	MW067180	MW057513	Kantor *et al.* 2022
Buccinidae Gen. sp.	MNHN-IM-2013-60365	Guadeloupe, Grande Terre	MW077040	MW067293	MW067219	MW057556	Kantor *et al.* 2022
Fascicolaria bullisi	FMNH UF-351146	USA, Florida	KT753988	KT753874	KT753755	KT754118	Couto *et al.* 2016
Peristernia Gen. sp.	MNHN-IM-2013-17660	Papua New Guinea	KT753926	KT753819	KT753693	KT754057	Couto *et al.* 2016

Institutional abbreviations are as follows: BAU, Department of Biology and Biotechnologies “Charles Darwin”, Sapienza University of Rome; MNHN, Muséum national d'Histoire naturelle, Paris; ANSP, Academy of Natural Sciences of Philadelphia; FMNH, Florida Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; MZSP, Museum of Zoology, University of São Paulo.

(G4) were available. Analyses were performed on large datasets including selected sequences from all fasciolariid subfamilies (using the two buccinoideans as outgroup), or on reduced datasets focusing only on the Fusininae (using a fasciolariine, *Fasciolaria bullisi* Lyons, 1972, and a peristerniine, *Peristernia* sp., as outgroups). The Bayesian information criterion implemented in jModelTest v. 2.1.7 (Darriba & Posada, 2012) was used to identify the best substitution models and parameters for each gene partition; the substitution models selected for each partition were the following: GTR+I (COI 1st codon position), HKY (COI 2nd codon position), GTR+G (COI 3rd codon position), HKY+I+G (16S), GTR+I+G (28S), and HKY+I+G (H3).

Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian approaches. ML analyses were run on the IQ-TREE web server using W-IQ-TREE v. 1 (Trifinopoulos *et al.*, 2016; with 1000 ultrafast bootstrap replicates). Bayesian analyses were performed using MrBayes v. 3.2.3 (Ronquist *et al.* 2012; 10^7 generations, trees sampled every 1,000 generations, 25% burn-in) on the CIPRES Science Gateway (Miller *et al.*, 2010). Convergence of MCMC was assumed to have occurred when the effective sample size was >200 and the potential scale reduction factor was approximately 1, as calculated with Tracer v. 1.7 (Rambaut *et al.*, 2018). Only nodes with ultrafast bootstrap values (UfB) ≥0.95 or posterior probabilities (PP) values ≥0.95 were considered to be highly supported.

Abbreviations

MNHN: Muséum National d'Histoire Naturelle, Paris.
MHNG: Muséum d'Histoire Naturelle, Genève.
P.R.: private collection Paolo Russo, Venezia.
UfB: ultrafast bootstrap values in Maximum Likelihood analyses.
PP: posterior probabilities of nodes in Bayesian Analyses.

Results

All single-gene trees are reported in Supplementary materials (Figs S1-S8). In our multilocus G3 and G4 trees (Figs 1, 2) the included fasciolariids always formed three

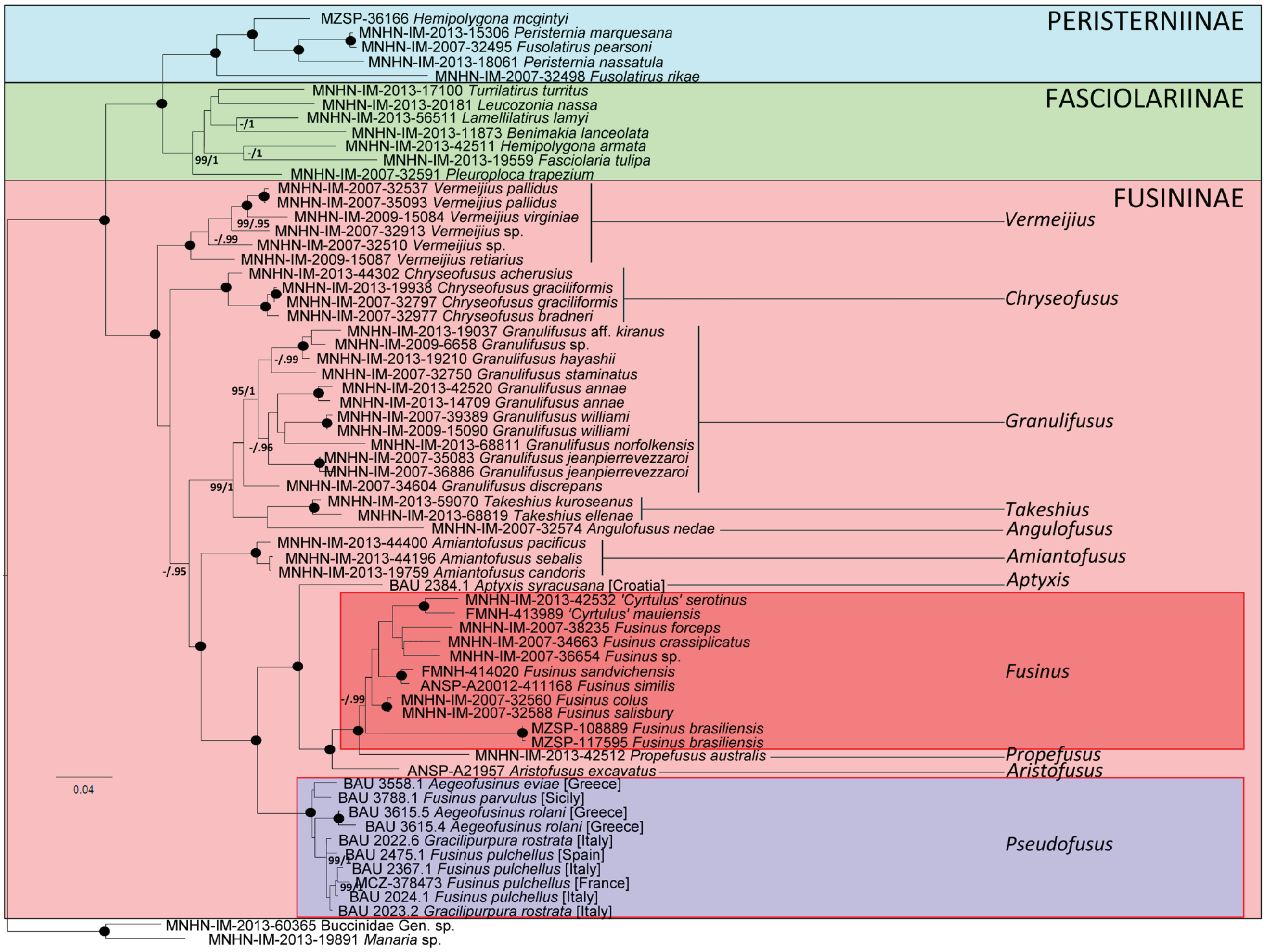

Fig. 1: ML tree (G3 dataset) portraying the relationships among lineages of Fasciolariidae. Lineages of Fusininae corresponding to currently accepted genera are marked. A clade corresponding to a restricted concept of *Fusinus* s.s. (see also Couto *et al.*, 2016, and Kantor *et al.*, 2018) is highlighted in red; in violet a clade of Mediterranean species currently classified in *Aegeofusinus, Fusinus* and *Gracilipurpura*. Numbers at nodes correspond to ultrafast bootstrap support for ML, and posterior probability for BI, respectively (only UfB ≥0.95 and PP ≥0.95 are reported; closed circles indicate 100% BS and 1 PP).

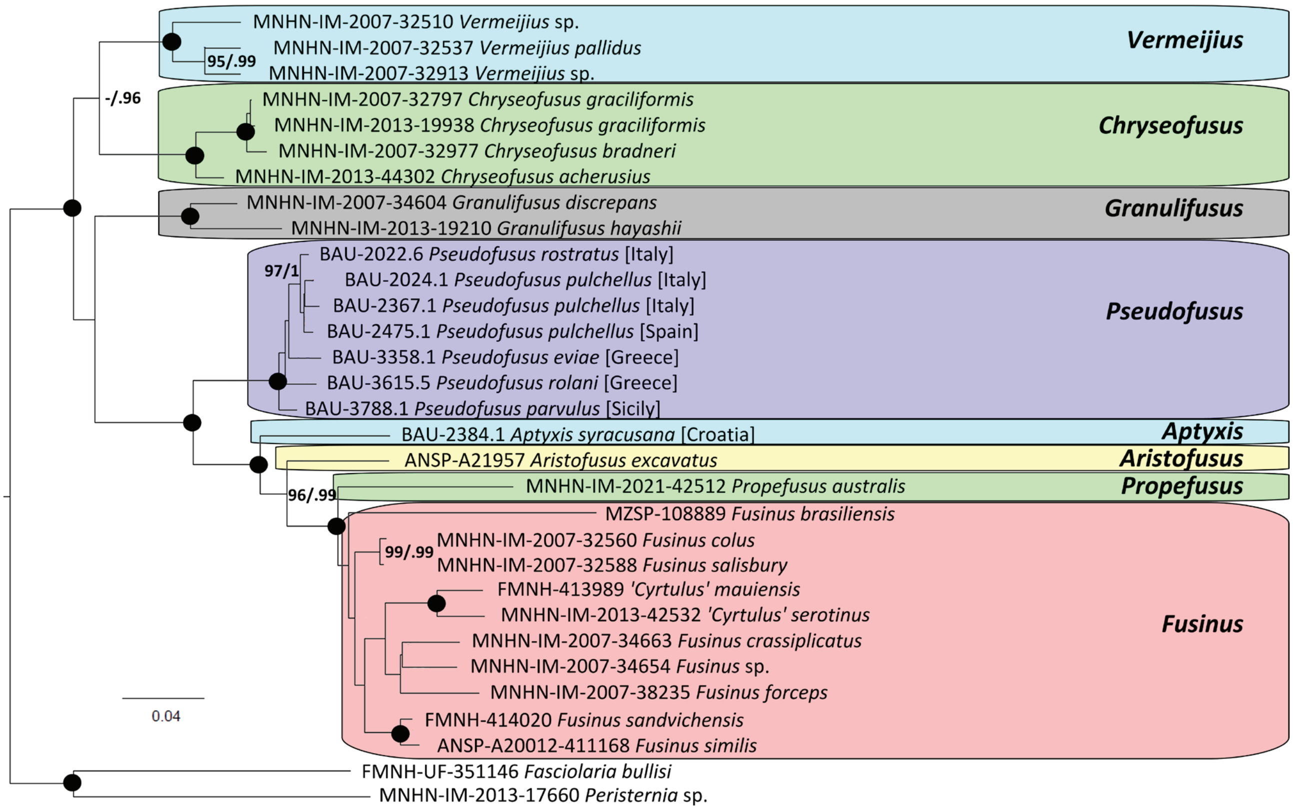

Fig. 2: ML tree of selected taxa (G4 dataset), showing the relationships among fusinine genus level lineages. Numbers at nodes correspond to ultrafast bootstrap support for ML, and posterior probability for BI, respectively (only UfB ≥0.95 and PP ≥0.95 are reported; closed circles indicate 100% BS and 1 PP).

distinct clades – as in Couto *et al.* (2016) and Kantor *et al.* (2018) – corresponding to the three subfamilies Fasciolariinae, Peristerniinae and Fusiniinae, highly supported by both, PP and UfB.

Within the Fusininae we retrieved almost all recognised genera as monophyletic, with high UfB and PP supports, in all G3 and G4 analyses. We could not unambiguously resolve the relationships among most of the genera. However, in the G3 analyses we recovered a clade (UfB 82%, PP 1) with *Amiantofusus* as the sister to a maximally supported clade, including species ascribed to *Fusinus* s.s., *Aristofusus, Propefusus, Cyrtulus* and the Mediterranean native fusinines; recognition of *Cyrtulus* as a distinct genus would make *Fusinus* as currently recognised polyphyletic. This pattern was also strongly supported in the G4 analysis, with the clade *Aptyxis syracusana* + *Aristofusus* + *Propefusus* + *Fusinus* s.s. as sister to the remaining Mediterranean fusinines. The latter formed a maximally supported monophyletic group including *Aegeofusinus eviae, A. rolani, Gracilipurpura rostrata*, *Fusinus pulchellus* and *F. parvulus* (with the two *Aegeofusinus* never forming a monophyletic unit in any analysis).

Discussion

All our analyses confirmed the monophyly of the Fusininae as previously reported by Couto *et al.* (2016) and Kantor *et al.* (2018). The inclusion of the additional Mediterranean taxa did not alter the internal phylogenetic pattern of the Fusininae, where at least nine lineages worthy of genus level classification were identified. Six of them corresponded to the genera *Amiantofusus, Angulofusus, Chryseofusus, Granulifusus, Takashius* and *Vermeijius* as delimited by Kantor *et al.* (2018).

Our results are in agreement with the view of Vermeij & Snyder (2018) that *Fusinus* s.s. (type species *Murex colus*) should be restricted to the group of large-shelled species from the Indo-West Pacific (Fig. 3); however, it should also include – as shown by Couto *et al.* (2016) and Kantor *et al.* (2018) – the morphologically divergent '*Cyrtulus' serotinus* Hinds, 1843 (from Marquesas) and '*Cyrtulus*' *mauiensis* (Callomon & Snyder, 2006) (from Hawaii). Conversely, *Aristofusus excavatus* (G. B. Sowerby II, 1880) and *Propefusus australis* (Quoy & Gaimard, 1833) may be kept as representing distinct genera (with five and three species, respectively) as suggested by their morphology (Vermeij & Snyder, 2018). In this framework, *Fusinus* s.s. is quite evidently not the appropriate genus for the small-shelled Mediterranean fusinines. The Mediterranean species here analysed split into two distinct lineages: one represented by *Aptyxis syracusana* (thus justifying the use of *Aptyxis* for this species, which is also supported by radular differences; see below) and the other including the remaining assayed species. For the latter, the pattern is suggestive of a single radiation of the small fusinines of the Mediterranean Sea currently ascribed to *Fusinus* and *Aegeofusinus*. In fact, the two Aegean species assayed here, which are among those

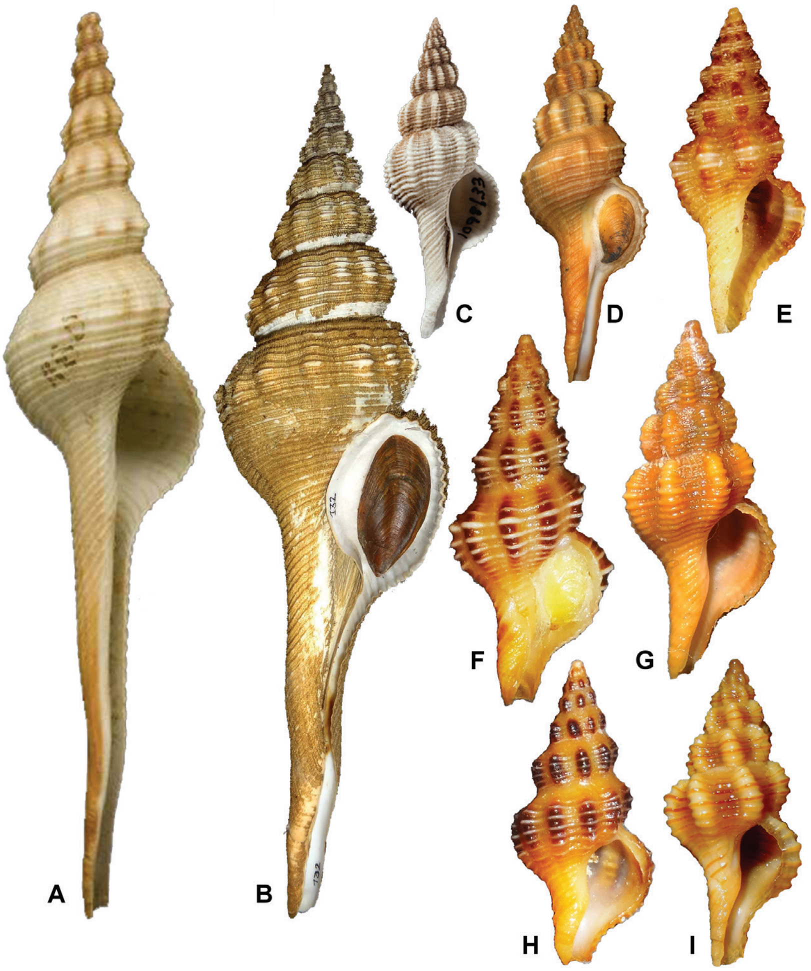

***Fig. 3*: Representative vouchers of species of Fusininae (shells not to scale). A: *Fusinus colus* (Linnaeus, 1758) (type species of *Fusinus*), syntype, courtesy of Linnaean Society, length 113 mm; B: *Fusinus salisbury* Fulton, 1930, East China Sea, coll. P.R., length 246 mm; C, D: *Pseudofusus rostratus* (Olivi, 1792) (type species of *Pseudofusus* Monterosato); C: probable syntype of *Fusus strigosus* Lamarck, 1822, "Méditerranée", MHNG INVE 51731, length 48.5 mm; D: Northern Adriatic, coll. P.R., length 39 mm; E: *Pseudofusus pulchellus* (Philippi, 1844), Sicily Channel, coll. P.R., length 15 mm; F: *Pseudofusus rolani* (Buzzurro & Ovalis, 2005), Saronikos Gulf, coll. P.R., length 13.7 mm; G: *Pseudofusus parvulus* (Monterosato, 1884), Porto Palo (Sicily), coll. P.R., length 15 mm; H: *Pseudofusus margaritae* (Buzzurro & Russo, 2007) (type species of *Aegeofusinus*), Kàrpathos Is., coll. P.R., length 15.5 mm; I: *Pseudofusus eviae* (Buzzurro & Russo, 2007), Astypalea Is., coll. P.R., length 12.7 mm.

recently (Russo, 2017) ascribed to the genus *Aegeofusinus* (*A. eviae* and *A. rolani*, the latter very similar morphologically to the type species *A. margaritae*), belong in this radiation but do not represent a distinct lineage. Concerning all these species, we show herein (see below) that the name *Gracilipurpura* was not introduced for *Murex rostratus*; however, there is a genus name available, *Pseudofusus* Monterosato, 1884, which can be used.

Therefore, we propose the following arrangement for the systematics of the Mediterranean Fusininae. The scheme is derived from the present results, is extended to the non-assayed nominal species by inference on morphological similarity, and will serve as a framework for a future revision of the Mediterranean fusinine fauna.

Systematics

Class Gastropoda Cuvier, 1795

Order Neogastropoda Wenz, 1938
Family Fasciolariidae Gray, 1853
Subfamily Fusininae Wrigley, 1927

Genus *Aptyxis* Troschel, 1868

Aptyxis Troschel, 1868: 61, 64. Type species by monotypy: *Murex syracusanus* Linnaeus, 1758

Remarks

Russo (2015), based on shell and radular morphology (see also Bouchet & Warén, 1985:160, fig. 381; Russo, 2016), resurrected this genus for the type species, *Murex syracusanus* Linnaeus, 1758, and for *Fusus luteopictus* Dall, 1877. For the latter species, Snyder & Vermeij (2016) established the new genus *Hesperaptyxis* that should be tested for validity by molecular data. Landau *et al.* (2013) included in the genus *Aptyxis* the fossil *Fusus palatinus* Strausz, 1954, from the Middle Miocene of Turkey, which would serve in future studies to calibrate the age of this lineage.

Genus *Pseudofusus* Monterosato, 1884

Pseudofusus Monterosato, 1884: 117. Type species by subsequent designation (Crosse, 1885): *Murex rostratus* Olivi, 1792

Aegeofusinus, Russo, 2017 (type species by original designation: *Fusinus margaritae* Buzzurro & Russo, 2007)

Gracilipurpura sensu Vermeij & Snyder (2018:71) not Jousseaume, 1880: 335

Carinofusus Ceulemans, Landau & Van Dingen, 2014 (type species by original designation: *Clavella neogenica* Cossmann, 1901)

Remarks

Monterosato (1884: 117) explicitly considered *Fusus* Lamarck as unfit to host the small Mediterranean spindle shells, which he suggested to place in "*Aptysis*" (sic! lapsus calami for *Aptyxis*) and in another "section" to be called *Pseudofusus,* with the following resulting classification: *Aptyxis syracyusana, Pseudofusus rostratus, P. pulchellus, P. rusticulus, P. labronicus.*

Pseudofusus Monterosato 1884 is the first available name certainly applied to the clade of *Murex rostratus*. Monterosato has repeatedly used *Pseudofusus* (Monterosato 1890; 1891; 1917) as also did Carus (1889: 405-406), Pallary (1900: 267; 1904: 225; 1914), Praus Franceschini (1906: 58), Coen (1914: 7, 24; 1917: 318; 1933: 173; 1937: scheda), Bellini (1902: 97; 1929: 31), Franchini & Zanca (1977:8). Others (Malatesta, 1960; Bouchet & Warén, 1985; Snyder, 2003; Buzzurro & Russo, 2007) regarded *Pseudofusus* as a junior synonym of *Fusinus*.

Vermeij & Snyder (2018:71), proposed to classify *Murex rostratus* (and a group of related fossil species) in *Gracilipurpura* Jousseaume, 1880 (type species "*Fusus strigosus* Lamk.": Jousseaume, 1880: 335; "*Fusus strigosus* Lin.", Jousseaume, 1881: 331). *Fusus strigosus* was actually described by Lamarck (1822: 130), from the Gulf of Taranto (vernacular name: "Fuseau de Tarente") without any image. A probable syntype in the museum of Genève (Finet & Snyder, 2012: fig. 8B; Fig. 3C) is clearly a specimen of *Murex rostratus* Olivi. From here the suggestion by Vermeij & Snyder (2018), to use *Gracilipurpura* for the species that has long been called *Fusinus rostratus* (Olivi). However, it is quite evident from Jousseaume's description ("*Genre Gracillipurpura (nob.) type Fusus strigosus Lin., coquille allongée à spire conique, tours rapeux ornés de gros plis longitudinaux aux deux extrémités; bord columellaire appliqué en arrière et à peine détaché en avant, canal médiocre déjeté a gauche et fermé à l'état adulte"* (Jousseaume, 1881: 331-332) that he was not dealing with a fasciolariid but rather with an ocenebrine muricid (*canal déjeté a gauche et fermé à l'état adulte*). In fact, Jousseaume (1880, 1881) introduced *Gracilipurpura* in the framework of a major revision of the Muricidae, and placed it after "*Tritonalia* (Flem)" (=*Ocenebra* Gray, 1847) and before the fossil *Lyropurpura* Jousseaume, 1880, two typical ocenebrine muricid lineages. He evidently misidentified *Fusus strigosus* Lamarck. This misidentification of *Fusus strigosus* had previously occurred also with Blainville (1828) who redescribed *Fusus strigosus* Lamarck, modifying the description, using the same vernacular name (*"Fuseaux"*), and indicating the same locality (Gulf of Taranto); admitting that he did not know the types, he figured under this name (Blainville, 1828: pl. 4D, fig. 3) a typical deep water specimen of the ocenebrine *Hadriania craticulata* Bucquoy & Dautzenberg, 1882 (as also pointed out by Weinkauff, 1868: 100). This is, therefore, a case of misidentified type species (ICZN, 1999); the use of *Gracilipurpura* can be stabilized by selecting as type species either the fasciolariid species denoted by the name used by Jousseaume (*Fusus strigosus = Murex rostratus*), or the muricid species actually intended by Jousseaume (i.e. *Hadriania craticulata*, albeit using a wrong name). The first option would have the only advantage of maintaining the very recently (Vermeij & Snyder, 2018) proposed use of *Gracilipurpura* for *Murex rostratus*, extending it also to the remaining species of this clade; however, it would be completely disrespectful of the evident original intention of Jousseaume to introduce a genus name for an ocenebrine muricid lineage. The second option makes *Gracilipurpura* an objective senior synonym of *Hadriania* Bucquoy & Dautzenberg, 1882; it is noteworthy that the affected species, *Hadriania craticulata* Bucquoy & Dautzenberg, 1882, has already one of the most troubled nomenclatural histories of the Mediterranean fauna. Therefore, respecting the original intention of Jousseaume, we select and fix as type species of *Gracilipurpura* Jousseaume, 1880 (according to the ICZN, 1999) the taxonomic species actually involved in the misidentification, i.e. *Hadriania craticulata* Bucquoy & Dautzenberg, 1882 (= *Fusus strigosus* sensu Jousseaume, 1880, not *Fusus strigosus* Lamarck, 1822).

We include the following nominal taxa from the Mediterranean and the Ibero-Moroccan Gulf in *Pseudofusus*:

***Pseudofusus rostratus* (Olivi, 1792)**
Pseudofusus albacarinoides (Hadorn, Afonso & Rolán, 2009)
Pseudofusus alternatus (Buzzurro & Russo, 2007)
Pseudofusus angeli (Russo & Angelidis, 2016)
Pseudofusus buzzurroi (Prkić & Russo, 2008)
Pseudofusus clarae (Russo & Renda in Russo, 2013)
Pseudofusus corallinus (Russo & Germanà, 2014)
Pseudofusus cretellai (Buzzurro & Russo, 2008)
Pseudofusus dimassai (Buzzurro & Russo, 2007)
Pseudofusus dimitrii (Buzzurro & Ovalis in Buzzurro & Russo, 2007)
Pseudofusus eviae (Buzzurro & Russo, 2007)
Pseudofusus fioritai (Russo & Pagli, 2019)
Pseudofusus insularis (Russo & Calascibetta, 2018)
Pseudofusus labronicus Monterosato, 1884
Pseudofusus margaritae (Buzzurro & Russo, 2007)
Pseudofusus parvulus (Monterosato, 1884)
Pseudofusus patriciae (Russo & Olivieri, 2013)
Pseudofusus profetai (Nofroni, 1982)
Pseudofusus pulchellus (Philippi, 1840)
Pseudofusus raricostatus (Del Prete, 1883)
Pseudofusus rolani (Buzzurro & Ovalis, 2005)

Pseudofusus rusticulus (Monterosato, 1880)
Pseudofusus ventimigliai (Russo & Renda in Russo, 2013)

A few species have wide ranges (*P. rostratus*, *P. pulchellus*, *P. parvulus*) whereas most taxa have restricted to very restricted ranges. All species have a paucispiral protoconch, indicating a non-planktotrophic larval development (probably entirely intracapsular), which may be related to the geographic pattern. Two of the involved species, *P. rostratus* and *P. pulchellus*, are very hard or impossible to separate morphologically in the area of the Alboran Sea (Gofas, 2011). Present results did not unequivocally nor consistently resolve the assayed specimens morphologically ascribed to either species, suggesting that they represent either a single species, or a pair of species that have diverged very recently. It is hoped that enlarging the sampling will help clarifying this issue.

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Supplementary Data

The following supplementary information is available online for the article:

Fig. S1: Phylogenetic relationships among fasciolariids as illustrated by the **Bayesian** majority consensus tree of the **16S** alignment. The tree is rooted on two buccinoideans (the Eosiphonidae *Manaria* sp., voucher MNHN-IM-2013-19891, and an undetermined Buccinidae, voucher MNHN-IM-2013-60365). Support values are given as posterior probabilities for the Bayesian analysis based on 107 generations, 25% burnin (only values ≥0.95 are shown).

Fig. S2: Phylogenetic relationships among fasciolariids as illustrated by the **Bayesian** majority consensus tree of the **28S** alignment. The tree is rooted on two buccinoideans (the Eosiphonidae *Manaria* sp., voucher MNHN-IM-2013-19891, and an undetermined Buccinidae, voucher MNHN-IM-2013-60365). Support values are given as posterior probabilities for the Bayesian analysis based on 107 generations, 25% burnin (only values ≥0.95 are shown).

Fig. S3: Phylogenetic relationships among fasciolariids as illustrated by the **Bayesian** majority consensus tree of the **COI** alignment. The tree is rooted on two buccinoideans (the Eosiphonidae *Manaria* sp., voucher MNHN-IM-2013-19891, and an undetermined Buccinidae, voucher MNHN-IM-2013-60365). Support values are given as posterior probabilities for the Bayesian analysis based on 107 generations, 25% burnin (only values ≥0.95 are shown).

Fig. S4: Phylogenetic relationships among fasciolariids as illustrated by the **Bayesian** majority consensus tree of the **H3** alignment. The tree is rooted on two buccinoideans (the Eosiphonidae *Manaria* sp., voucher MNHN-IM-2013-19891, and an undetermined Buccinidae, voucher MNHN-IM-2013-60365). Support values are given as posterior probabilities for the Bayesian analysis based on 107 generations, 25% burnin (only values ≥0.95 are shown).

Fig.S5: Phylogenetic relationships among conoideans as illustrated by the **ML** majority consensus tree of the **16S** alignment. The tree is rooted on two buccinoideans (the Eosiphonidae *Manaria* sp., voucher MNHN-IM-2013-19891, and an undetermined Buccinidae, voucher MNHN-IM-2013-60365). Support values are given as ultrafast bootstrap support after ML analysis of 1000 pseudoreplicates (only values ≥95% are shown).

Fig. S6: Phylogenetic relationships among conoideans as illustrated by the **ML** majority consensus tree of the **28S** alignment. The tree is rooted on two buccinoideans (the Eosiphonidae *Manaria* sp., voucher MNHN-IM-2013-19891, and an undetermined Buccinidae, voucher MNHN-IM-2013-60365). Support values are given as ultrafast bootstrap support after ML analysis of 1000 pseudoreplicates (only values ≥95% are shown).

Fig. S7: Phylogenetic relationships among conoideans as illustrated by the **ML** majority consensus tree of the **COI** alignment. The tree is rooted on two buccinoideans (the Eosiphonidae *Manaria* sp., voucher MNHN-IM-2013-19891, and an undetermined Buccinidae, voucher MNHN-IM-2013-60365). Support values are given as ultrafast bootstrap support after ML analysis of 1000 pseudoreplicates (only values ≥95% are shown).

Fig. S8: Phylogenetic relationships among conoideans as illustrated by the **ML** majority consensus tree of the **H3** alignment. The tree is rooted on two buccinoideans (the Eosiphonidae *Manaria* sp., voucher MNHN-IM-2013-19891, and an undetermined Buccinidae, voucher MNHN-IM-2013-60365). Support values are given as ultrafast bootstrap support after ML analysis of 1000 pseudoreplicates (only values ≥95% are shown).