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

GIULIA FASSIO, PAOLO RUSSO, GIUSEPPE BONOMOLO, ALEXANDER E. FEDOSOV, MARIA VITTORIA MODICA, ELISA NOCELLA, MARCO OLIVERIO

doi: 10.12681/mms.29935

To cite this article:

Fassio, G., Russo, P., Bonomolo, G., Fedosov, A. E., Modica, M. V., Nocella, E., & OLIVERIO, M. (2022). A molecular framework for the systematics of the Mediterranean spindle-shells (Gastropoda, Neogastropoda, Fasciolariidae, Fusininae). Mediterranean Marine Science, 23(3), 623–636. https://doi.org/10.12681/mms.29935
A molecular framework for the systematics of the Mediterranean spindle-shells (Gastropoda, Neogastropoda, Fasciolariidae, Fusininae)

Giulia FASSIO1, Paolo RUSSO2, Giuseppe BONOMOLO3, Alexander E. FEDOSOV4,5, Maria Vittoria MODICA6, Elisa NOCELLA1,6 and Marco OLIVERIO1

1 Department of Biology and Biotechnologies “Charles Darwin”, Zoology, Sapienza University of Rome, Viale dell’Università 32, I-00185 Roma, Italy
2 Santa Croce 421, 30135 Venezia
3 Via Giuseppe Mazzini 9 - 61022 Vallefoglia, Pesaro-Urbino
4 A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninski prospect 33, Moscow 119071, Russia
5 Institut de Systématique, Évolution, Biodiversité, ISYEB, UMR7205 (CNRS, EPHE, MNHN, UPMC), Muséum national d’histoire naturelle, Sorbonne Universités, 55 Rue Buffon, 75005 Paris Cedex 05
6 Department of Biology and Evolution of Marine Organisms, Stazione Zoologica Anton Dohrn, Villa Comunale, I-80121, Naples, Italy

Corresponding author: Marco Oliverio; marco.oliverio@uniroma1.it

Contributing Editor: Serge GOFAS

Received: 18 March 2022; Accepted: 20 April 2022; Published online: 24 June 2022

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 horseconchs, 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 unsta-
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 kuroeansus* 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 spindleshells 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 *Agegeofusinus* 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 spindleshells 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*, *Agegeofusinus rolani*, *A. eviae*.

Two buccinoidean species, corresponding to the vouchers 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 mm³ clip of foot tissue by using a ‘salting out’ protocol (Aljanabi & Martínez, 1997), or a proteinase K/phenol–chloroform extraction protocol (Oliverio & Mariotti, 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 800-bp region of the mitochondrial 16S rDNA, with the primers 16SA (Palumbi, 1996) and CGLEuR (Hayashi, 2003); a 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 BIOTQAQ 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 |
|---------------|--------------|-----------|
| **Aegeoacusinus Russo, 2017** | | |
| *Aegeoacusinus angeli* (Russo & Angelidis, 2016) | Aegean Sea (Chalki Is.) | |
| *Aegeoacusinus eviae* (Buzzurro & Russo, 2007) | Aegean Sea (Astypalea Is.) | ✓ |
| *Aegeoacusinus margaritae* (Buzzurro & Russo, 2007) | Aegean Sea (Karpathos Is.) | |
| *Aegeoacusinus patriciae* (Russo & Olivieri, 2013) | Aegean Sea (Crete Is.) | |
| *Aegeoacusinus profetai* (Nofroni, 1982) | Aegean Sea (Karpathos Is.) | |
| *Aegeoacusinus 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 cretella* Buzzurro & Russo, 2008 | Alboran Sea and Ibero-Moroccan Gulf | |
| *Fusinus dimassai* Buzzurro & Russo, 2007 | Messina Strait and Lampedusa Is. | |
| *Fusinus dimritii* Buzzurro & Ovalis in Buzzurro & Russo, 2007 | Aegean Sea (Limnos Is.) | |
| *Fusinus floritai* 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 ventrimigliai* 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.

| 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°49'11" 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 | 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 | 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°49’11" 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    |
| *Pleurolopa 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
| Taxon                        | Voucher ID          | Locality                                                                 | COI       | 16S rRNA | 28S       | H3       | References          |
|-----------------------------|---------------------|---------------------------------------------------------------------------|-----------|----------|-----------|----------|---------------------|
| *Granulifusus jeanpierrevezzaroi* | MNHN-IM-2007-36886 | New Caledonia, 22°1'52" S, 167°6'22" E, 320–380 m                       | MG838147  | -        | MG936663  | MG838015 | Kantor et al. 2018 |
| *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 norfolkensis*  | MNHN-IM-2013-68811 | New Caledonia, 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 Pamilaracan L, 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, 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°39'9" 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

| 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°73" 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 sandwichensis_       | 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*
| Taxon             | Voucher ID        | Locality                                      | GenBank accession numbers | References   |
|------------------|-------------------|-----------------------------------------------|---------------------------|--------------|
| *Fusinus brasiliensis* | MZSP-117595       | Southeast Brazil                              | KT753986                  | Kutcho et al. 2016 |
| *Propfusus australis* | MNHN-IM-2013-42512 | Western Australia, Albany, 35°3′52" S, 117°56′30" E | KT753923                  | Kutcho et al. 2016 |
| *Aristofusus excavatus* | ANSP-A21957       | Barbados                                       | KT754000                  | Kutcho et al. 2016 |
| *Pseudofusus rolandi*   | BAU-3615.4        | Greece, Attica, Anavayssos                     | ON166821                  | This work    |
| *Pseudofusus rolandi*   | BAU-3615.5        | Anavayssos Greece, Attica, Anavayssos         | ON166822                  | This work    |
| *Pseudofusus parvulus*  | BAU-3788.1        | Italy, Marettimo Island, 37°58′03.1″N, 12°04′40.6″E, 35 m | ON166823                  | This work    |
| *Pseudofusus eviae*     | BAU-3558.1        | Greece, Astypalea Island, 80 m                 | ON166820                  | This work    |
| *Pseudofusus rostratus* | BAU-2022.6        | Italy, Venezia Lagoon                         | ON166814                  | This work    |
| *Pseudofusus rostratus* | BAU-2023.2        | Italy, off Chioggia, 25–28 m                   | ON166815                  | This work    |
| *Pseudofusus pulchellus* | BAU-2367.1       | Italy, Capo Linaro, 45 m                       | ON166817                  | This work    |
| *Pseudofusus pulchellus* | BAU-2024.1       | Italy, Sapri, 40 m                            | ON166816                  | This work    |
| *Pseudofusus pulchellus* | BAU-2475.1       | Spain, Fuengirola                             | ON166819                  | This work    |
| *Pseudofusus pulchellus* | MCZ-378473       | France, Banyuls sur Mer                        | KT753996                  | Kutcho et al. 2016 |

**Buccinoidea**

| Taxon            | Voucher ID       | Locality                  | GenBank accession numbers | References   |
|------------------|------------------|----------------------------|---------------------------|--------------|
| *Manaria sp.*    | MNHN-IM-2013-19891 | Solomon Islands, Huon Golf | MW077004                  | Kantor et al. 2022 |
| *Buccinidae Gen. sp.* | MNHN-IM-2013-60365 | Guadeloupe, Grande Terre | MW077040                  | Kantor et al. 2022 |
| *Fascicolaria bullisi* | FMNH UF-351146 | USA, Florida               | KT753988                  | Couto et al. 2016 |
| *Peristernia Gen. sp.* | MNHN-IM-2013-17660 | Papua New Guinea          | KT753926                  | Couto et al. 2016 |

Institutional abbreviations are as follows: BAU, Department of Biology and Biotechnologies “Charles Darwin”, Sapienza University of Rome; MNHN, Musée 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.
Analyses were performed on large datasets including selected sequences from all fasciolariid subfamilies (using the two bucinoideans as outgroup), or on reduced datasets focusing only on the Fusininae (using a fasciolarine, Fasciolaria bullisi Lyons, 1972, and a peristernine, 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 (UB) ≥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.
UB: 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
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. rolandi, 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
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 Bouche & Warén, 1985:160, fig. 381; Russo, 2016), resurrected this genus for the type species, *Murex syracusanus* Linnaeus, 1758, and for *Fusus luteopicus* Dall, 1877. For the latter species, Snyder & Vermeij (2016) established the new genus *Hesperaptyxis* that should be tested for validity by molecular data. Landsau et al. (2013) included in the genus *Aptyxis* the fossil *Fusus palatinus* Straus, 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

*Ageofusinus*, 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* Coissmann, 1901)

**Remarks**

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

Monterosato 1884 is the first available name certain 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) *Gracilipurpura* Jousseaume, 1880, not *Fusus strigosus* Lin., 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 buzzuroi* (Prici & Russo, 2008)

*Pseudofusus clarae* (Russo & Renda in Russo, 2013)

*Pseudofusus corallinus* (Russo & Germanà, 2014)

*Pseudofusus cretei* (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 raricosatus* (Del Prete, 1883)

*Pseudofusus rolanii* (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 assigned 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.

Acknowledgements

We thank Costas Kontadakis (Athens) and Angelo Fiorita (Porto Cesareo), who provided specimens for this study. Domenico Pacifici and Flavia Scoccia (Sapienza University of Rome) are acknowledged for the help with the laboratory work. Samples used in this study were collected during expeditions organized by the MNHN, Paris; among others: CONCALIS (doi: 10.17600/8100010), EXBODI (doi: 10.17600/11100080), EBISCO (doi: 10.17600/5100080), KANACONO (doi: 10.17600/16003900), KARUBENTHOS 2 (doi: 10.17600/15005400), KAVIENG 2014 (doi: 10.17600/14004400), PAPUA NIUGINI (doi: 10.17600/7100070), TARASOC (doi: 10.17600/9100040), TERRASSES (doi: 10.17600/8100100). Work partly supported by a Sapienza grant (“InvEvo”: RM11916B-804DEA4F).

References

Aljanabi, S.M., Martinez, I., 1997. Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. Nucleic Acids Research, 25 (22), 4692-4693.
Bandel, K., 1993. Caenogastropoda during Mesozoic times. Scripta Geologica, Special Issue 2, 7-56.
Bellini, R., 1902. Contribuzione alla conoscenza della fauna dei molluschi marini dell’isola di Capri. Bollettino della Societá dei Naturalisti in Napoli, (1) 15, 85-121.
Bellini R., 1929. I Molluschi del Golfo di Napoli (studi precedenti, l’ambiente, enumerazione e sinonimie). Annuario del Museo Zoologico della R. Universitá di Napoli, (n.s.), 6, 1-87.
Blainville, H.M.D de [Henri Marie Ducrotay], 1828 [1828-1830]. Malacozoaires ou animaux mollusques. Faune française ou histoire naturelle, générale et particulière des animaux que se trouvent en France. Chez F.G. Levrault, Paris, 320 pp (31 pls).
Bouchet, P., Warén, A., 1985. Revision of the Northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca, Gastropoda). Bollettino Malacologico. Supplement 1, 121-296.
Buzzurro, G., Russo, P., 2007. Fusinus del Mediterraneo. Published by the authors, 280 pp.
Carus, J.V., 1889 [1889-1893]. Prodromus Faunae Mediterraneae sive Descriptio Animalium Maris Mediterranei Incolarum quam comparatia silva rerum quatenus innotuit adiectis locis et nominibus vulgaribus eorumque auctoribus in commodum Zoologorum. Vol. 2. E. Schweizerbart’sche Verlagshandlung, Stuttgart, 854 pp.
Coen, G.S., 1914. Contributo allo studio della Fauna malacologica Adriatica. Regio Comitato Talassografico Italiano, Memoria 46, 3-34, pls 1-7.
Coen, G.S., 1917. Di un nuovo Fusus Adriatico. Atti della Società Italiana di Scienze Naturali, 56, 317-319.
Coen, G., 1933. Saggio di una Sylloge Molluscorum Adriaticorum. Regio Comitato Talassografico Italiano, Memoria 192, VII+1-186, 10 pls.
Coen, G.S., 1937. Nuovo saggio di una Sylloge Molluscorum Adriaticorum. Regio Comitato Talassografico Italiano, Memoria 240, 1-173, pls 1-10.
Colgan, D.J., Ponder, W.F., Eggler, P.E., 2000. Gastropod evolutionary rates and phylogenetic relationships assessed using partial 28S rDNA and histone H3 sequences. Zoologica Scripta, 29, 29-63.
Couto, D.R., Bouchet, P., Kantor, Y.I., Simone, L.R.L., Giribet, G., 2016. A multilocus molecular phylogeny of Fasciolariidae (Neogastropoda: Buccinoidea). Molecular Phylogenetics and Evolution, 99, 309-322.
Crosse, H., 1885. Nomenclatura generica e specifica di alcune conchiglie mediterrane, pel Marchese di Monterosato [book review]. Journal de Conchyliologie, 33, 139-142.
Darriba, D., Posada, D., 2012. jModelTest 2.0 manual. Nature Methods, 9, 772.
Finet, Y., Snyder, M.A., 2012. Illustrations and taxonomic placement of the Recent Fusus and Fasciolaria in the Lamarck collection of the Museum d’Histoire Naturelle, Geneva (Caenogastropoda, Buccinoidea, Gastropoda). Zootaxa, 3507 (1), 1-37.
Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology, 3, 294-299.
Franchini, D.A., Zanca, M., 1977. The Genus Fusinus in the Mediterranean Sea. La Conchiglia, 9 (99-100), 16-19.
Galindo, L.A., Puillandre, N., Strong, E.E., Bouchet, P., 2014. Using microwave to prepare gastropods for DNA barcoding. Molecular Ecology Resources, 14, 700-705.
Gofas, S., 2011. Familia Fasciolariidae. p. 287-289. In: Moluscos marinos de Andalucia. Vol. 1. Gofas S., Moreno D., Salas C. (Eds). Servicio de Publicaciones e Intercambio Científico, Universidad de Málaga.
Hayashi, S., 2003. The molecular phylogeny of the Buccinidae (Caenogastropoda: Neogastropoda) as inferred from the complete mitochondrial 16S rRNA gene sequences of selected representatives. Molluscan Research, 25, 85-98.
ICZN (International Commission on Zoological Nomenclature), 1999. International code of zoological nomenclature. Art 70.3. Edn 4. International Trust for Zoological Nomenclature, London, 106 pp.

Joussauwe, F.P., 1880. Division méthodique de la famille des purpuridiés. Le Naturaliste, 1 (1), 335-336.

Joussauwe, F.P., 1881. Etude de Purpuridae et description des espèces nouvelles. Revue et Magasin de Zoologie pure et appliquée, 3rd serie T.7, 314-347 (“1879”).

Jovelin, R., Justine, J., 2001. Phylogenetic relationships within the polyplacophoraylate monogeneans (Platyhelminthes) inferred from partial 28S rDNA sequences. International Journal for Parasitology, 31, 393-401.

Kantor, Y., Fedosov, A.E., Snyder, M.A., Bouchet, P., 2018. Pseudolatirus Bellardi, 1884 revisited, with description of two new genera and five new species (Neogastropoda: Fasciolariidae). European Journal of Taxonomy, 433, 1-57.

Kantor, Y., Fedosov, A., Snyder, M.A., Bouchet, P., 2022a. Takashius nom. nov. (Neogastropoda: Buccinoidea: Fasciolariidae), a replacement name for Okatius Kantor et al., 2018 non D.R. Smith, 1981. R. Thechnica, 32 (2), 60.

Kantor, Y.I., Fedosov, A.E., Kosyan, A.R., Puillandre, N., Sorokin, P.A. et al., 2022b. Molecular phylogeny and revised classification of the Buccinoidea (Neogastropoda). Zoological Journal of the Linnean Society, 194, 789-857.

Katoh, K., Rozewicki, J., Yamada, K. D., 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics, 20, 1160-1166.

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution, 30, 772-780.

Lamarck, M. de, 1822. Histoire Naturelle des Animaux sans Vertèbres. Tome septième. Paris chez l’Auteur, 462 pp.

Landau, B.M., Harzhauser, M., Islamoglu, Y., da Silva, C.M., 2013. Systematics and palaeobiogeography of the gastropods of the middle Miocene (Serravallian) Karaman Basin, Turkey. Cenozoic Research, 11-13, 1-584.

Leal, J.H.L., 1991. Marine Prosobranch Gastropods from Oceanic Islands Off Brazil: Species Composition and Biogeography. Universal Book Services/Dr. W. Backhuys, 418 pp.

Malatesta, A., 1960. Malacofoa pleistocenica di Grammichele. Memorie per servire alla descrizione della Carta Geologica d’Italia, 12, 1-392, 19 pls.

Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE 2010) New Orleans, LA, 1-8.

MolluscaBase (Eds.), 2022. MolluscaBase. https://www.molluscabase.org (Accessed 20 June 2022).

Monterosato, T., 1884. Nomenclatura generica e specifica di alcune conchiglie mediterranee. Stabilimento Tipografico Virzi, Palermo, 152 pp.

Monterosato, T., 1890. Conchiglie di profondità del mare di Palermo. Naturalista Siciliano, 9 (8), 181-191.

Monterosato, T., 1891. Molluschi fossili queratiani si S. Flavia. Naturalista Siciliano, 10 (5), 96-104.

Monterosato, T., 1917. Molluschi delle coste Cirenaiche raccolti dall’Ing. Camillo Crema. Memorie del Comitato Talas-sografico Italiano, Memoria 106, 1-14.

Oliviero, M., Mariottini, P., 2001. A molecular framework for the phylogeny of Coralliophila and related muricoids. Journal of Molluscan Studies, 67, 215-224.

Pallary, P., 1900. Coquilles marines du littoral du Département d’Oran. Journal de Conchyliologie, 48 (3), 211-422.

Pallary, P., 1904. Addition a la faune malacologique du Golfe de Gabès. Journal de Conchyliologie, 52, 212-248.

Pallary, P., 1914. Liste de mollusques du Golfe de Tunis. Bulletin de la Société d’Histoire Naturelle de l’Afrique du Nord, 1, 12-27.

Palumbi, S.R., 1996. Nucleic acids II: the polymerase chain reaction. Molecular Systematics, 2, 205-247.

Paus Francescini, C., 1906. Elenco delle conchiglie del Golfo di Napoli e del Mediterraneo. Annuario del Museo Zoologico della R. Università di Napoli (N.S.), 2, 1-68.

Ptikić, J., Russo, P., 2008. Fusinus buzzerroii (Gastropoda: Fasciolariidae), a new species from Croatian coasts. Iberus, 26 (2), 177-183.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology, 67, 901-904.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D., Darling, A. et al., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology, 61, 539-542.

Russo, P., 2013. Tre nuove specie di Fusinus (Gastropoda: Fasciolariidae) per il Mare Mediterraneo. Bollettino Malacologico, 49 (1), 1-11.

Russo, P., 2015. On the systematic position of Murex syracusanus Linnaeus, 1758 (Gastropoda, Fasciolariidae) with revaluation of the genus Aptyxis. Bollettino Malacologico, 51 (2), 79-86.

Russo, P., 2016. On the grammatical gender of Aptyxis Troesch, 1884 (Gastropoda, Fasciolariidae). Bollettino Malacologico, 52, 76.

Russo, P., 2017. New genus Aegeofusinus (Gastropoda: Fasciolariidae) to include small endemic species of the Aegean sea. Bollettino Malacologico, 53, 63-68.

Russo, P., Angelidis, A., 2016. A new species of Fusinus (Gastropoda, Fasciolariidae) from the Aegean Sea. Bollettino Malacologico, 52 (1), 68-73.

Russo, P., Calascibetta, S., 2018. Fusinus insularis (Gastropoda: Fasciolariidae), new species of the South West Tyrrenhian Sea. Bollettino Malacologico, 54 (2), 134-138.

Russo, P., Germană, A., 2014. Una nuova specie mediterranea di Fusinus (Gastropoda, Fasciolariidae). Bollettino Malacologico, 50, 54-58.

Russo, P., Pagli, A., 2019. Fusinus Fioritae n. sp. (Gastropoda: Fasciolariidae) from the central Apulia, Gulf of Taranto, Ionian Sea, Mediterranean Sea. Bollettino Malacologico, 55 (1), 39-44.

Snyder, M.A., 2003. Catalogue of the marine gastropod family Fasciolariidae. Academy of Natural Sciences of Philadelphia, Special Publication, 21iii + 1-431.

Snyder, M.A., Vermeij, G.J., 2016. Hesperaptyxis, a new genus for some western American Fasciolariidae (Gastropoda), with the description of a new species. The Nautilus, 130 (3), 122-126.
tion and the evolution of predatory prosobranch gastropods. *Palaeontology, 23*, 375-409.
Trifinopoulos, J., Nguyen, L.-T., Von Haeseler, A., Minh, B.Q., 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44, W232-W235.
Troschel, F.H., 1868. *Das Gebiss der Schnecken zur Begründung einer natürlichen Classification*. Vol. 2. Nicolaische Verlagsbuchhandlung, Berlin, 409 pp.
Vermeij, G.J., Snyder, M.A., 2018. Proposed genus-level classification of large species of Fusininae (Gastropoda, Fasciolariidae). *Basteria*, 82 (4-6), 57-82.
Weinkauff, H.C., 1868. *Die Conchylien des Mittelmeeres, ihre geographische und geologisches Verbreitung*. Vol. 2. T. Fischer, Cassel, VI + 512 pp.

**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).