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Two new species of the genus *Amiantofusus* (Gastropoda: Fasciolariidae) from seamounts in the tropical western Pacific, with remarks on the taxonomy of *A. candoris* and *A. sebalis*

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During two scientific expeditions to the seamounts near the Mariana Trench in the tropical western Pacific, two undescribed gastropod species belonging to the genus *Amiantofusus* Fraussen et al., 2007 were collected from the upper bathyal zone. In the present study, we describe and illustrate them as new species. *Amiantofusus granulus* sp. nov. was collected from Magellan and Caroline Seamounts at depths of 1357–1473 m, and *Amiantofusus tchangsii* sp. nov. was discovered from Caroline Seamounts at depths of 1893–2291 m. The new species are distinguished from each other and congeners by shell morphology. Phylogenetic analyses based on the cytochrome oxidase *c* subunit I (COI) gene using Bayesian inference indicate that *Amiantofusus granulus* sp. nov. is a sister group to other congeners, and *Amiantofusus tchangsii* sp. nov. shows a close relationship with *Amiantofusus* sp. JQ950210 from the Philippines. The results provide additional support for the assignment of the new species to the genus *Amiantofusus* and their separation from congeners. In addition, our molecular analysis reveals that *Amiantofusus candoris* Fraussen et al., 2007 and *Amiantofusus sebalis* Fraussen et al., 2007 have almost identical COI sequences. Their taxonomic relationship is briefly discussed, and it is concluded that *A. candoris* should be regarded as a junior synonym of *A. sebalis*.

KEYWORDS

Buccinoidea, Mariana Trench, deep sea, phylogeny, diversity

ZooBank registration LSIDs

Article: urn:lsid:zoobank.org:pub:BA88C7BB-B164-4960-BEEE-5CC03DD4D3AB

Amiantofusus granulus sp. nov.: urn:lsid:zoobank.org:act:C756BA82-9D30-4610-8FD6-0A80FFCE0442

Amiantofusus tchangsii sp. nov.: urn:lsid:zoobank.org:act:B43E0C27-6F7B-429F-BC33-165A9FF3BA01

Introduction

Members of the genus *Amiantofusus* possess shells that are quite similar to those of the family Buccinidae but differ in having a particular protoconch morphology with striking semilunar axial riblets, fasciolariid-like radula, and a distinctive soft-part anatomy (Fraussen et al., 2007; Couto et al., 2016; Couto and Simone, 2019). The genus was originally proposed by Fraussen et al. (2007) to accommodate a small group of deep-sea fasciolariid species. In that publication, Fraussen et al. (2007) designated *Fusus amiantus* Dall, 1889 from the Atlantic Ocean as the type species and described seven other species from the Indo-west Pacific region, including *Amiantofusus borbonicus* Fraussen et al., 2007 and *Amiantofusus cartilago* Fraussen et al., 2007, from the western Indian Ocean and the other five species from the western Pacific. Since then, no additional species have been formally introduced to the genus, although several undescribed species have been reported (Fraussen et al., 2007; Kantor et al., 2012). To date, all known species inhabit the water ranging from relatively shallow depths (down to 300 m) to the upper bathyal zone [1665 m, represented by *Amiantofusus amiantus* (Dall, 1889)].

During two scientific expeditions conducted by the Institute of Oceanology, Chinese Academy of Sciences (IOCAS), two and five specimens belonging to the family Fasciolariidae were collected from two seamounts near the Mariana Trench with the aid of the submersible ROV FAXIAN. Examinations of the shells and radulae revealed that these specimens represent two new species that belong to the genus *Amiantofusus*. During the molecular analysis, we also found that *Amiantofusus sebalis* Fraussen et al., 2007 is genetically very close to *Amiantofusus candoris* Fraussen et al., 2007. In the present study, we formally describe the species and regard *A. candoris* as a junior synonym of *A. sebalis*.

Materials and methods

Sample collection and preservation

Specimens were collected from the upper bathyal zone during the two dives of the Remotely Operated Vehicle (ROV) *Faxian* (IOCAS; mother ship R/V KEXUE) at the two seamounts near the Mariana Trench (Figure 1). The specimens were photographed *in situ* before being sampled by the ROV. Soon after collection, the specimens were fixed in 99.5% ethanol. All examined specimens have been deposited in the Marine Biological Museum of Chinese Academy of Sciences (MBMCAS) at Qingdao, China.

Light and scanning electron microscopies

Shells and soft parts were examined *via* a stereo dissecting microscope (Zeiss SteREO Discovery. V12). For SEM studies, radulae were extracted from the buccal mass by gross dissection, cleaned using 10% NaOH for 1–2 h to remove the surrounding

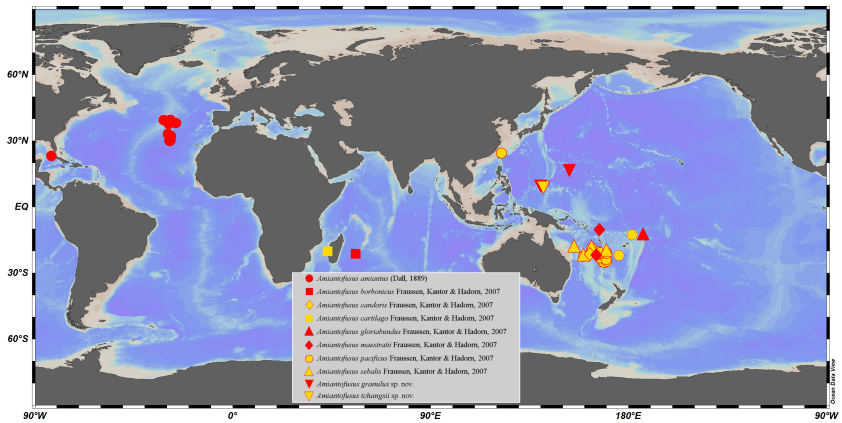

FIGURE 1
Geographic distribution of known *Amiantofusus* species. Data from Dall (1889); Gofas (2000); Fraussen et al. (2007), and the present study.

tissue, rinsed in distilled water, air-dried, coated with gold, and examined with a Hitachi S-3400N SEM with an accelerating voltage of 5 kV. For the identity and terminology of the radula, we followed Fraussen et al. (2007) and Couto and Simone (2019).

DNA extraction and sequencing

One specimen of *Amiantofusus granulus* sp. nov. and three specimens of *Amiantofusus tchangsii* sp. nov. were subjected to molecular analysis. Genomic DNA was extracted with a Column Genomic DNA Isolation Kit (Beijing TIANGEN, China) according to the manufacturer's instructions. DNA was eluted in an elution buffer and stored at –20°C until use. The COI region was amplified by polymerase chain reaction (PCR) using the primers LCO1490 (forward: 5'-GGTCAACAA ATCATAAAGATATTGG-3') and HCO2198 (reverse: 5'-TTAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al., 1994). PCRs were carried out in a total volume of 25 µl, including 2 µl DNA template, 0.5 µl of each 10 µM primers, 0.5 µl of 10 mM dNTPs, 2.5 µl of 10× buffer, and 0.5 U Taq DNA polymerase. Thermal cycling was performed under the following conditions: 95°C for 3 min (initial denaturation), followed by 35 cycles of 95°C for 30 s (denaturation), 42°C for 45 s (annealing), 72°C for 60 s (extension), and a final extension at 72°C for 10 min. The PCR products were verified on a GelRed-stained 1.5% agarose gel and purified with a Column PCR Product Purification Kit (Shanghai Sangon, China), and sequencing was performed with TsingKe Biological Technology (TsingKe Biotech, Beijing, China).

Phylogenetic analyses and genetic distance

For phylogenetic analyses, COI sequences from the present study and representative COI sequences of the family Fasciolariidae downloaded from GenBank were used (Table 1). The species used for phylogenetic analyses represent all the genera currently recognized. Sequence alignments were generated with MAFFT 7 (Katoh and Standley, 2013) using the "G-INS-i (accurate)" strategy. No stop codons, insertions, or deletions were observed in the COI sequences. Ragged parts at both ends were removed with trimAl (Capella-Gutierrez et al., 2009) using the "-automated1" command. ModelFinder (Kalyaanamoorthy et al., 2017) was used to select the best-fit model using the AICc criterion. Bayesian inference phylogenies were inferred using MrBayes 3.2.7 (Ronquist et al., 2012) under the GTR+I+G model. Metropolis-coupled Monte Carlo Markov chains were run using the following parameters: ngen=5,000,000, nchains=4, samplefreq=1000, diagnfreq=1000, and temp=0.05, with split frequencies of less than 0.01 before the analyses were terminated. A 25% burn-in was applied before constructing the majority-rule consensus tree. The tree log was checked to ensure that all chain swap information scores fell into the range 0.1–0.7. Tracer 1.7 (Rambaut et al., 2018) was used to assess the convergence. We followed Couto et al. (2016) to use the species of *Buccinum* (Buccinidae) to root the tree. The results were visualized using FigTree v. 1.4.4. The software MEGA X (Kumar et al., 2018) was employed to calculate the pairwise distances of COI sequences using a Kimura 2-parameter model.

Results

Systematics

Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea Rafinesque, 1815
Family Fasciolariidae Gray, 1853
Subfamily Fusininae Wrigley, 1927
Genus ***Amiantofusus*** Fraussen et al., 2007
Type species. *Fusus amiantus* Dall, 1889, Atlantic, type by original designation

***Amiantofusus granulus* sp. nov.**
Figures 2A, 3A–E, 4A–B

Material examined

Holotype: MBM286510; collection number: M5153; 33.7 mm, 10°01′N 140°06′E, 1473 m, 29 May 2019, from type locality.

Paratype: MBM286711; collection number: M1032; one specimen, 21.9 mm, 17°05′N 153°08′E, ~1357 m, 8 April, 2018.

Description

Shell (Figures 3A–E) fusiform, relatively thick, white or yellowish in color. Protoconch and upper teleoconch whorls lost, with only last four whorls remaining. Suture thin, shallow. Teleoconch whorls convex, subsutural area slightly constricted. Axial sculpture of thin, regularly spaced ribs, numbering 19 and 21 on penultimate and the last whorl, respectively. Spiral sculpture with numerous prominent cords of different strength, primary ones forming small, rounded granules on the axial ribs. Both axial and spiral sculptures becoming weak on the shell base. Aperture large, ovate, inner surface white, outer lip sharped; columellar lip weakly callused, anterior part slightly curved. Siphonal canal relatively long, semitubular.

Radula (Figures 4A, B) rachiglossan, with a formula of 1 + 1+1, asymmetric. Rachidian teeth small, narrow, with an elongated base; distal end simple, with a large central cusp. Right lateral teeth with six major cusps along the posterior margin and a small knob at the inner end, left lateral teeth with five major cusps and a small knob.

TABLE 1 List of representatives of the family Fasciolariidae and outgroup species used for phylogenetic analysis using the COI gene, with GenBank accession number, voucher number (where available), and original references.

Genus	Species	Accession number	Voucher	References
Amiantofusus Fraussen, Kantor & Hadorn, 2007	*Amiantofusus sebalis*	KT753958.1	MNHN:IM:2013-44196	Couto et al. (2016)
	Amiantofusus pacificus	KT753947.1	MNHN:IM:2013-44400	Couto et al. (2016)
	Amiantofusus pacificus	KT753918.1	MNHN:IM:2009-13533	Couto et al. (2016)
	Amiantofusus sebalis	KT753911.1	MNHN:IM:2007-32837	Couto et al. (2016)
	Amiantofusus candoris	KT753912.1	MNHN:IM:2013-19759	Couto et al. (2016)
	Amiantofusus sp.	JQ950210.1	MNHN-IM-2007-34648	Kantor et al. (2012)
	***Amiantofusus granulus* sp. nov.**	**OP114412**	**M5153**	**This study**
	***Amiantofusus tchangsii* sp. nov.**	**OP114413**	**M5296**	**This study**
	***Amiantofusus tchangsii* sp. nov.**	**OP114414**	**M5348**	**This study**
	***Amiantofusus tchangsii* sp. nov.**	**OP114415**	**M5461**	**This study**
Angulofusus Fedosov & Kantor, 2012	*Angulofusus nedae*	KT753984.1	MNHN:IM:2007-32574	Couto et al. (2016)
Aptyxis Troschel, 1868	*Aptyxis syracusanus*	KT753968.1	MNHN:IM:2013-32440	Couto et al. (2016)
Aurantilaria Snyder, Vermeij & Lyons, 2012	*Aurantilaria aurantiaca*	KT754013.1	MZSP 101904	Couto et al. (2016)
Australaria Snyder, Vermeij & Lyons, 2012	*Australaria australasia*	KT753990.1	MNHN:IM:2013-42516	Couto et al. (2016)
Benimakia Habe, 1958	*Benimakia fastigium*	KT754010.1	FMNH UF-369083	Couto et al. (2016)
	Benimakia lanceolata	KT753959.1	MNHN:IM:2013-11873	Couto et al. (2016)
Cinctura Hollister, 1957	*Cinctura hunteria*	KT754011.1	MCZ:Mala:382637	Couto et al. (2016)
Chryseofusus Hadorn & Fraussen, 2003	*Chryseofusus bradneri*	MN752200.1	MNHN IM 2009-15108	Kantor et al. (2020
	Chryseofusus graciliformis	KT753963.1	MNHN:IM:2013-19938	Couto et al. (2016)
	Chryseofusus acherusius	KT753956.1	MNHN:IM:2013-44302	Couto et al. (2016)
Fasciolaria Lamarck, 1799	*Fasciolaria bullisi*	KT753988.1	FMNH UF-351146	Couto et al. (2016)
Filifusus Snyder, Vermeij & Lyons, 2012	*Filifusus filamentosus*	KT753909.1	MNHN:IM:2013-13107	Couto et al. (2016)
Fusinus Rafinesque, 1815	*Fusinus sandvichensis*	KT754009.1	FMNH 414020	Couto et al. (2016)
	Fusinus pulchellus	KT753996.1	MCZ:Mala:378473	Couto et al. (2016)
	Fusinus agatha	KT753993.1	MZSP 53680	Couto et al. (2016)
Fusolatirus Kuroda & Habe, 1971	*Fusolatirus rikae*	KT753976.1	MNHN:IM:2007-32498	Couto et al. (2016)
	Fusolatirus pachyus	KT753961.1	MNHN:IM:2007-35084	Couto et al. (2016)
Gracilipurpura Jousseaume, 1880	*Gracilipurpura rostrata*	MN064616.1	–	Couton et al. (2019)
Granulifusus Kuroda & Habe, 1954	*Granulifusus hayashi*	KT753955.1	MNHN:IM:2013-19210	Couto et al. (2016)
	Granulifusus staminatus	KT753973.1	MNHN:IM:2007-32750	Couto et al. (2016)
	Granulifusus niponicus	KT753935.1	MNHN:IM:2013-19903	Couto et al. (2016)
Hemipolygona Rovereto, 1899	*Hemipolygona mcgintyi*	KT754023.1	MZSP 36166	Couto et al. (2016)
	Hemipolygona armata	KT753974.1	MNHN:IM:2013-42511	Couto et al. (2016)
Lamellilatirus Lyons & Snyder, 2008	*Lamellilatirus lamyi*	KT754007.1	MNHN:IM:2013-56511	Couto et al. (2016)
Latirolagena G. F. Harris, 1897	*Latirolagena smaragdulus*	KT753964.1	MNHN:IM:2007-32547	Couto et al. (2016)
Latirus Montfort, 1810	*Latirus amplustre*	KT754021.1	FMNH UF-410623	Couto et al. (2016)
	Latirus polygonus	KT753995.1	MZSP 99782	Couto et al. (2016)
	Latirus pictus	KT753967.1	MNHN:IM:2013-10540	Couto et al. (2016)
Leucozonia Gray, 1847	*Leucozonia nassa*	KT754019.1	MZSP 112955	Couto et al. (2016)
Nodolatirus Bouchet & Snyder, 2013	*Nodolatirus nodatus*	KT753906.1	MNHN:IM:2013-42534	Couto et al. (2016)
Opeatostoma Berry, 1958	*Opeatostoma pseudodon*	KT754025.1	MZSP 68483	Couto et al. (2016)
Pararetifusus Kosuge, 1967	*Pararetifusus carinatus*	MK583342.1	–	Vaux et al. (2017)
Peristernia Mörch, 1852	*Peristernia chlorostoma*	MW277916.1	508060-Mollusca	Paulay et al., unpublished
	Peristernia gemmata	KT753980.1	MNHN:IM:2013-42528	Couto et al. (2016)
	Peristernia nassatula	KT753957.1	MNHN:IM:2013-18061	Couto et al. (2016)
Pleuroploca P. Fischer, 1884	*Pleuroploca trapezium*	KT753962.1	MNHN:IM:2007-32591	Couto et al. (2016)
	Pleuroploca filamentosa	JQ950197.1	MNHN-IM-2007-32592	Kantor et al. (2012)
Polygona Schumacher, 1817	*Polygona infundibulum*	MW125081.1	USNM:IZ:1450670	Pappalardo et al. (2021)

(Continued)

TABLE 1 Continued

Genus	Species	Accession number	Voucher	References
	Polygona bernadensis	KT754001.1	MNHN:IM:2013-56077	Couto et al. (2016)
	Polygona angulata	KT753985.1	MZSP 112907	Couto et al. (2016)
Pseudolatirus Bellardi, 1884	*Pseudolatirus* sp.	MG838144.1	MNHN-IM-2007-38356	Kantor et al. (2019)
	Pseudolatirus sp.	MG838142.1	MNHN-IM-2013-59070	Kantor et al. (2019)
Pustulatirus Vermeij & Snyder, 2006	*Pustulatirus praestantior*	KT754014.1	FMNH UF-359664	Couto et al. (2016)
Triplofusus Olsson & Harbison, 1953	*Triplofusus giganteus*	KT754003.1	MCZ:Mala:382636	Couto et al. (2016)
Turrilatirus Vermeij & M. A. Snyder, 2006	*Turrilatirus turritus*	KT753981.1	MNHN:IM:2013-17100	Couto et al. (2016)
	Turrilatirus craticulatus	KT753920.1	MNHN:IM:2007-32504	Couto et al. (2016)
Vermeijius Kantor, Fedosov, Snyder & Bouchet, 2018	*Vermeijius retiarius*	MG838129.1	MNHN-IM-2009-15087	Kantor et al. (2019)
Buccinum Linnaeus, 1758 (outgroup)	*Buccinum koreana*	KX519501.1	BK005	Zhang and Zhang (2017)
	Buccinum undatum	KF644029.1	11BFMOL-0347	Layton et al. (2014)

Newly sequenced species are in bold.

Operculum (Figure 3A) semitransparent, pale brown, very thin, elongate-oval, with terminal nucleus.

Type locality: Caroline seamounts, near the Mariana Trench, 1473 m deep, 10°01′N 140°06′E.

Etymology: The name of the new species refers to the nature of the axial ribs with granules.

Distribution and habitat: To date, this species is known from the two seamounts near the Mariana Trench—Kocebu Guyot and Caroline seamounts, where it lives on basalt rock at depths of 1375–1473 m.

Remarks: *Amiantofusus granulus* sp. nov. is characterized by its large shell sculptured with broad but weak spiral cords separated by fine interspaces and thin, regularly spaced axial ribs and numerous, small, rounded granules on the axial ribs. Within the genus, only one species, *Amiantofusus gloriabundus* Fraussen et al., 2007, has similar granules on the axial ribs. However, the latter can be clearly separated from the new species in having a slightly broader shell (a width/height ratio of the last whorl of 0.72 instead of 0.64) with a more convex outline of the last whorl, the much more developed spiral cords separated by well-defined interspaces and the weaker axial ribs that are slightly lower in number (17 on penultimate and 20 on the last whorl vs. 19 on penultimate and 21 on the last whorl).

***Amiantofusus tchangsii* sp. nov.**

Figures 2B, 3F–K, 4C–D

Material examined

Holotype: MBM287288; collection number: M5296; 30.6 mm, 10°05′N 140°10′E, 1237 m, 1 June 2019, from type locality;

Paratype 1: MBM287289; collection number: M5461; 35.9 mm, 10°03′N 140°09′E, 1816–2291 m, 9 June 2019;

Paratype 2: MBM287280; collection number: M5348; 36.7 mm, 10°04′N 140°11′E, 893 m, 2 June 2019;

Paratype 3: MBM287291; collection number: M7041; 36.3 mm, 10°05′N 140°15′E, 1087 m, 8 June 2019;

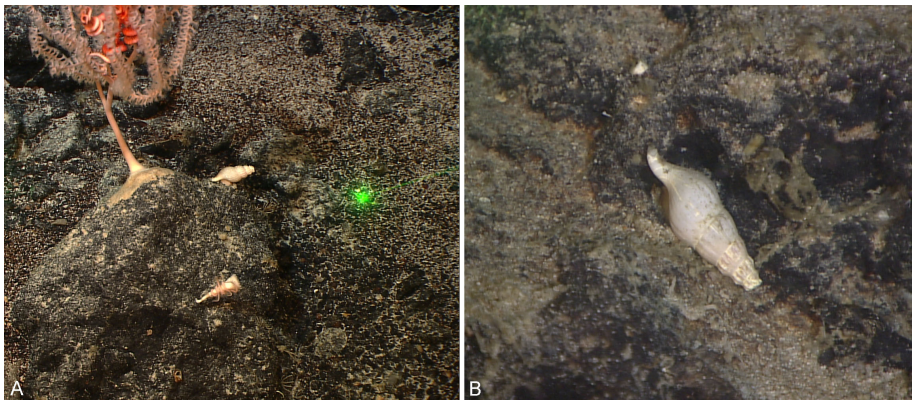

FIGURE 2
In situ image of *Amiantofusus* species on natural substrate. **(A)** *Amiantofusus granulus* sp. nov.; **(B)** *Amiantofusus tchangsii* sp. nov.

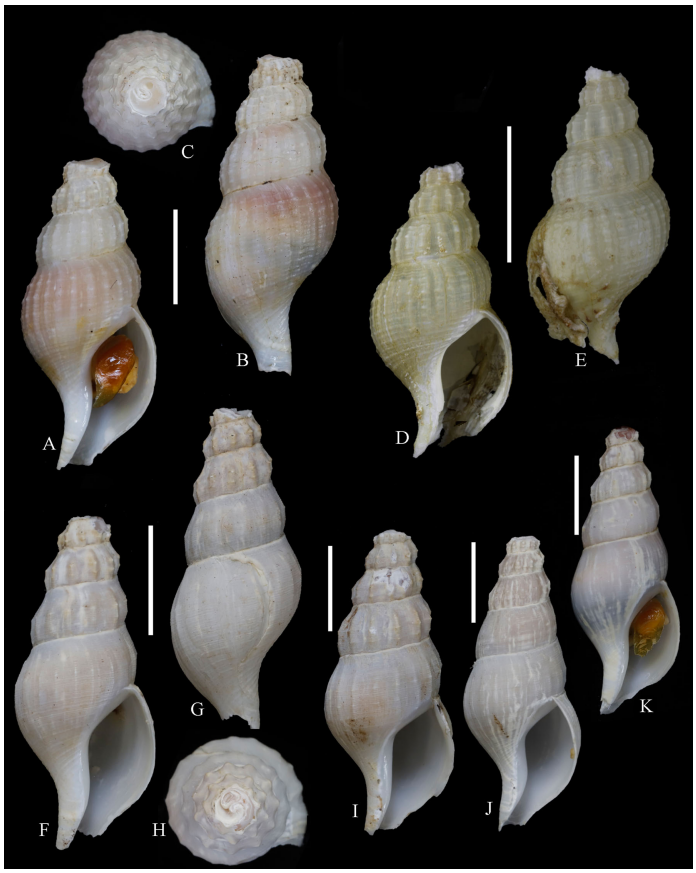

FIGURE 3
Amiantofusus species. **(A–E)** *Amiantofusus granulus* sp. nov. **(A–C)** Holotype, MBM286510, 32.8 mm; **(D, E)** paratype, MBM286711, 21.8 mm; **(F–K)** *Amiantofusus tchangsii* sp. nov. **(F–H)** Holotype, MBM287288, 30.6 mm; **(I)** paratype 1, MBM287289, 35.9 mm; **(J)** paratype 2, MBM287280, 36.7 mm; **(K)** paratype 3, MBM287291, 36.3 mm. Scale bars = 10 mm.

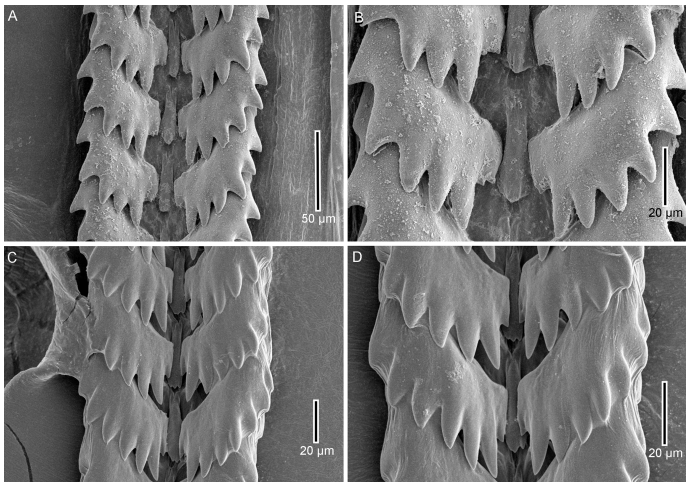

FIGURE 4
Radulae. **(A, B)** Radula of *Amiantofusus granulus* sp. nov., MBM286510; **(C, D)** radula of *Amiantofusus tchangsii* sp. nov., MBM287291.

Paratype 4: MBM287292; collection number: M7042; 40.6 mm, 10°05′N 140°15′E, 1084 m, 8 June 2019.

Description

Shell (Figures 3F–K) fusiform, relatively thick, white or yellowish in color. Protoconch and upper teleoconch whorls lost, with only last four or five whorls remaining. Suture thin, shallow. Teleoconch whorls convex, subsutural area slightly constricted. Axial ribs thin and sharp, widely spaced, numbering 16–17 on penultimate whorl, becoming reduced and almost absent on the ventral and dorsal sides of the last whorl. Spire whorls with two weak primary spiral cords, forming spiny nodules on the axial ribs. Secondary spiral cords numerous, densely spaced. Aperture large, ovate, inner surface whitish, outer lip sharped; columellar lip weakly callused, anterior part slightly curved. Siphonal canal relatively long, semitubular.

Radula (Figures 4C, D) rachiglossan, with a formula of 1 + 1+1, asymmetric. Rachidian teeth small, narrow, with an elongated base; distal end tricuspid. Right lateral teeth with seven major cusps along the posterior margin and a small knob at the inner end, left lateral teeth with six major cusps and a small knob.

Operculum (Figure 3K) semitransparent, light yellow, very thin, ovate, with terminal nucleus.

Type locality: Caroline seamounts, near the Mariana Trench, 1237 m deep, 10°05′N 140°10′E.

Etymology: The new species is named after the late professor Si Tchang (Xi Zhang) for his pioneering work on malacology in China.

Distribution and habitat: To date, this species is only known from the Caroline seamounts, where it lives on basalt rock at depths of 893–2291 m.

Remarks: In general, the shell shape of *Amiantofusus tchangsii* sp. nov. is similar to that of *Amiantofusus pacificus* Fraussen et al., 2007. The latter species has a remarkable degree of variability, and six forms were mentioned by Fraussen et al. (2007). Nonetheless, all the forms have strong axial ribs and spiral cords, which are clearly different from those of *Amiantofusus tchangsii* sp. nov. In addition, *Amiantofusus pacificus* differs from the new species in having less major cusps (four instead of six to seven) on the lateral teeth (see Couto and Simone, 2019). In addition, our phylogenetic tree shows that *Amiantofusus tchangsii* sp. nov. together with an unnamed species formed a sister group with *Amiantofusus pacificus* (see below). The COI pairwise distance between *Amiantofusus tchangsii* sp. nov. and *Amiantofusus pacificus* ranges from 3.6% to 4.1%, a divergence much higher than the known intraspecific variation of *Amiantofusus* spp. (0.2–1.0%).

Amiantofusus tchangsii sp. nov. has a similar appearance in sculpture to *Amiantofusus* species 2 Fraussen et al., 2007, which is known from a single shell from Vanuatu. That shell has three to four primary spiral cords along the spire whorls instead of two and has a slender shape.

Phylogenetic analysis and genetic distance

One and three partial sequences for the COI region were successfully amplified and sequenced from *Amiantofusus granulus* sp. nov. and *Amiantofusus tchangsii* sp. nov., respectively, and have been deposited in GenBank (accession numbers: OP114412–OP114415). The Bayesian phylogenetic tree (Figure 5) was reconstructed using available COI sequences from the present study and GenBank. In our phylogenetic analyses, none of the three currently recognized subfamilies (Fasciolariinae, Fusininae, and Peristerniinae) was recovered as monophyly. Fasciolariinae and Peristerniinae were clustered together: some species of Peristerniinae (e.g., *Hemipolygona armata*, *Nodolatirus nodatus*, and *Benimakia fastigium*) nested within Fasciolariinae, and Fusininae formed a paraphyletic clade. In the clade Fusininae, the two new species fell into the genus *Amiantofusus*, which forms a monophyletic sister group (PP = 1) with *Granulifusus* + *Pseudolatirus* + *Angulofusus*. This topology is consistent with the ML analysis of Couto et al. (2016) based on multiple genes. Within the genus, *Amiantofusus granulus* sp. nov. independently formed a sister group with all other congeners (PP = 0.99), while *Amiantofusus*

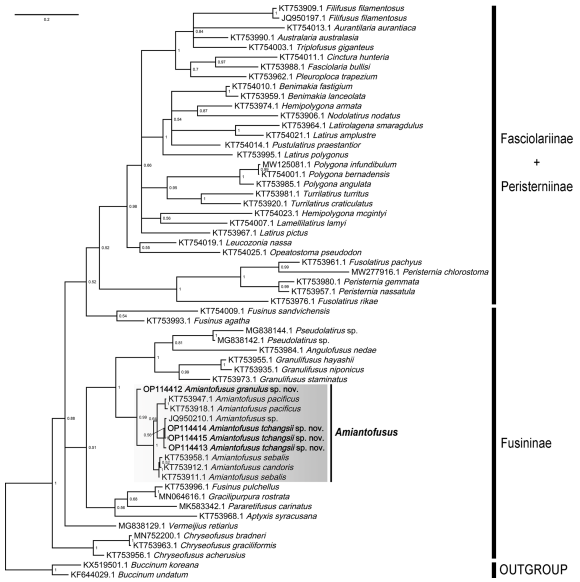

FIGURE 5
Phylogenetic tree inferred by Bayesian analysis (BI) showing the systematic position of *Amiantofusus granulus* sp. nov. and *Amiantofusus tchangsii* sp. nov. within the family Fasciolariidae. Numbers adjacent to nodes refer to BI posterior probability.

TABLE 2 Estimates of *p*-distances of the mitochondrial COI gene among *Amiantofusus* species and studied sequences.

	A. sebalis	*A. pacificus*	*A. candoris*	*A. tchangsii*	*A. granulus*
A. sebalis	**0.6%**				
A. pacificus	3.6–4.6%	**0.8%**			
A. candoris	0.5–0.8%	3.8–4.3%	–		
A. tchangsiii	3.1–4.3%	3.6–4.1%	3.2–3.8%	**0.2–1.0%**	
A. granulus	5.0–5.3%	5.3–5.5%	5.1%	5.5–5.8%	–

Intraspecific distances in bold. – means no data.

tchangsii sp. nov. together with an unnamed species, *Amiantofusus* sp. from the Philippines, formed a sister group with *Amiantofusus pacificus* (PP = 0.56).

The inter- and intraspecific genetic divergences of the COI were calculated to investigate the genetic distances in *Amiantofusus*. For the COI alignment, the interspecific distances range from 3.1% to 5.8%, and the intraspecific distances are in the range of 0.2–1% (Table 2).

Discussion

Generic assignment and species delineation

Both the morphology and molecular phylogenetic analyses support the assignment of the two new species to the genus *Amiantofusus* Fraussen et al., 2007. *Amiantofusus* species are conchologically quite similar to Buccinidae but have a fasciolariid radula (Fraussen et al., 2007; Couto and Simone, 2019). The radula has a small, narrow, tricuspid central tooth with an elongated base and broad, slightly curved lateral teeth with several (usually four to seven) major cusps accompanied by a small knob or cusp at both ends. The two new species described in the present study conform to these characteristics. In our molecular phylogenetic tree, the genus *Amiantofusus*, including the two new species, was recovered as a monophyletic group with full support (PP=1). This result provides additional support for the systematic placement of the new species in the genus *Amiantofusus*.

Amiantofusus granulus sp. nov. and *Amiantofusus tchangsii* sp. nov. can be clearly separated from other congeners by the shell shape, the sculpture, and the number of cusps on the lateral teeth. The separations were confirmed by the *p*-distance analyses, which showed that the uncorrected *p*-distance for the COI among *Amiantofusus granulus* sp. nov. and other congeners is 5.0–5.8%; among Amiantofusus tchangsii sp. nov. and other congeners it is 3.1-5.8%. These divergences are both much higher than the known intraspecific variation of *Amiantofusus* spp. (0.2–1%) (see Table 2) and thus warrant separations of *Amiantofusus granulus* sp. nov. and *Amiantofusus tchangsii* sp. nov. from other congeners.

Our phylogenetic tree showed that *Amiantofusus tchangsii* sp. nov. together with an unnamed species, *Amiantofusus* sp. from the Philippines, formed a fully supported branch (PP = 1). This unnamed species, deposited in the Muséum National d'Histoire Naturelle, Paris (voucher number: MNHN-IM-2007-34648), may be conspecific with *Amiantofusus tchangsii* sp. nov., as the COI *p*-distance between the two is 0.2–1%. The divergences fall within the range of intraspecific variation of the genus (0.2–1%; see Table 2).

Geographic distribution of *Amiantofusus* species

Among the 10 currently known species of *Amiantofusus*, *A. amiantus* (Dall, 1889), the type species of the genus, is the only species recorded from the Atlantic Ocean (Fraussen et al., 2007). All other species are known from the Indo-west Pacific region: *A. borbonicus* Fraussen et al., 2007 and *A. cartilago* Fraussen et al., 2007 from the western Indian Ocean and the other seven species including the present two new species from the Western Pacific (Figure 1). Such a wide and disjunct distribution indicates that there are likely many more species awaiting discovery. *Amiantofusus* species have a multispiral protoconch with a large diameter, indicating planktotrophic larval development (Gofas, 2000; Fraussen et al., 2007). Larvae with this developmental mode typically have a high dispersion potential and, consequently, broad geographic distribution (Bouchet and Warén, 1979; Lima and Lutz, 1990; Barroso et al., 2022). This is clearly reflected in several *Amiantofusus* species. The most evident case is *A. pacificus* Fraussen et al., 2007, which has a fairly wide distribution range from Taiwan, China *via* the North Fiji Basin to the northern and southern New Caledonia, the southern Coral Sea, Vanuatu, and Tonga (Fraussen et al., 2007). Another example is *A. amiantus* (Dall, 1889), which exhibits an amphi-Atlantic distribution. If the unnamed species *Amiantofusus* sp. from the Philippines, as mentioned above, is indeed conspecific with *Amiantofusus tchangsii* sp. nov., it would largely extend the distribution of *A. tchangsii* sp. nov. from the Caroline seamounts to the Philippines.

On a vertical scale, all species inhabit the water from relatively shallow depths (down to 300 m) to the upper

bathyal zone. *Amiantofusus tchangsii* sp. nov. represents the deepest record of the genus (down to 1816–2291 m depth), with *A. pacificus* Fraussen et al., 2007 being the shallowest (minimum depth of 364 m).

Synonym

During the genetic analyses, it came to light that *Amiantofusus sebalis* Fraussen et al., 2007 is genetically very close to *Amiantofusus candoris* Fraussen et al., 2007. The COI pairwise distance between the two is only 0.5–0.8%, which falls within the range of intraspecific variation of the genus (0.2–1.0%; see Table 2). This result indicates that the two species are likely conspecific. In the original description, Fraussen et al. (2007) compared the two species morphologically and concluded that *Amiantofusus sebalis* differs from *Amiantofusus candoris* in terms of the strength of the sculpture, the size of the protoconch, and the shell shape. Some of these differences, however, are also observed between different individuals of *Amiantofusus tchangsii* sp. nov., e.g., the shell shape varies from broad (Figures 3F–I) to slender (Figures 3J–K), and axial ribs being prominent on the penultimate and body whorl in some individuals (Figures 3F–I) but reduced (Figure 3J) or almost obsolete in others (Figure 3K). Thus, it is reasonable to conclude that the differences mentioned by Fraussen et al. (2007) are, in fact, intraspecific variations. We consider *Amiantofusus candoris* to be a morph of *Amiantofusus sebalis*, probably connected to shallower waters. As *Amiantofusus sebalis* was described based on many more specimens, while the few specimens of *Amiantofusus candoris* cover a limited range, we herein regard *A. candoris* Fraussen et al., 2007 as a junior synonym of *A. sebalis* Fraussen et al., 2007.

Conclusion

We describe two new species, *Amiantofusus granulus* sp. nov. and *Amiantofusus tchangsii* sp. nov., from the seamounts in the tropical western Pacific. Both their morphology and molecular phylogenetic analyses support the assignment of the two species to the genus *Amiantofusus*, and with separation from other congeners. Based on the very close COI *p*-distance between *Amiantofusus sebalis* and *A. candoris*, the two species are suggested to be synonymized. *Amiantofusus* has a wide but sparse distribution: one species from Atlantic, two from the western Indian Ocean, and the other seven species including the present two new species from the western Pacific. Such a broad and disjunct distribution indicates that there may well be many more species awaiting discovery. More explorations are needed to evaluate the species diversity and the geographic distribution of these deep-sea gastropods.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article.

Author contributions

SQZ conceived of and designed the study. SQZ and KF analyzed the morphological and molecular data and drafted the original manuscript, which was revised and improved by SPZ. All authors gave final approval for submission and publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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