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Monograph

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The Indo-Pacific *Amalda* (Neogastropoda, Olivoidea, Ancillariidae) revisited with molecular data, with special emphasis on New Caledonia

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³[urn:lsid:zoobank.org:author:40BCE11C-D138-4525-A7BB-97F594041BCE](https://zoobank.org/author:40BCE11C-D138-4525-A7BB-97F594041BCE)

⁴[urn:lsid:zoobank.org:author:FC9098A4-8374-4A9A-AD34-475E3AAF963A](https://zoobank.org/author:FC9098A4-8374-4A9A-AD34-475E3AAF963A)

Abstract. In the ancillariid genus *Amalda*, the shell is character rich and 96 described species are currently treated as valid. Based on shell morphology, several subspecies have been recognized within *Amalda hilgendorfi*, with a combined range extending at depths of 150–750 m from Japan to the South-West Pacific. A molecular analysis of 78 specimens from throughout this range shows both a weak geographical structuring and evidence of gene flow at the regional scale. We conclude that recognition of subspecies (*richeri* Kilburn & Bouchet, 1988, *herlaari* van Pel, 1989, and *vezzaroi* Cossignani, 2015) within *A. hilgendorfi* is not justified. By contrast, *hilgendorfi*-like specimens from the Mozambique Channel and New Caledonia are molecularly segregated, and so are here described as new, as *Amalda miriky* sp. nov. and *A. cacao* sp. nov., respectively. The New Caledonia *Amalda montrouzieri* complex is shown to include at least three molecularly separable species, including *A. allaryi* and *A. alabaster* sp. nov. Molecular data also confirm the validity of the New Caledonia endemics *Amalda aureomarginata*, *A. fuscilingua*, *A. bellonarum*, and *A. coriolis*. The existence of narrow range endemics suggests that the species limits of *Amalda* with broad distributions, extending, e.g., from Japan to Taiwan (*A. hinomotoensis*) or even Indonesia, the Strait of Malacca, Vietnam and the China Sea (*A. mamillata*) should be taken with caution.

Keywords. *Amalda hilgendorfi* species complex, deep-water *Amalda*, *Cox1*, integrative taxonomy.

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Introduction

The genus *Amalda* H. Adams & A. Adams, 1853 is broadly distributed in the tropical waters of the World Ocean from the intertidal to several hundred meters. Presently, the genus includes 96 Recent species, classified in seven nominal subgenera (Kantor *et al.* 2017), some of them at times treated as full genera. The genus has been reviewed on conchological grounds in a series of papers by Gratecap (2012, 2014, 2016a, 2016b). The type species *Amalda tankervillei* (Swainson, 1825) inhabits the tropical western Atlantic and two more species occur in the tropical and subtropical Atlantic (Rosenberg 2009); the remaining ones are Indo-Pacific, with a particularly rich fauna in Australia (32 species: Gratecap 2016a) and the Indo-West Pacific (19 species: Gratecap 2016b). However, until the recent paper by Gemmel *et al.* (2020), *Amalda* has remained practically overlooked from the molecular point of view, with sequences of only 5 species deposited in GenBank, essentially originating from the molecular phylogeny of the superfamily Olivoidea by Kantor *et al.* (2017). Gemmel *et al.* (2020) presented a molecular phylogeny based on the entire mitogenome and long nuclear rRNA gene cassette data, targeting primarily New Zealand species of *Amalda*. These included species attributed to the subgenera *Baryspira* P. Fischer, 1883 (including the type species *A. australis* (G.B. Sowerby I, 1830) and *Gracilispira* Olsson, 1956 (including the type species *A. novaezelandiae* (G.B. Sowerby II, 1859); as well as six Indo-Pacific species, mostly based on the MNHN collections that also form the basis of the present paper.

The New Caledonian *Amalda* were treated by Kilburn & Bouchet (1988) who described four new species and one new subspecies in addition to the previously known *Amalda montrouzieri* (Souverbie, 1860); three additional species were described by Bozzetti (2007) and Cossignani (2013). With the exception of *A. montrouzieri* and *A. hilgendorfi*, all are endemic to New Caledonia. Since the paper by Kilburn & Bouchet, a considerable amount of material has been collected by the expeditions organized by MNHN with IRD and other partners in different parts of the tropical Indo-Pacific, including New Caledonia. The major goal of the present work is to revise the New Caledonian fauna of *Amalda* based on molecular data. For comparative purposes, material from other regions of Indo-Pacific was also sequenced.

Material and methods

Material

Specimens, including material suitable for sequencing was collected during the Indo-West Pacific *Tropical Dee-Sea Benthos* expeditions: MIRIKY, INHACA 2011 in Madagascar and Mozambique; TERRASSES, EXBODI, NORFOLK 2, KANACONO (<https://doi.org/10.17600/16003900>), EBISCO, KANADEEP 1 (<https://doi.org/10.17600/17003800>), and CONCALIS in New Caledonia; NanHai 2014 and ZhongSha 2015 in the South China Sea; PANGLAO 2005 in the Philippines; SALOMON 2 (<https://doi.org/10.17600/4100090>), SALOMONBOA 3 (<https://doi.org/10.17600/7100070>) in the Solomon Islands; BIOPAPUA, PAPUA NIUGINI, MADEEP, KAVIENG in Papua New Guinea. For comparative purposes, material represented by empty shells and specimens not suitable for sequencing was also examined. The list of this material is provided in the ‘Material Examined’ section of each species. Additional material from other sources, mostly collected by fishermen or divers, including WESTERN AUSTRALIA 2011 was also examined and, where possible, sequenced.

Until 2012, live specimens for molecular analysis were anaesthetized with an isotonic solution of MgCl₂ and fixed in 96% ethanol. Specimens collected during later expeditions were processed with a microwave oven (Galindo *et al.* 2014): the living molluscs in small volumes of sea water were exposed to microwaves for 10–60 s, depending on specimen size. Bodies were immediately removed from shells and dropped in 96% ethanol. Specimens are registered in the MNHN collection and sequences are deposited in BOLD (Barcode of Life Datasystem) and GenBank (Table 1).

The sequences of *Cox1* fragments of five species of New Zealand *Amalda* representing the subgenera *Baryspira* and *Gracilispira* were kindly made available to us by M. Gemmel (Massey University, Palmerston North, New Zealand) and are included in our analysis for comparative purposes.

Table 1 (continued on next six pages). List of sequenced specimens analyzed, including voucher registration and GenBank accession numbers. Original sequences highlighted in **bold** typeface. The BOLD ID refers to the The Barcode of Life Data System.

MNHN registration	Genus	Species	Cruise	Station	Country	Coordinates	Depth	BOLD ID	GenBank accession	Source
IM-2007-43583	<i>Amalda</i>	<i>alabaster</i> sp. nov.	TERRASSES	DW3078	S New Caledonia	22°29' S, 167°30' E	180–210 m	NEOGA955-10	MT556153	This study
IM-2007-43621	<i>Amalda</i>	<i>alabaster</i> sp. nov.	TERRASSES	DW3093	S New Caledonia	22°06' S, 167°03' E	190–200 m	NEOGA961-10	MT556102	This study
IM-2007-43622	<i>Amalda</i>	<i>alabaster</i> sp. nov.	TERRASSES	DW3093	S New Caledonia	22°06' S, 167°03' E	190–200 m	NEOGA962-10	MT556133	This study
IM-2007-43624	<i>Amalda</i>	<i>alabaster</i> sp. nov.	TERRASSES	DW3093	S New Caledonia	22°06' S, 167°03' E	190–200 m	NEOGA964-10	MT556056	This study
IM-2007-43627	<i>Amalda</i>	<i>alabaster</i> sp. nov.	TERRASSES	DW3093	S New Caledonia	22°06' S, 167°03' E	190–200 m	NEOGA966-10	MT556086	This study
IM-2007-43636	<i>Amalda</i>	<i>alabaster</i> sp. nov.	TERRASSES	DW3093	S New Caledonia	22°06' S, 167°03' E	190–200 m	NEOGA970-10	MT556107	This study
IM-2007-43639	<i>Amalda</i>	<i>alabaster</i> sp. nov.	TERRASSES	DW3093	S New Caledonia	22°06' S, 167°03' E	190–200 m	NEOGA972-10	MT556121	This study
IM-2007-43642	<i>Amalda</i>	<i>alabaster</i> sp. nov.	TERRASSES	DW3093	S New Caledonia	22°06' S, 167°03' E	190–200 m	NEOGA974-10	MT556073	This study
IM-2013-63897	<i>Amalda</i>	<i>cf. alabaster</i>	EXBODY	CP3813	E New Caledonia	21°46' S, 166°38' E	251–281 m	NEOGA1484-20	MT556059	This study
IM-2007-43628	<i>Amalda</i>	<i>allaryi</i>	TERRASSES	DW3128	S New Caledonia	22°43' S, 167°17' E	90–100 m	NEOGA1429-20	MT556047	This study
IM-2007-43630	<i>Amalda</i>	<i>allaryi</i>	TERRASSES	DW3128	S New Caledonia	22°43' S, 167°17' E	90–100 m	NEOGA1406-20	MT556035	This study
IM-2007-43640	<i>Amalda</i>	<i>allaryi</i>	TERRASSES	DW3128	S New Caledonia	22°43' S, 167°17' E	90–100 m	NEOGA973-10	MT556039	This study
IM-2007-43551	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3125	S New Caledonia	22°55' S, 167°17' E	480–500 m	NEOGA950-10	MT556045	This study
IM-2007-43576	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	CP3117	S New Caledonia	22°51' S, 167°16' E	500 m	NEOGA954-10	MT556157	This study
IM-2007-43606	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3125	S New Caledonia	22°55' S, 167°17' E	480–500 m	NEOGA959-10	MT556155	This study
IM-2007-43611	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3127	S New Caledonia	23°00' S, 167°16' E	400–420 m	NEOGA1428-20	MT556067	This study
IM-2007-43612	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3127	S New Caledonia	23°00' S, 167°16' E	400–420 m	NEOGA960-10	MT556074	This study
IM-2007-43623	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	CP3116	S New Caledonia	22°50' S, 167°15' E	460–490 m	NEOGA963-10	MT556115	This study
IM-2007-43637	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3127	S New Caledonia	23°00' S, 167°16' E	400–420 m	NEOGA971-10	MT556096	This study
IM-2007-43644	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3122	S New Caledonia	22°47' S, 167°12' E	390–410 m	NEOGA1407-20	MT556066	This study
IM-2007-43645	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3122	S New Caledonia	22°47' S, 167°12' E	390–410 m	NEOGA975-10	MT556091	This study
IM-2007-43646	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3122	S New Caledonia	22°47' S, 167°12' E	390–410 m	NEOGA976-10	MT556128	This study
IM-2007-43647	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3122	S New Caledonia	22°47' S, 167°12' E	390–410 m	NEOGA977-10	MT556075	This study
IM-2007-43648	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3122	S New Caledonia	22°47' S, 167°12' E	390–410 m	NEOGA978-10	MT556160	This study
IM-2007-43651	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3123	S New Caledonia	22°53' S, 167°13' E	420–450 m	NEOGA980-10	MT556123	This study
IM-2007-43652	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3123	S New Caledonia	22°53' S, 167°13' E	420–450 m	NEOGA981-10	MT556098	This study
IM-2007-43653	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3123	S New Caledonia	22°53' S, 167°13' E	420–450 m	NEOGA982-10	MT556119	This study

Table 1 (continued).

MNHN registration	Genus	Species	Cruise	Station	Country	Coordinates	Depth	BOLD ID	GenBank accession	Source
IM-2007-43654	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3123	S New Caledonia	22°53' S, 167°13' E	420–450 m	NEOGA983-10	MT556037	This study
IM-2007-43655	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3123	S New Caledonia	22°53' S, 167°13' E	420–450 m	NEOGA984-10	KX233276	This study
IM-2007-43656	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3123	S New Caledonia	22°53' S, 167°13' E	420–450 m	NEOGA985-10	MT556097	This study
IM-2007-43659	<i>Amalda</i>	<i>aureomarginata</i>	TERRASSES	DW3123	S New Caledonia	22°53' S, 167°13' E	420–450 m	NEOGA987-10	MT556076	This study
IM-2009-11962	<i>Amalda</i>	<i>aureomarginata</i>	NORFOLK 2	DW2147	S New Caledonia	22°50' S, 167°16' E	496 m	NEOGA1441-20	MT556171	This study
IM-2007-33273	<i>Amalda</i>	<i>bellonarum</i>	EBISCO	DW2572	Coral Sea	20°23' S, 158°45' E	324–330 m	NEOGA672-10	MT571641	This study
IM-2007-33287	<i>Amalda</i>	<i>cacao</i> sp. nov.	EBISCO	DW2533	Coral Sea	22°17' S, 159°27' E	360–370 m	NEOGA678-10	MT556108	This study
IM-2009-22262	<i>Amalda</i>	<i>contusa</i>	INHACA 2011	MR27	Mozambique	26°06'18" S, 32°58' 00" E	17 m	NEOGA1459-20	MT556166	This study
IM-2009-22263	<i>Amalda</i>	<i>contusa</i>	INHACA 2011	MR4	Mozambique	26°06'18" S, 32°58' 00" E	17–19 m	MITR1063-15	KR087230	Fedosov <i>et al.</i> 2015
IM-2009-22264	<i>Amalda</i>	<i>contusa</i>	INHACA 2011	MR4	Mozambique	26°06'18" S, 32°58'00" E	17–19 m	NEOGA1460-20	MT556038	This study
IM-2007-33298	<i>Amalda</i>	<i>coriolis</i>	EBISCO	CP2492	Coral Sea	24°44' S, 159°39' E	285 m	NEOGA1416-20	MT556082	This study
IM-2013-63899	<i>Amalda</i>	<i>coriolis</i>	KANADEEP	DW4938	Coral Sea	25°28' S, 159°50' E	300–400 m	NEOGA1477-20	MT556141	This study
IM-2007-43584	<i>Amalda</i>	<i>fuscilingua</i>	TERRASSES	DW3114	S New Caledonia	22°44' S, 167°14' E	350–380 m	NEOGA956-10	MT556027	This study
IM-2007-43603	<i>Amalda</i>	<i>fuscilingua</i>	TERRASSES	DW3121	S New Caledonia	22°45' S, 167°13' E	380–400 m	NEOGA958-10	MT556054	This study
IM-2007-43634	<i>Amalda</i>	<i>fuscilingua</i>	TERRASSES	DW3121	S New Caledonia	22°45' S, 167°13' E	380–400 m	NEOGA968-10	MT556156	This study
IM-2007-43635	<i>Amalda</i>	<i>fuscilingua</i>	TERRASSES	DW3114	S New Caledonia	22°44' S, 167°14' E	350–380 m	NEOGA969-10	MT556114	This study
IM-2007-43643	<i>Amalda</i>	<i>fuscilingua</i>	TERRASSES	DW3122	S New Caledonia	22°47' S, 167°12' E	390–410 m	NEOGA1430-20	MT556151	This study
IM-2007-43649	<i>Amalda</i>	<i>fuscilingua</i>	TERRASSES	DW3122	S New Caledonia	22°47' S, 167°12' E	390–410 m	NEOGA979-10	KX233275	Kantor <i>et al.</i> 2016
IM-2007-43650	<i>Amalda</i>	<i>fuscilingua</i>	TERRASSES	DW3122	S New Caledonia	22°47' S, 167°12' E	390–410 m	NEOGA1414-20	MT556116	This study
IM-2007-43657	<i>Amalda</i>	<i>fuscilingua</i>	TERRASSES	DW3123	S New Caledonia	22°53' S, 167°13' E	420–450 m	NEOGA986-10	MT556104	This study
IM-2013-44009	<i>Amalda</i>	<i>hayashii</i>	NanHai 2014	CP4099	Taiwan	22°13' N, 120°24' E	310–346 m	NEOGA1469-20	MT556164	This study
IM-2013-44413	<i>Amalda</i>	<i>hayashii</i>	NanHai 2014	CP4115	South China Sea	20°03' N, 120°24' E	265–300 m	NEOGA1466-20	MT556094	This study
IM-2013-44415	<i>Amalda</i>	<i>hayashii</i>	NanHai 2014	CP4115	South China Sea	20°03' N, 120°24' E	265–300 m	NEOGA1468-20	MT556149	This study
IM-2013-44432	<i>Amalda</i>	<i>hayashii</i>	NanHai 2014	CP4115	South China Sea	20°03' N, 120°24' E	265–300 m	NEOGA1462-20	MT556112	This study
IM-2013-44444	<i>Amalda</i>	<i>hayashii</i>	NanHai 2014	CP4116	South China Sea	20°03' N, 114°11' E	262–298 m	NEOGA1463-20	MT556081	This study

Table 1 (continued).

MNHN registration	Genus	Species	Cruise	Station	Country	Coordinates	Depth	BOLD ID	GenBank accession	Source
IM-2013-44451	<i>Amalda</i>	<i>hayashii</i>	NanHai 2014	CP4116	South China Sea	20°03' N, 114°11' E	262–298 m	NEOGA1464-20	MT556146	This study
IM-2013-44454	<i>Amalda</i>	<i>hayashii</i>	NanHai 2014	CP4116	South China Sea	20°03' N, 114°11' E	262–298 m	NEOGA1467-20	MT556106	This study
IM-2013-44457	<i>Amalda</i>	<i>hayashii</i>	NanHai 2014	CP4116	South China Sea	20°03' N, 114°11' E	262–298 m	NEOGA1465-20	MT556060	This study
IM-2013-61748	<i>Amalda</i>	<i>hayashii</i>	ZhongSha 2015	CP4136	South China Sea	20°03' N, 114°33' E	249–250 m	NEOGA1470-20	MT556058	This study
IM-2007-31950	<i>Amalda</i>	<i>hilgendorfi</i>	PANGLAO 2005	CP2362	Philippines	8°57' N, 123°33' E	679–740 m	NEOGA460-10	MT556165	This study
IM-2007-33272	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	DW2607	Coral Sea	19°33' S, 158°40' E	400–413 m	NEOGA671-10	MT556129	This study
IM-2007-33286	<i>Amalda</i>	<i>hilgendorfi</i>	SALOMON 2	CP2260	Solomon Islands	8°04' S, 156°55' E	399–427 m	NEOGA1424-20	MT556100	This study
IM-2007-33288	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	CP2643	Coral Sea	20°51' S, 160°59' E	557–565 m	NEOGA679-10	MT556148	This study
IM-2007-33289	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	DW2484	Coral Sea	23°51' S, 161°43' E	400–616 m	NEOGA680-10	MT556152	This study
IM-2007-33290	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	CP2621	Coral Sea	20°06' S, 160°21' E	691–750 m	NEOGA1415-20	MT556170	This study
IM-2007-33293	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	DW2485	Coral Sea	23°52' S, 161°42' E	525–550 m	NEOGA681-10	MT556036	This study
IM-2007-33294	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	DW2485	Coral Sea	23°52' S, 161°42' E	525–550 m	NEOGA682-10	MT556105	This study
IM-2007-33303	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	DW2625	Coral Sea	20°05' S, 160°20' E	627–741 m	NEOGA685-10	MT556042	This study
IM-2007-33312	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	DW2609	Coral Sea	19°33' S, 158°40' E	436–431 m	NEOGA1425-20	MT556072	This study
IM-2007-33313	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	CP2621	Coral Sea	20°06' S, 160°21' E	691–750 m	NEOGA690-10	MT556033	This study
IM-2007-33321	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	DW2612	Coral Sea	19°33' S, 158°41' E	392 m	NEOGA694-10	MT556068	This study
IM-2007-33322	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	CP2643	Coral Sea	20°51' S, 160°59' E	557–565 m	NEOGA1436-20	MT556168	This study
IM-2007-33329	<i>Amalda</i>	<i>hilgendorfi</i>	EBISCO	DW2612	Coral Sea	19°33' S, 158°41' E	392 m	NEOGA1426-20	MT556077	This study
IM-2007-33427	<i>Amalda</i>	<i>hilgendorfi</i>	PANGLAO 2005	CP2363	Philippines	8°06' N, 123°25' E	437–439 m	NEOGA1427-20	MT556088	This study
IM-2007-34785	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2956	N New Caledonia	18°58' S, 163°19' E	400–415 m	NEOGA805-10	MT556169	This study
IM-2007-42673	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2996	N New Caledonia	18°01' S, 163°01' E	487–500 m	NEOGA900-10	MT556061	This study
IM-2007-42674	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2996	N New Caledonia	18°01' S, 163°01' E	487–500 m	NEOGA901-10	MT556134	This study
IM-2007-42675	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2996	N New Caledonia	18°01' S, 163°01' E	487–500 m	NEOGA902-10	MT556145	This study
IM-2007-43661	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGA989-10	MT556147	This study
IM-2007-43662	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGA990-10	MT556026	This study
IM-2007-43663	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGA991-10	MT556167	This study
IM-2007-43664	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGA1408-20	MT556064	This study

Table 1 (continued).

MNHN registration	Genus	Species	Cruise	Station	Country	Coordinates	Depth	BOLD ID	GenBank accession	Source
IM-2007-43665	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGAI1409-20	MT556144	This study
IM-2007-43666	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGA992-10	MT556046	This study
IM-2007-43667	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGAI1410-20	MT556092	This study
IM-2007-43668	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGAI1411-20	MT556095	This study
IM-2007-43669	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGA993-10	MT556025	This study
IM-2007-43670	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGA994-10	MT556080	This study
IM-2007-43671	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGA995-10	MT556131	This study
IM-2007-43673	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGAI1412-20	MT556127	This study
IM-2007-43674	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGA997-10	MT556062	This study
IM-2007-43676	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGAI1413-20	MT556163	This study
IM-2007-43677	<i>Amalda</i>	<i>hilgendorfi</i>	TERRASSES	DW3118	S New Caledonia	22°51' S, 167°15' E	350–380 m	NEOGA999-10	MT556093	This study
IM-2009-5572	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2997	N New Caledonia	18°02' S, 163°02' E	430–438 m	NEOGAI1417-20	MT556132	This study
IM-2009-11915	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2997	N New Caledonia	18°02' S, 163°02' E	430–438 m	NEOGAI1446-20	MT556044	This study
IM-2009-11916	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	CP2958	N New Caledonia	18°58' S, 163°15' E	432–448 m	NEOGAI1447-20	MT556083	This study
IM-2009-11917	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2997	N New Caledonia	18°02' S, 163°02' E	430–438 m	NEOGAI1445-20	MT556125	This study
IM-2009-11918	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2997	N New Caledonia	18°02' S, 163°02' E	430–438 m	NEOGAI1456-20	MT556030	This study
IM-2009-11920	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2995	N New Caledonia	18°00' S, 163°03' E	450–495 m	NEOGAI1448-20	MT556135	This study
IM-2009-11937	<i>Amalda</i>	<i>hilgendorfi</i>	NORFOLK 2	DW2147	S New Caledonia	22°50' S, 167°16' E	496 m	NEOGAI1449-20	MT556078	This study
IM-2009-11938	<i>Amalda</i>	<i>hilgendorfi</i>	NORFOLK 2	DW2147	S New Caledonia	22°50' S, 167°16' E	496 m	NEOGAI1450-20	MT556024	This study
IM-2009-11945	<i>Amalda</i>	<i>hilgendorfi</i>	NORFOLK 2	DW2147	S New Caledonia	22°50' S, 167°16' E	496 m	NEOGAI1451-20	MT556049	This study
IM-2009-11949	<i>Amalda</i>	<i>hilgendorfi</i>	NORFOLK 2	DW2147	S New Caledonia	22°50' S, 167°16' E	496 m	NEOGAI1452-20	MT556063	This study
IM-2009-11950	<i>Amalda</i>	<i>hilgendorfi</i>	NORFOLK 2	DW2147	S New Caledonia	22°50' S, 167°16' E	496 m	NEOGAI1453-20	MT556101	This study
IM-2009-11961	<i>Amalda</i>	<i>hilgendorfi</i>	SALOMONBOA 3	CP2799	Solomon Islands	8°41' S, 161°02' E	430–635 m	NEOGAI1440-20	MT556113	This study
IM-2009-11963	<i>Amalda</i>	<i>hilgendorfi</i>	NORFOLK 2	DW2147	S New Caledonia	22°50' S, 167°16' E	496 m	OLIV009-16	KX233274	Kantor <i>et al.</i> 2016
IM-2009-11964	<i>Amalda</i>	<i>hilgendorfi</i>	NORFOLK 2	DW2147	S New Caledonia	22°50' S, 167°16' E	496 m	NEOGAI1442-20	MT556120	This study
IM-2009-11965	<i>Amalda</i>	<i>hilgendorfi</i>	NORFOLK 2	DW2147	S New Caledonia	22°50' S, 167°16' E	496 m	NEOGAI1443-20	MT556161	This study
IM-2009-11966	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2997	N New Caledonia	18°02' S, 163°02' E	430–438 m	NEOGAI1454-20	MT556137	This study
IM-2009-11968	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2979	N New Caledonia	18°16' S, 162°54' E	350 m	OLIV010-16	KX233273	Kantor <i>et al.</i> 2016

Table 1 (continued).

MNHN registration	Genus	Species	Cruise	Station	Country	Coordinates	Depth	BOLD ID	GenBank accession	Source
IM-2009-22139	<i>Amalda</i>	<i>hilgendorfi</i>	SALOMONBOA 3	CP2799	Solomon Islands	8°41' S, 161°02' E	430–635 m	NEOGAI1444-20	MT556130	This study
IM-2009-22244	<i>Amalda</i>	<i>hilgendorfi</i>	BIOPAPUA	CP3669	Papua New Guinea	04°08' S, 151°56' E	382–389 m	NEOGAI1458-20	MT556051	This study
IM-2009-23330	<i>Amalda</i>	<i>hilgendorfi</i>	BIOPAPUA	CP3669	Papua New Guinea	04°08' S, 151°56' E	382–389 m	NEOGAI1461-20	MT556028	This study
IM-2009-33734	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2979	N New Caledonia	18°16' S, 162°54' E	350 m	NEOGAI1457-20	MT556111	This study
IM-2009-33764	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2995	N New Caledonia	18°00' S, 163°03' E	450–495 m	NEOGAI1455-20	MT556122	This study
IM-2013-19909	<i>Amalda</i>	<i>hilgendorfi</i>	Papua Niugini	CP4006	Papua New Guinea	6°03' S, 148°08' E	440–475 m	NEOGAI1489-20	MT556154	This study
IM-2013-44995	<i>Amalda</i>	<i>hilgendorfi</i>	MADEEP	CP4255	Papua New Guinea	2°28' S, 150°44' E	333–420 m	NEOGAI1478-20	MT556050	This study
IM-2013-44996	<i>Amalda</i>	<i>hilgendorfi</i>	MADEEP	CP4255	Papua New Guinea	2°28' S, 150°44' E	333–420 m	NEOGAI1475-20	MT556031	This study
IM-2013-48047	<i>Amalda</i>	<i>hilgendorfi</i>	KANADEEP	DW4975	Coral Sea	19°45' S, 158°35' E	386–428 m	NEOGAI1474-20	MT556057	This study
IM-2013-58045	<i>Amalda</i>	<i>hilgendorfi</i>	KAVIENG 2014	DW4418	Papua New Guinea	2°27' S, 150°40' E	335–340 m	NEOGAI1479-20	MT556085	This study
IM-2013-58068	<i>Amalda</i>	<i>hilgendorfi</i>	KAVIENG 2014	CP4420	Papua New Guinea	2°24' S, 150°36' E	335–340 m	NEOGAI1480-20	MT556034	This study
IM-2013-58069	<i>Amalda</i>	<i>hilgendorfi</i>	KAVIENG 2014	CP4420	Papua New Guinea	2°24' S, 150°36' E	335–340 m	NEOGAI1481-20	MT556124	This study
IM-2013-58070	<i>Amalda</i>	<i>hilgendorfi</i>	KAVIENG 2014	CP4420	Papua New Guinea	2°24' S, 150°36' E	335–340 m	NEOGAI1488-20	MT556138	This study
IM-2013-58290	<i>Amalda</i>	<i>hilgendorfi</i>	KAVIENG 2014	CP4437	Papua New Guinea	2°23' S, 150°37' E	416–535 m	NEOGAI1491-20	MT556109	This study
IM-2013-58291	<i>Amalda</i>	<i>hilgendorfi</i>	KAVIENG 2014	CP4437	Papua New Guinea	2°23' S, 150°37' E	416–535 m	NEOGAI1482-20	MT556162	This study
IM-2013-58292	<i>Amalda</i>	<i>hilgendorfi</i>	KAVIENG 2014	CP4437	Papua New Guinea	2°23' S, 150°37' E	416–535 m	NEOGAI1490-20	MT556069	This study
IM-2013-58293	<i>Amalda</i>	<i>hilgendorfi</i>	KAVIENG 2014	CP4437	Papua New Guinea	2°23' S, 150°37' E	416–535 m	NEOGAI1483-20	MT556142	This study
IM-2013-63430	<i>Amalda</i>	<i>hilgendorfi</i>	KANACONO	DW6746	S New Caledonia	22°59' S, 167°43' E	494–508 m	NEOGAI1471-20	MT556090	This study
IM-2013-63900	<i>Amalda</i>	<i>hilgendorfi</i>	KANADEEP	DW4975	Coral Sea	19°45' S, 158°35' E	386–428 m	NEOGAI1485-20	MT556089	This study
IM-2013-63901	<i>Amalda</i>	<i>hilgendorfi</i>	KANADEEP	DW4976	Coral Sea	19°44' S, 158°32' E	360–380 m	NEOGAI1486-20	MT556029	This study
IM-2013-69557	<i>Amalda</i>	<i>hilgendorfi</i>	KANACONO	DW4722	S New Caledonia	22°54' S, 167°17' E	496–505 m	NEOGAI1472-20	MT556055	This study
IM-2013-69558	<i>Amalda</i>	<i>hilgendorfi</i>	KANACONO	DW4722	S New Caledonia	22°54' S, 167°17' E	496–505 m	NEOGAI1473-20	MT556079	This study
IM-2013-86077	<i>Amalda</i>	<i>hilgendorfi</i>	CONCALLIS	DW2995	N New Caledonia	18°00' S, 163°03' E	450–495 m	NEOGAI1499-20	MT556158	This study
IM-2019-616	<i>Amalda</i>	<i>hilgendorfi</i>	from fishermen		Japan, Amamiyoshima	appr. 28°15' N, 129°49' E	220–280 m	NEOGAI1493-20	MT556118	This study
IM-2019-617	<i>Amalda</i>	<i>hilgendorfi</i>	from fishermen		Japan, Amamiyoshima	appr. 28°15' N, 129°49' E	220–280 m	NEOGAI1494-20	MT556139	This study
IM-2019-621	<i>Amalda</i>	<i>hilgendorfi</i>	from fishermen		Japan, Amamiyoshima	appr. 28°15' N, 129°49' E	220–280 m	NEOGAI1498-20	MT556084	This study

Table 1 (continued).

MNHN registration	Genus	Species	Cruise	Station	Country	Coordinates	Depth	BOLD ID	GenBank accession	Source
IM-2019-618	<i>Amalda</i>	<i>hinomotoensis</i>	from fishermen		Japan, S Honshu	appr. 34°30' N, 138°00' E	70–100 m	NEOGA1495-20	MT556071	This study
IM-2019-619	<i>Amalda</i>	<i>hinomotoensis</i>	from fishermen		Japan, S Honshu	appr. 34°30' N, 138°00' E	70–100 m	NEOGA1496-20	MT556043	This study
IM-2007-36842	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	CP3183	Madagascar	12°37' S, 48°14' E	420–436 m	NEOGA1437-20	MT556150	This study
IM-2007-36866	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	CP3183	Madagascar	12°37' S, 48°14' E	420–436 m	NEOGA1418-20	MT556065	This study
IM-2007-36868	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	CP3183	Madagascar	12°37' S, 48°14' E	420–436 m	NEOGA1419-20	MT556052	This study
IM-2007-36934	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	CP3188	Madagascar	12°31' S, 48°22' E	298–301 m	NEOGA1432-20	MT556053	This study
IM-2007-36956	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	CP3183	Madagascar	12°37' S, 48°14' E	420–436 m	NEOGA1420-20	MT556126	This study
IM-2007-36970	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	CP3188	Madagascar	12°31' S, 48°22' E	298–301 m	NEOGA1421-20	MT556140	This study
IM-2007-36973	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	DW3212	Madagascar	12°34' S, 47°54' E	367–369 m	NEOGA1439-20	MT556103	This study
IM-2007-38032	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	CP3188	Madagascar	12°31' S, 48°22' E	298–301 m	NEOGA1438-20	MT556099	This study
IM-2007-38039	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	CP3188	Madagascar	12°31' S, 48°22' E	298–301 m	NEOGA1433-20	MT556041	This study
IM-2007-38064	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	DW3216	Madagascar	12°34' S, 47°52' E	296–350 m	NEOGA1434-20	MT556143	This study
IM-2007-38071	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	DW3216	Madagascar	12°34' S, 47°52' E	296–350 m	NEOGA1435-20	MT556087	This study
IM-2007-38073	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	DW3216	Madagascar	12°34' S, 47°52' E	296–350 m	NEOGA1422-20	MT556048	This study
IM-2007-38074	<i>Amalda</i>	<i>miriky</i> sp. nov.	MIRIKY	DW3216	Madagascar	12°34' S, 47°52' E	296–350 m	NEOGA1423-20	MT556040	This study
IM-2013-63898	<i>Amalda</i>	<i>monilifera</i>	WESTERN AUSTRALIA 2011	WB28	Western Australia	33°40'12" S, 114°56'36" E	0–15 m	NEOGA1476-20	MT556110	This study
IM-2013-80199	<i>Amalda</i>	<i>montrouzieri</i>	Nouméa		New Caledonia, Prory Bay		12–15 m	NEOGA1492-20	MT556159	This study
IM-2007-38287	<i>Amalda</i>	<i>optima</i>	MAINBAZA	CP3130	Mozambique Channel	25°53' S, 33°07' E	112–127 m	NEOGA1431-20	MT556070	This study
IM-2013-63891	<i>Amalda</i>	sp.	BIOPAPUA	DW3694	Papua New Guinea	02°10' S, 147°16' E	200–219 m	NEOGA1487-20	MT556032	This study
Outgroups										
IM-2007-34786	<i>Belloliva</i>	<i>exquisita</i> (Angas, 1871)	CONCALLIS	DW2973	N New Caledonia	18°14' S, 163°06' E	275–288 m	OLIV004-16	KX233314	Kantor <i>et al.</i> 2017
IM-2013-47678	<i>Belloliva</i>	<i>amoni</i> (Sterba & Lorenz, 2005)	KAVIENG 2014	KS11	Papua-New Guinea	02°33.02' S, 150°48.02' E	7 m	OLIV070-16	KX233351	Kantor <i>et al.</i> 2017
IM-2007-39045	<i>Ancilla</i>	<i>aureocallosa</i> (Kilburn & Jenner, 1977)	MAINBAZA	CP3143	Mozambique Channel	23°32' S, 35°46' E	264–277 m	OLIV007-16	KX233284	Kantor <i>et al.</i> 2017

Table 1 (continued).

MNHN registration	Genus	Species	Cruise	Station	Country	Coordinates	Depth	BOLD ID	GenBank accession	Source
IM-2009-15460	<i>Ancilla</i>	<i>thomassini</i> Zilburn, 1981	ATIMO VATAE	TB13	South Madagascar	25°01.05' S, 47°00.00' E	2–4 m	OLIV011-16	KX233307	Kantor <i>et al.</i> , 2017
IM-2007-31958	<i>Ancillina</i>	cf. <i>sumatrana</i> (Thiele, 1925)	PANGLAO 2005	CP2358	Philippines, Bohol Sea	8°52' N, 123°37' E	569–583 m	NEOGA465-10	MT556117	This study
IM-2009-25009	<i>Entomoliva</i>	<i>mirabilis</i> Bouchet & Kilburn, 1991	EXBODI	DW3906	New Caledonia	19°50' S, 165°33' E	490–580 m	OLIV066-16	KX233317	Kantor <i>et al.</i> , 2017
IM-2007-31949	<i>Turrancilla</i>	<i>glans</i> (E.A. Smith, 1899)	PANGLAO 2005	CP2333	Philippines, Bohol Sea	9°38' N, 123°44' E	584–596 m	NEOGA459-10	KX233370	Kantor <i>et al.</i> , 2017
IM-2019-620	<i>Turrancilla</i>	<i>apicalis</i> (Ninomya, 1988)	from fishermen		Japan	appr. 32°34' N, 132°22' E		NEOGA1497-20	MT556136	This study
IM-2009-24350	<i>Olivella</i>	<i>minuta</i> (Link, 1807)	KARUBENTHOS 2012	GM19	Guadeloupe	16°21.3' N, 61°44.92' W	1 m	OLIV063-16	KX233349	Kantor <i>et al.</i> , 2017
IM-2013-52004	<i>Agaronia</i>	<i>annotata</i> (Marrat, 1871)	Port ZANAGA	DW515	Congo	4°43'14" S, 11°49'4" E	8–9 m	OLIV074-16	KX233272	Kantor <i>et al.</i> , 2017
IM-2007-39266	<i>Calyptoliva</i>	<i>bugeae</i> Kantor <i>et al.</i> , 2016	TARASOC	DW3380	Tuamotu	15°39' S, 146°56' W	970–1060 m	OLIV008-16	KX233316	Kantor <i>et al.</i> , 2017
IM-2007-33275	<i>Oliva</i>	<i>lacamentai</i> Greifeneder & Blöcher, 1985	EBISCO	DW2573	New Caledonia, North Bellona	20°21' S, 158°46' E	345–351 m	NEOGA673-10	KX233379	Kantor <i>et al.</i> , 2017
IM-2007-31988	<i>Oliva</i>	<i>amethystina</i> (Roding, 1798)	Santo 2006	DR09	Vanuatu	15°34'36.00" S, 167°13'47.98" E	12 m	NEOGA476-10	KR087289	Kantor <i>et al.</i> , 2017

Sequencing and phylogenetic reconstruction

The total genomic DNA was extracted from muscle tissue with the semi-automated ABI PRISM™ 6100 Nucleic Acid Prep Station following the manufacturer's instructions. A fragment of 650 bp of the *Cox1* mitochondrial gene was amplified using universal primers LCO11490 and HCO2198 (Folmer *et al.* 1994). DNA amplification was performed in 25- μ L PCR reactions, containing approximately 3 ng of template DNA, 2.5 mM magnesium chloride (MgCl₂), 0.26 mM of each nucleotide, 0.3 mM of each primer, 5% dimethylsulphoxide (DMSO) and 1.5 units of QBIOTAQ polymerase (MP Biomedicals). Amplification products were generated by an initial denaturation step of 4 min at 94°C followed by 30 cycles of denaturation at 94°C for 30 s, annealing at 48°C for 40 s and extension at 72°C for 1 min. PCR products were sequenced in both directions to ensure the accuracy of base calls.

Sequences were aligned using the FFT-NS-I strategy in MAFFT ver. 7 (Katoh & Toh 2010; Katoh *et al.* 2019; <http://mafft.cbrc.jp/alignment/server/>). We used BioEdit ver. 7.0.5.3 (Hall 1999) to check for poorly aligned sites and MEGA ver. 5.05 (Tamura *et al.* 2011) to translate protein-coding sequences to screen for premature stop codons. Phylogenetic reconstructions were estimated using Bayesian Inference (BI) and Maximum Likelihood (ML). All nucleotide sites were conserved and three partitions corresponding to first, second and third codon positions were analyzed independently. A generalized time reversible model with a gamma law (G, four categories) and a proportion of invariants (I) was selected for both BI and ML analyses as it is the most inclusive model of nucleotide evolution. BI analyses were performed in two parallel runs in MrBayes (Huelsenbeck *et al.* 2001) and consisted of six Markov chains and 10 000 000 generations with default number of chain swaps and sampling frequency of one tree in each 500 generations. A chain temperature of 0.02 was used in all analyses. The convergence of each analysis was checked using Tracer ver. 1.4.1 (Rambaut *et al.* 2014); the two runs were considered converged if all effective sample size (ESS) values exceeded 200. Consensus trees were calculated after discarding the first 25% trees as burn-in. Best-scoring ML trees were estimated using RAXML (Stamatakis 2014). One hundred independent searches, each starting from distinct random trees, were conducted. The robustness of nodes was assessed using rapid bootstrapping with 1000 bootstrap replicates. All analyses were implemented in the Cipres Science Gateway (<https://www.phylo.org/>) portal ver. 3.3. (Miller *et al.* 2010), using MrBayes ver. 3.2.6 on XSEDE and RAXML-HPC2 on XSEDE (ver. 8.1.11). Species delimitation analyses were conducted using the Automatic Barcode Gap Discovery (ABGD) method of Puillandre *et al.* (2012) that uses detection of the 'barcode gap' in the distribution of genetic pairwise distances. The ABGD method was implemented based on all available *Cox1* sequences and using the online version of the program (<https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html>) with default parameters.

Nodes with Bootstraps values (B) lower than 70% and Posterior Probabilities (PP) lower than 0.90 are considered non-supported; B-values between 70 to 90 and PP-values between 0.90 to 0.95 will be regarded as moderately supported and B > 90 and PP > 0.95 shall be treated as highly supported.

To visualize the relationships between haplotypes and their geographic distribution of the widely distributed *A. hilgendorfi* (von Martens, 1897), a Median-Joining Network (MJN) was constructed using the program NETWORK ver. 5.0.1.0 (Bandelt *et al.* 1999) with equal weights for variable sites (epsilon=0) and connection cost calculation method. To delete superfluous median vectors and links that are not contained in the shortest tree, a post-processing maximum parsimony calculation was run.

Unless stated otherwise, all illustrated specimens with MNHN registration numbers were sequenced.

Morphological studies

The terminology of shell characters follows Kantor *et al.* (2017). The primary spire callus covers most of the spire, including at least part of the protoconch, leaving in most cases only the first protoconch whorl exposed. Therefore, for comparative purposes, we measured only the diameter of the first whorl, following the method described by Bouchet & Kantor (2004). The radula was examined when available. It was cleaned in dilute bleach, mounted on glass cover slips and air dried; the cover slips were glued to aluminum stubs, then coated with gold and studied on scanning electron microscope TeScan TS5130MM in the Institute of Ecology and Evolution of the Russian Academy of Sciences (IEE RAS).

Abbreviations

AL	=	aperture length
dd	=	empty shell
juv	=	juvenile
lv	=	live collected specimen
SL	=	shell length
SW	=	shell width
stn	=	station

Repositories

MMM	=	Museo Malacologico, Cupra Marittima, Italy
MNHN	=	Muséum national d'histoire naturelle, Paris, France
NBC	=	Naturalis Biodiversity Center, Leiden, The Netherlands
NHMUK	=	The Natural History Museum, London, UK
UMUT	=	University Museum, University Tokyo, Japan
ZMA	=	Zoologisch Museum Amsterdam [now in Naturalis, Leiden, The Netherlands]
ZMB	=	Museum für Naturkunde, Berlin, Germany

Results

Molecular analysis and species delimitation

The trees obtained with ML and BI analyses have similar topologies, with a few differences in the robustness of some nodes (Fig. 1). The genus *Amalda* is not supported, either in the ML tree or in the BI tree (Posterior Probability, PP=0.83).

The ABGD method estimated seven a priori thresholds. Extreme threshold values led to partitions where each of the 64 *Cox1* haplotypes of *Amalda* (not taking into account outgroups) was considered as a different Primary Species Hypothesis (PSH), or conversely where almost all haplotypes were considered as a single PSH. Five intermediate a priori thresholds led to five partitions with 38, 38, 33, 31 and 22 PSHs detected within *Amalda*. Vouchers of the four inferred PSHs (*A. australis* + *A. depressa* (G.B.Sowerby II, 1839), *A. novaezelandiae*, *A. mucronata* (G.B.Sowerby I, 1830), *A. benthicola* (Dell, 1956)) in the partition scheme with 22 PSHs were not available for study. *Amalda australis* and *A. depressa* were not recognized as separate species in any of the obtained partition schemes, except the one comprising 64 PSHs. An examination of the shell morphology supported only 17 out of the remaining 18 PSHs. Indeed, two closely related PSHs, hereafter referred to as *A. miriky* sp. nov., showed no difference in shell morphology. Populations within this species are expected to be spatially structured because of the high level of habitat fragmentation and the reduced dispersal ability of the larvae as inferred from protoconch morphology. Consequently, we can expect that ABGD may split the dataset at the population level rather than at the species level. The 17 PSHs supported by both the shell morphology and the genetic clustering were hereafter treated as Secondary Species Hypotheses (SSH).

Based on these 17 SSHs, an examination of the published data and a comparison with the type specimens allowed to apply species names to 12 of them (Fig. 1). Among the remaining five SSHs, two are represented by multiple sequenced specimens and are described herein as new species, *A. miriky* sp. nov. and *A. alabaster* sp. nov. Three more are represented by a single sequenced specimen. Specimen MNHN IM-2007-33287 is very distinct morphologically and several additional, not sequenced specimens are present in our material. A comparison with other known species of *Amalda* leaves no doubt that these correspond to a new species, which is described here as *A. cacao* sp. nov. Sister to it is a single, seemingly subadult, specimen MNHN IM-2013-63891 from Papua New Guinea, and no comparable additional specimens are present in the available material. Although it definitely represents a separate species, we abstain from its description for the moment (see below for discussion). Finally,

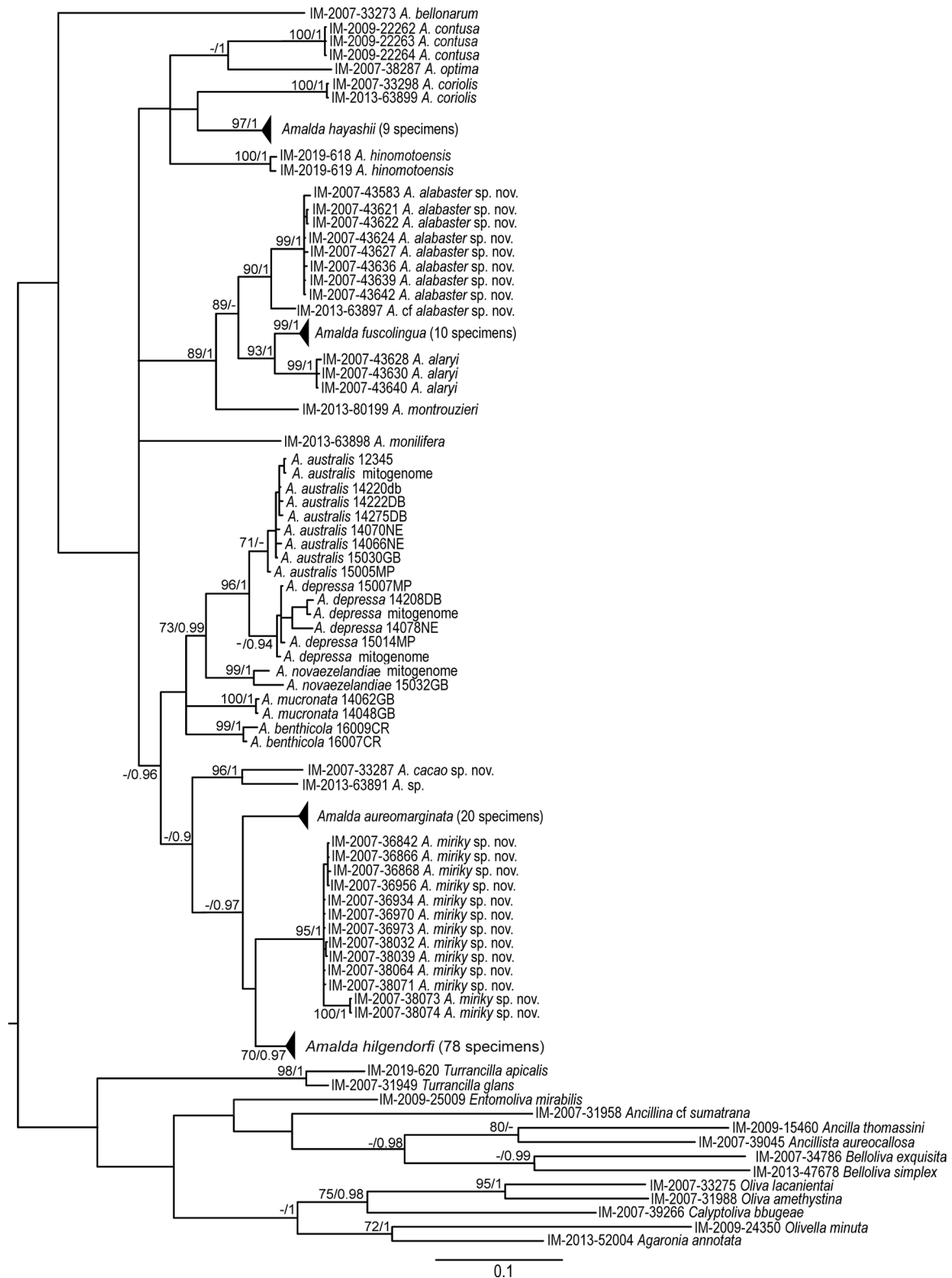


Fig. 1. Bayesian tree (MrBayes) for the *Cox1* gene. Bootstrap supports (≥ 70) and posterior probabilities (> 0.90) values are shown for each supported node. The unit for the scale is “substitutions/site”. The clades of *Amalda hayashii* Ninomiya, 1988, *A. fuscolingua* Kilburn & Bouchet, 1988 and *A. aureomarginata* Kilburn & Bouchet, 1988 containing multiple specimens with minimal genetic distances are collapsed. The clade of *A. hilgendorfi* (von Martens, 1897) is collapsed and shown on Fig. 2.

the specimen MNHN IM-2013-63897 is sister to *A. alabaster* sp. nov., with a high support both in ML and BI trees. Morphologically, it is similar to *A. alabaster* sp. nov. Since no additional material suitable for sequencing is available at the moment we also do not provide a formal description (see below).

The largest clade, very heterogeneous both molecularly and morphologically, is represented in our material by 78 sequenced specimens from different regions of the West Pacific. It is highly supported in the BI tree (PP=0.97), and moderately supported in the ML tree (B=70). Among these specimens, three were collected in Japan. They are similar to the type of *Ancilla hilgendorfi* and we applied this name to that clade.

The haplotypes network obtained from *Cox1* sequences showed high genetic disparity, with a total of thirty haplotypes separated by high number of mutation steps (Fig. 3). The haplotypes network on the other hand displays a pronounced geographic structure (with 29 of 30 haplotypes represented in only one major region). A striking pattern here is the presence of two highly divergent assemblages of haplotypes at same sampling sites around Île des Pins (showed in yellow on Fig. 3), and huge disparity of haplotypes in specimens from Papua New Guinea (Bismarck Sea) (recovered in five unrelated clusters, purple on Fig. 3). One distinctive and large group (highlighted by a green rectangle on Fig. 3) included individuals exclusively sampled from New Caledonia EEZ, except for one specimen from Papua New Guinea.

While the terminal groups (SSH) are well supported, at least in the Bayesian analysis, the deeper nodes are mostly not resolved, a situation typical with a single genetic marker. Two groupings are however statistically supported: a clade uniting *A. alabaster* sp. nov., *A. fuscolingua*, *A. allaryi* and *A. montrouzieri*, and (only in BA) a second one including all remaining New Caledonian (except *A. bellonarum*) and New Zealand species.

Systematic descriptions

Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Neogastropoda Wenz, 1938
Family Ancillariidae Swainson, 1840

Genus *Amalda* H. Adams & A. Adams, 1853

Type species

Ancillaria tankervillii Swainson, 1825, by subsequent designation by Cossmann (1899).

Remarks

Amalda tankervillii occurs in Venezuela in shallow water (6 to 70 m) and is conchologically quite different from the other species included in the genus (Fig. 4M). Neither its anatomy nor the molecular data have been examined. Based on shell characters, Voskuil (1991) compared *Ancillaria tankervillii* with species of *Eburna* Lamarck, 1801 and concluded that *Amalda* s. str. should be considered a subgenus of *Eburna*, while the Indo-Pacific species of *Amalda* probably belong to a separate genus *Baryspira* P. Fischer, 1883. Although *A. tankervillii* is indeed somewhat different from Indo-Pacific species in being thin, broadly oval, with a large inflated last whorl and a very low spire, in the absence of molecular and anatomical data the opinion of Voskuil (1991) remains speculative. Herein, we follow the generally accepted taxonomic concept of *Amalda* and do not attempt to revise its generic/subgeneric structure, which will require a much broader molecular taxon sampling than is currently available, as well, as sequencing additional genetic markers.

Amalda hilgendorfi (von Martens, 1897)

Figs 2–4, 5–6, 7A–G, 8I–J

Ancillaria hilgendorfi von Martens, 1897: 167, pl. 16 figs 26–27.

Amalda hilgendorfi richeri Kilburn & Bouchet, 1988: 285–287, figs 18–22 [not figs 23–24 = *Amalda cacao* sp. nov.].

Amalda vernedei herlaari van Pel, 1989: 14, figs 1–3.

Amalda hilgendorfi vezzaroi Cossignani, 2015: 24–25, text figures.

Baryspira hilgendorfi – Kira 1962: 208, pl. 71 fig. 1. — Kuroda *et al.* 1971: 300 [Japanese text], 196 [English text], pl. 54. fig. 1.

Amalda aureomarginata Northern New Caledonia form – Kilburn & Bouchet 1988: 284, Fig. 13.

Amalda aureomarginata Chesterfield form – Kilburn & Bouchet 1988: 284, figs 14–17.

?*Amalda (Alcospira) hilgendorfi* – Ninomiya 1990: pl. 2 fig. 5.

Amalda hilgendorfi – Okutani 2000: 523, pl. 260 fig. 2 (erroneously labelled *A. hayashii* on the plate) [not pl. 260 fig. 3 = *A. hayashii*]. — Gratecap 2016b: 4, 12, figs 3–4. — Tsuchida 2017: 995, pl. 288 fig. 3.

Amalda vernedei herlaari – Poppe 2008: pl. 546, figs 7–9.

Amalda hilgendorfi richeri – Gratecap 2014 (part): 14, 19, figs 19–23 [not figs 24–25 = *Amalda cacao* sp. nov.]

Type material

JAPAN • Holotype of *Ancillaria hilgendorfi*; ZMB 31632.

NEW CALEDONIA • Holotype of *Amalda hilgendorfi richeri*; North of New Caledonia, Grand Passage; 18°57' S, 163°14' E; 480 m deep; MNHN IM-2000-1378.

ARAFURA SEA • Holotype of *Amalda vernedei herlaari*; Arafura Sea; 150 fathoms [270 m]; formerly ZMA Moll. no. 3.88.040, now NBC.

PHILIPPINES • Holotype of *Amalda hilgendorfi vezzaroi*; Philippines, Aliguay island; MMM.

Description

SHELL. Variable, narrowly to broadly fusiform with high, acuminate spire; thin to thick microshagreened primary callus impressed at suture, forming distinct to very distinct, obtuse keel above suture. Protoconch exposed, medium large (n=2, first whorl diameter 0.75–0.92 mm), border with teleoconch indistinct. Secondary callus very thin to distinct, tongue-shaped, broadening in middle part and rounded apically, extending on last three whorls, seemingly less shagreened than primary callus. Plication plate with 2–7 weak ridges, sometimes nearly obsolete. Olivoid groove from narrow and distinct to broad and shallow or nearly obsolete, labral tooth distinct, obtuse. Upper anterior band usually thickened, sometimes heavily. Colour variable, from pale yellowish to brown, olivoid band always lighter than body whorl cloak, anterior band the darkest anterior zone of shell, plication plate usually nearly white, primary callus bordered by lighter narrow band (or line). Height to 81 mm, exceptionally up to 98 mm.

RADULA (n=16 of different morphs). Lateral teeth very similar in all species of *Amalda*, unicuspid, hook-shaped (Fig. 7A). Central tooth normally tricuspid with central cusp shortest. Some variation in central tooth shape (Fig. 7B–G); central cusp from extremely short, nearly obsolete, to subdivided in two cusplets, or with additional denticles on side. Cusps of the central tooth either with smooth edges, or serrated (Fig. 7G). Morphological variation not related to geographical distribution.

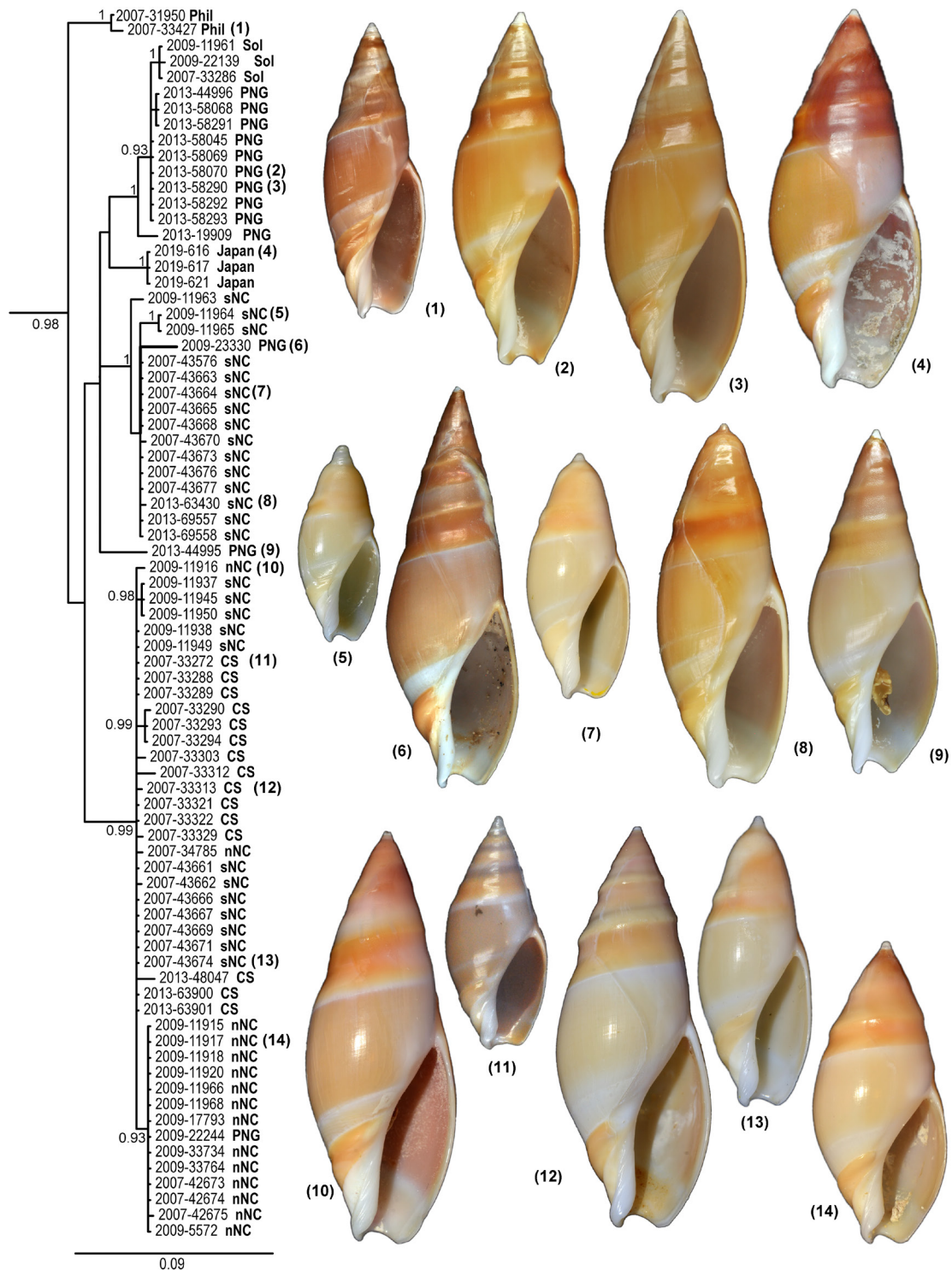


Fig. 2. Molecular phylogeny of *Amalda hilgendorfi* (von Martens, 1897) produced by a Bayesian analysis of the *Cox1* gene dataset. Outgroups and other species of *Amalda* have been removed from the tree. Only posterior probabilities $\geq 90\%$ are shown. The unit for the scale is “substitutions/site”. The geographical distribution and morphological morphs are coded for each specimen: Phil=Philippines; Sol=Solomon Islands; PNG=Papua New Guinea; sNC=South New Caledonia; nNC=North New Caledonia; CS=Coral Sea. Numbers in parentheses at the tips of the tree link the MNHN IM voucher number to the corresponding photo on the right.

Remarks

Molecular analysis demonstrated high heterogeneity of this species with several subclades, mostly geographically determined (Fig. 2), with groupings from Japan, the Philippines, Papua New Guinea and the Solomon Islands, north of New Caledonia and the Coral Sea, and south of New Caledonia and Norfolk Ridge. This structure is, however, not clear-cut; for example, individuals with identical haplotypes are found in northern New Caledonia (MNHN IM-2009-33734) and Papua New Guinea (MNHN IM-2009-22244) (Haplotype #18, Fig. 3). At the same time, the specimens collected in the south of New Caledonia are grouped in two different subclades, one of which also includes one specimen from Papua New Guinea, while the second one includes specimens from southern and northern New Caledonia and the Coral Sea, as well as one specimen from Papua New Guinea.

This suggests that despite a non-planktotrophic larval development, larval dispersal in *A. hilgendorfi* over time can take place across large geographic distances. The presence in New Caledonia of two highly divergent genetic groups (marked by green oval and green rectangle on Fig. 3), both with affinities with haplotypes from Papua New Guinea, suggests that larval exchange between these distant regions might have been quite frequent.

The species is variable in shell shape and colouration. Several morphs could be distinguished, mostly geographically determined and not necessarily distinct molecularly. This has resulted in the description of three subspecies. Moreover, morphologically very similar sympatric specimens may belong to different subclades. For a better characterization of the variability, we describe these morphs separately.

General distribution

Amalda hilgendorfi is broadly distributed in the West Pacific, recorded from Japan, the Philippines, Papua New Guinea and the Solomon Islands, eastern Australia, the Coral Sea, and New Caledonia.

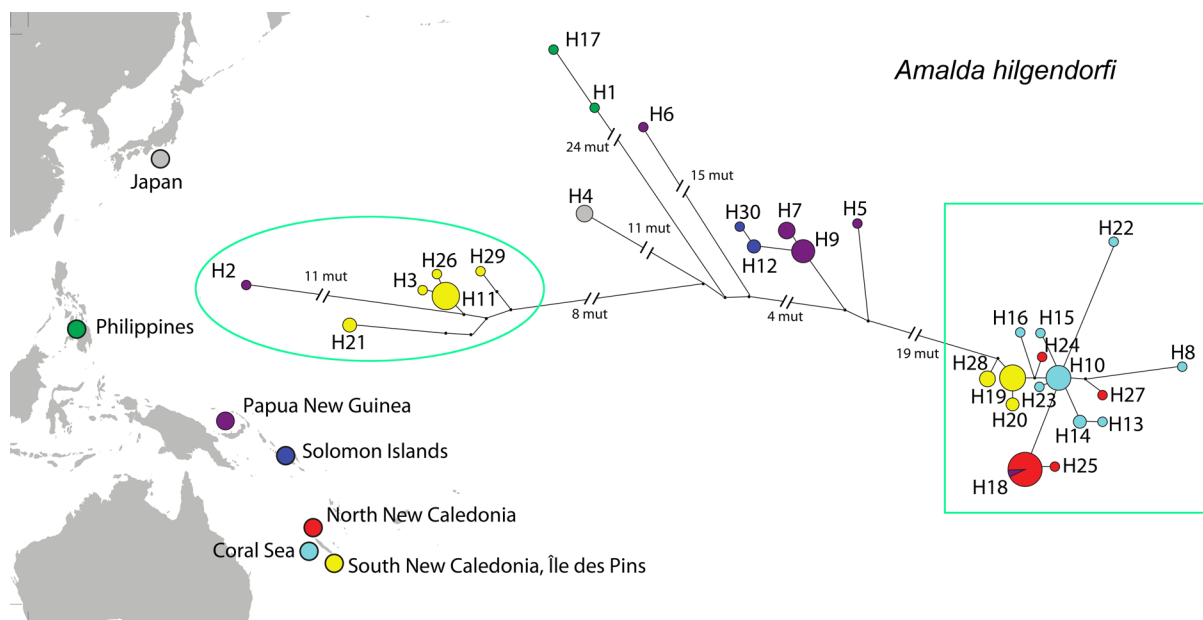


Fig. 3. Median-joining haplotype network based on *Cox1* sequences of *Amalda hilgendorfi* (von Martens, 1897). Circles are colour coded by general location reported on the map and sized according to each haplotype's relative abundance. Lengths of the lines connecting haplotype circles are proportional to the number of nucleotide differences among haplotypes. Green rectangle and oval encircle assemblages of haplotypes from New Caledonia (each including a specimen from Papua New Guinea).

Nominotypical (Japan) morph

Figs 2 (as Japan), 4A–D

Material examined

Three sequenced specimens (Table 1).

Remarks

Morph with a single identified haplotype (Fig. 3).

Shell broad-fusiform (SL up to 53 mm, holotype 50 mm) dark-coloured, with chestnut-brown primary callus and well-defined light purplish secondary callus (Fig. 4A–D). Body cloak orange-brown. Olivoid band light yellowish. Upper anterior band strongly convex, of same colour as body whorl cloak, lower anterior band much lighter, yellowish. Plication plate white, with 3–4 indistinct to nearly obsolete plicae. First protoconch whorl diameter 0.8–0.92 mm (mean 0.88, n=3). Depth range 150–350 m (Tsuchida 2017), sequenced specimens from 230–280 m.

Philippines morph

Figs 2 (as Phil), 4E–G

Material examined

Two sequenced specimens (Table 1).

Remarks

Both sequenced specimens cluster together (Fig. 2), two haplotypes identified (Fig. 3).

Shell slender (largest specimen with SL 40.3 mm), coloured in different shades of brown, with lighter olivoid band and slightly convex upper anterior band having nearly median obtuse ridge (Fig. 4). In shell shape and colouration this form matches the subspecies *A. hilgendorfi vezzaroi* Cossignani, 2015, described from Aliguay Island, Philippines. This same morph is illustrated by Poppe (2008) as *Amalda vernedei herlaari* van Pel, 1989 (part: pl. 546 fig. 7) from Balut Island in 100–150 m; this illustrated shell attains 67 mm, which is significantly larger than ours. Depth range of sequenced specimens 437–740 m.

Papua New Guinea and Solomon Islands morph

Figs 2 (as PNG and Sol), 4H–L

Material examined

Sequenced material

16 sequenced specimens (Table 1).

Not sequenced material

SOLOMON SEA • 1 lv; SE Engeneer group Island; 10°45' S, 151°06' E; 470–526 m deep; MADEEP; stn DW4300; MNHN IM-2013-45679 • 1 lv; SE of d'Entrecasteaux Islands; 9°48' S, 151°33' E; 278–420 m deep; MADEEP; stn DW4314; MNHN IM-2013-45800.

PAPUA NEW GUINEA • 1 lv; N Cape King William; 6°3' S, 147°36' E; 450–480 m deep; PAPUA NIUGINI; stn DW3992; MNHN IM-2013-19808 • 1 lv; 6°00' S, 147°38' E; 785 m deep; PAPUA NIUGINI; stn DW3992; MNHN IM-2013-19856.



Fig. 4. *Amalda hilgendorfi* (von Martens, 1897). **A–D.** Typical morph, Japan. **A–C.** MNHN IM-2019-616, SL 53.1 mm. **D.** MNHN IM-2019-621, SL 50.0 mm. **E–G.** Philippine morph. **E.** MNHN IM-2007-31950, SL 38.7 mm. **F–G.** MNHN IM-2007-33427, SL 40.3 mm. **H–L.** Solomon Islands and Papua New Guinea (PNG) morph. **H.** Solomons, MNHN IM-2007-33286, SL 52.6 mm. **I.** PNG, MNHN IM-2013-44995, SL 51.3 mm. **J.** Solomons, MNHN IM-2009-11961, SL 32.9 mm. **K.** PNG, MNHN IM-2009-22244, SL 63.1 mm. **L.** PNG, MNHN IM-2009-23330, SL 69.3 mm. **M.** *Amalda tankervillei* (Swainson, 1825), Venezuela, Isla de Margarita, 30–35 m, collection of Ron Voskuil, RV 0175, SL 80 mm. Photo by Ron Voskuil *et al.* (2011) (<http://olivirv.myspecies.info/en/taxon-pages/ancillaria-tankervillei>). Shells (except M, reduced) at the same scale.

Remarks

The population from the Solomon Islands and Papua New Guinea is molecularly heterogeneous; although most of them forming a highly supported clade (Fig. 2), some specimens are scattered along the tree. One specimen (MNHN IM-2009-23330, Fig. 4L) groups with the morph from south of New Caledonia; while another (MNHN IM-2009-22244, Fig. 4K) groups with the specimens from north of New Caledonia sharing the same haplotype (Fig. 3). In total, seven haplotypes were identified (two from the Solomon Islands and five from Papua New Guinea).

Shell large (SL up to 81.2 mm (MNHN IM-2013-45800), although most specimens are below 55 mm), resembling the population from north of New Caledonia, although generally of darker orange-brown colour and lacking the purplish colouration of the callus that is often present in the northern New Caledonia morph. Upper teleoconch whorls sometimes with obtuse calloused carina. Upper anterior band either evenly strongly convex or with poorly defined submedian carina, lower anterior band always yellow-brown, although sometimes very light. Columellar ridges differently pronounced, 3–7 in number.

This form was described as *Amalda vernedei herlaari* van Pel, 1989 (Arafura Sea, no exact locality), and later considered a subspecies of *A. hilgendorfi* (Cossignani 2015). The shell can attain 98 mm (holotype of *Amalda vernedei herlaari*). Depth range 335–785 m.

New Caledonia morphs

Figs 2 (as CS, nNC, sNC), 5, 6, 7F-G

Remarks

The specimens from New Caledonia form two distinct and supported molecular subclades (Fig. 2). One of them includes only specimens from south of New Caledonia (mostly around Île des Pins), while the second one combines specimens from southern and northern New Caledonia as well as from the Coral Sea. Each subclade includes one specimen from Papua New Guinea (see above). Morphologically, the specimens from south of New Caledonia around Île des Pins are very similar, although they belong to different subclades. Conversely, specimens from the Coral Sea and north of New Caledonia are morphologically very variable, despite belonging to the same subclade.

Coral Sea morph

Figs 2 (as CS), 5A–F, 7G

Material examined**Sequenced material**

15 sequenced specimens (Table 1).

Not sequenced material

CORAL SEA • Material listed by Kilburn & Bouchet (1988) • 1 lv; 19°34' S, 158°40' E; 400–413 m deep; EBISCO; stn DW2607; MNHN IM-2007-33278 • 1 lv; 20°51' S, 161°00' E; 557–565 m deep; EBISCO; stn CP2643; MNHN IM-2007-33292 • 1 lv; 19°45' S, 158°40' E; 386–428 m deep; KANADEEP 1; stn DW4975; MNHN IM-2013-63902.

Remarks

Shell large (SL up to 66 mm), usually light coloured, rarely nearly white except light yellowish primary callus and anterior band. Very distinct callused carina occupying mid-whorl position appearing on fourth or fifth teleoconch whorl (Fig. 5A–B, D). Secondary callus indistinct. Young specimens oval (Fig. 5E–F), large ones fusiform. Upper part of plication plate light yellowish. Upper anterior band strongly convex, in large specimens with obtuse and very broad (about 2/3 of anterior band) ridge. At least one specimen

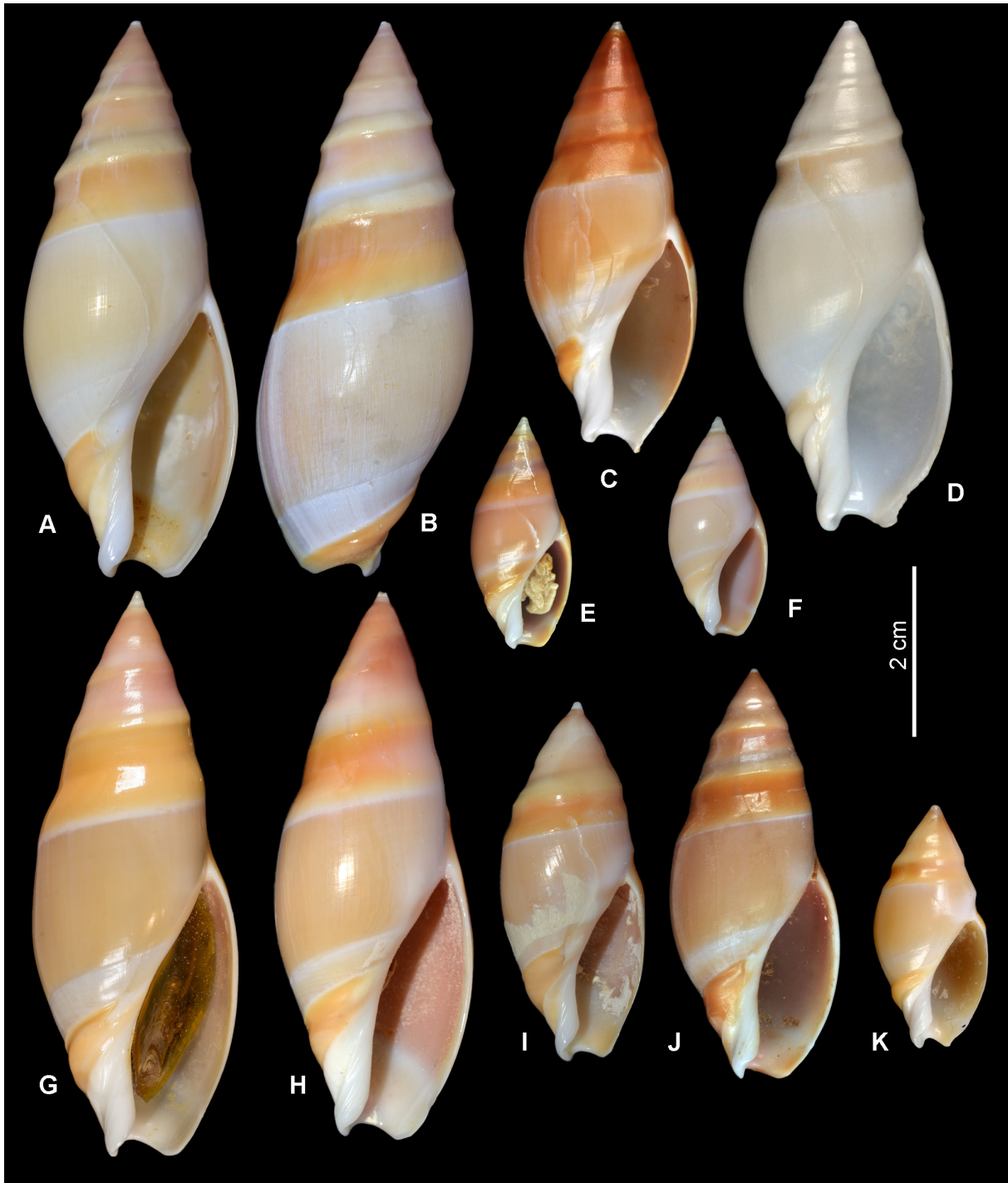


Fig. 5. *Amalda hilgendorfi* (von Martens, 1897). **A–F.** Coral Sea morph. **A–B.** MNHN IM-2007-33313, SL 66 mm. **C.** MNHN IM-2007-33289, SL 51.3 mm. **D.** MNHN IM-2007-33288, SL 60.3 mm. **E.** MNHN IM-2013-63901, SL 27.3 mm. **F.** MNHN IM-2007-33312, SL 25.9 mm. **G–K.** Northern New Caledonia morph = *A. hilgendorfi richeri* Kilburn & Bouchet, 1988. **G.** Holotype, MNHN IM-2000-1378, SL 66.9 mm. **H.** MNHN IM-2009-11916, SL 65 mm. **I.** MNHN IM-2009-11918, SL 43.2 mm. **J.** MNHN IM-2007-42675, SL 48.7 mm. **K.** MNHN IM-2009-11966, SL 29 mm. Shells at the same scale.

(SL 51.3 mm, MNHN IM-2007-33289, Fig. 5C) did not have a callused carina on the spire and had a uniformly white plication plate. Number of columellar ridges variable from 2–3 in small specimens to 6–7 in medium-sized and larger ones. First protoconch whorl diameter 0.75–0.92 mm (mean 0.82, n=5). The younger specimens of this morph are somewhat similar in colouration to *A. aureomarginata* and were erroneously identified as such by Kilburn & Bouchet (1988). Depth range 390–750 m.

Northern New Caledonia morph (“*A. hilgendorfi richeri*”)

Figs 2 (as nNC), 5G–K

Material examined

Sequenced material

15 sequenced specimens (Table 1).

Not sequenced material

Material listed by Kilburn & Bouchet (1988).

Remarks

Shell large (SL up to 76 mm), somewhat similar to the morph from the Coral Sea, although adult shells are more slender and the callused carina is less developed. Upper anterior band with more defined, relatively narrow, median carina. Plication plate uniformly white. Smaller specimens are more ovoid in shape, with relatively more pronounced carina and uniformly convex upper anterior band; the upper part of plication plate can be yellowish. Upper whorls often have a purplish tint. Number of columellar ridges variable, 2 to 6, regardless of specimen size. First protoconch whorl diameter 0.80–0.84 mm (mean 0.83, n=5). Depth range 360–750 m.

Southern New Caledonia morph (“*pupiform*”)

Figs 2 (as sNC), 6, 7F

Material examined

Sequenced material

26 sequenced specimens (all MNHN) (Table 1).

Not sequenced material

SOUTHERN NEW CALEDONIA • Material listed by Kilburn & Bouchet (1988) • 1 dd; Île des Pins; 22°48' S, 167°15' E; 440–470 m deep; TERRASSES; stn CP3115 • 1 dd; SW of Île des Pins; 22°54' S, 167°17' E; 496–505 m deep; KANACONO; stn DW4722 • 2 dd; W of Île des Pins; 22°50' S, 167°16' E; 480–505 m deep; VAUBAN 1978–1979; stn DR23 • 5 lv, 1 dd, S of Île des Pins; 22°53' S, 167°17' E; 570–610 m deep; BIOCAL; stn DW 46 • 1 dd; S of Grande Terre; 22°56' S, 167°17' E; 485–520 m deep; MUSORSTOM 4; stn CP215 • 1 dd; S of Grande Terre; 22°56' S, 167°17' E; 485–520 m deep; MUSORSTOM 4; stn DW223 • 2 worn dd; 22°51' S, 167°13' E; 445–460 m deep; MUSORSTOM 4; stn DW229 • 2 dd; S of Île des Pins; 22°52' S, 167°13' E; 415 m deep; SMIB 1; stn DW02 • 7 dd; S of Île des Pins; 22°55' S, 167°16' E; 490–495 m deep; SMIB 2; stn DW10 • 1 dd; Banc Éponge; 24°54' S, 168°22' E; 530 m deep; SMIB 3; stn CP04; • 1 worn dd; Kaimon Maru Bank; 24°45' S, 168°08' E; 233 m deep; SMIB 3; stn DW08 • 1 lv; SW of Île des Pins; 22°59' S, 167°19' E; 525 m deep; SMIB 3; stn DW21 • 1 lv, 1 dd; SW of Île des Pins; 23°03' S, 167°19' E; 503 m deep; SMIB 3; stn DW22.

Remarks

A very peculiar morph with medium-sized shell (SL up to 53.7 mm, usually less than 35 mm), occurring only in southern New Caledonia, mostly off Île des Pins, with a few specimens collected on Norfolk Ridge. Despite morphological similarity between specimens, these are genetically heterogeneous, belonging to

different highly divergent assemblages of haplotypes (marked by yellow in Fig. 3), some being closer to specimens from northern New Caledonia and the Coral Sea, while others constituting a subclade on the tree (Fig. 2). In total eight haplotypes were identified within this morph.

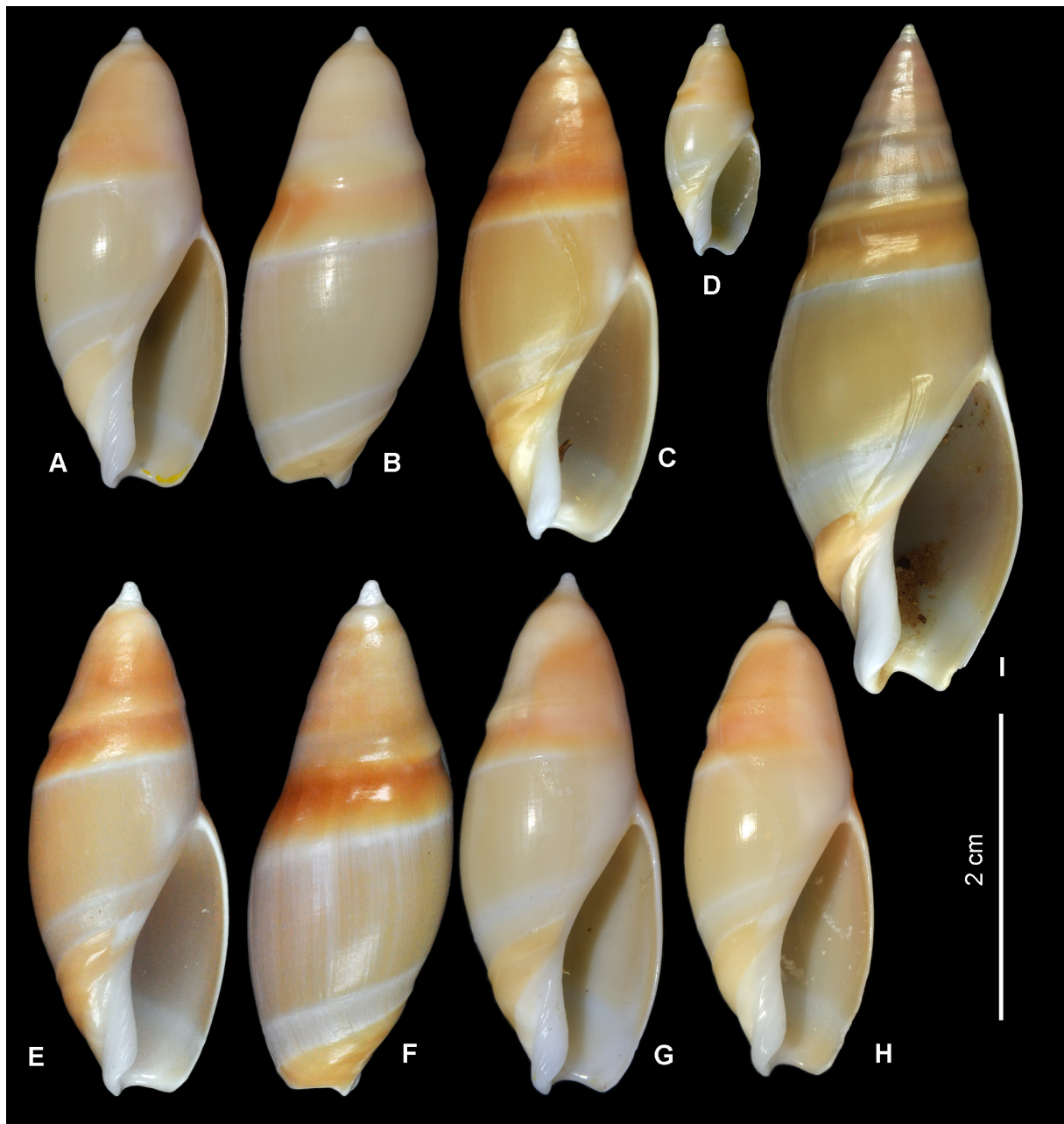


Fig. 6. *Amalda hilgendorfi* (von Martens, 1897). Southern New Caledonia morph. A–D and E–H belong to two molecularly distinct subclades. A–B. MNHN IM-2007-43664, SL 30.6 mm. C. MNHN IM-2007-43673, SL 34.2 mm. D. MNHN IM-2009-11964, SL 15.2 mm. E–F. MNHN IM-2007-43671, SL 33.8 mm. G. MNHN IM-2007-43674, SL 34.7 mm. H. MNHN IM-2009-11945, SL 31.6 mm. I. Norfolk Ridge, Banc Éponge, NORFOLK 1, stn DW 1693, 24°55' S, 168°21' E, 564–1144 m, SL 61 mm, specimen not sequenced, shell not to scale. Shells (except I, reduced) at the same scale.

Shell shape pupiform due to very strong development of primary and secondary calluses on upper teleoconch whorls, while uppermost 2.5–3 whorls (including those of protoconch) remain uncovered, revealing the papillate apex. Except the large development of the callus, the shell shape is rather similar to those in the north New Caledonia morph and some specimens with less developed callus (e.g., MNHN IM-2013-69558 or MNHN IM-2007-43673 on Fig. 6C) are practically indistinguishable (e.g., MNHN IM-2009-11918, Fig. 5I). Columellar ridges rather distinct, 6–7. Upper anterior band usually evenly convex, not subdivided by a ridge. First protoconch whorl diameter 0.84–0.90 mm (mean 0.86, n=5). Depth range 233–610 m.

On Norfolk Ridge and off southern New Caledonia, some specimens very similar to those from north of New Caledonia were found in deeper water in 560–650 m in addition to the pupiform morph. One specimen was collected on Banc Eponge (Fig. 6I) in a haul with a very large depth range, 564–1144 m, but the deepest record needs confirmation. Although none of these specimens were sequenced, there is no doubt of their identity.

Amalda aureomarginata Kilburn & Bouchet, 1988

Figs 7H, 8A–H, 9A

Amalda aureomarginata Kilburn & Bouchet, 1988: 282, 284, figs 9–12 [not figs 13–17=*Amalda hilgendorfi*].

Amalda aureomarginata – Gratecap 2014 (part): 13, 18, figs 5–8 [not fig. 9=*Amalda hilgendorfi*].

Type material

Holotype

SOUTHERN NEW CALEDONIA • 22°47' S, 167°15' E; 430–465 m deep; BIOCAL; stn 45; MNHN IM-2000-1345.

Material examined

Sequenced material

20 sequenced specimens (all MNHN) (Table 1).

Not sequenced material

SOUTHERN NEW CALEDONIA • 1 dd; S of Île des Pins; 22°55' S, 167°15' E; 450 m deep; SMIB 1; stn DW09 • 13 dd; SW of Île des Pins; 22°56' S, 167°15' E; 437 m deep; SMIB 3; stn DW25 • 5 dd; SW of Île des Pins; 22°55' S, 167°16' E; 450 m deep; SMIB 3; stn DW26 • 6 dd; SW of Île des Pins; 22°46' S, 167°11' E; 394 m deep; stn DW28 • 15 dd; SW of Île des Pins; 22°47' S, 167°12' E; 405 m deep; SMIB 3; stn DW29 • 2 dd; SW of Île des Pins; 22°55' S, 167°13' E; 383 m deep; SMIB 3; stn DW31 • 6 lv and dd; between Île des Pins and Grand Récif Sud; 22°56' S, 167°14' E; 400–420 m deep; SMIB 4; stn DW65 • 2 dd; between Île des Pins and Grand Récif Sud; 22°56' S, 167°15' E; 400–430 m deep; SMIB 4; stn DW66 • 2 dd; between Île des Pins and Grand Récif Sud; 22°55' S, 167°16' E; 430–440 m deep; SMIB 4; stn DW68 • 1 dd; between Île des Pins and Grand Récif Sud; 22°55' S, 167°15' E; 395–405 m deep; SMIB 4; stn DW69 • 2 dd; Antigonie Bank; 23°15' S, 168°04' E; 305–335 m deep; SMIB 5; stn DW104 • 2 dd; Antigonie Bank; 23°15' S, 168°04' E; 311–355 m deep; SMIB 8; stn DW185 • 2 dd; 23°17' S, 168°06' E; 390–540 m deep; SMIB 8; DW187 • ca 30 dd; S of Île des Pins; 22°48' S, 167°15' E; 444–445 m deep; BATHUS 2; stn DW719 • 3 dd; S of Île des Pins; 22°52' S, 167°16' E; 530–541 m deep; SMIB 8; stn DW720 • 4 dd; S of Île des Pins; 22°50' S, 167°27' E; 430–433 m deep; SMIB 8; stn DW723 • ca 15 lv and dd; southwest slope of the Dumbéa Pass; 22°52' S, 167°12' E; 400 m deep; SMIB 8; stn DW729 • 1 dd; Norfolk Ridge; 23°21' S, 168°02' E; 386–390 m deep; BATHUS 3;

stn DW829 • 2 dd; south of Grande Terre; 22°53' S, 167°12' E; 390–420 m deep; MUSORSTOM 4; stn DW230 • 4 dd; W of Île des Pins; 22°47' S, 167°12' E; 390–400 m deep; *Vauban* 1978–1979; stn DR16 • 4 dd; Crypthelia Bank; 23°20' S, 168°15' E; 207–276 m deep; NORFOLK 1; stn DW1728 • 25 dd; SW of Île des Pins; 22°57' S, 167°16' E; 427–433 m deep; NORFOLK 1; stn DW1733 • 20 dd; SW of Île des Pins; 22°54' S, 167°13' E; 403–429 m deep; NORFOLK 1; stn DW1734 • 20 lv and dd; SW of Île des Pins; 22°53' S, 167°13' E; 415–445 m deep; NORFOLK 1; stn DW1735 • 4 dd; SW of Île des

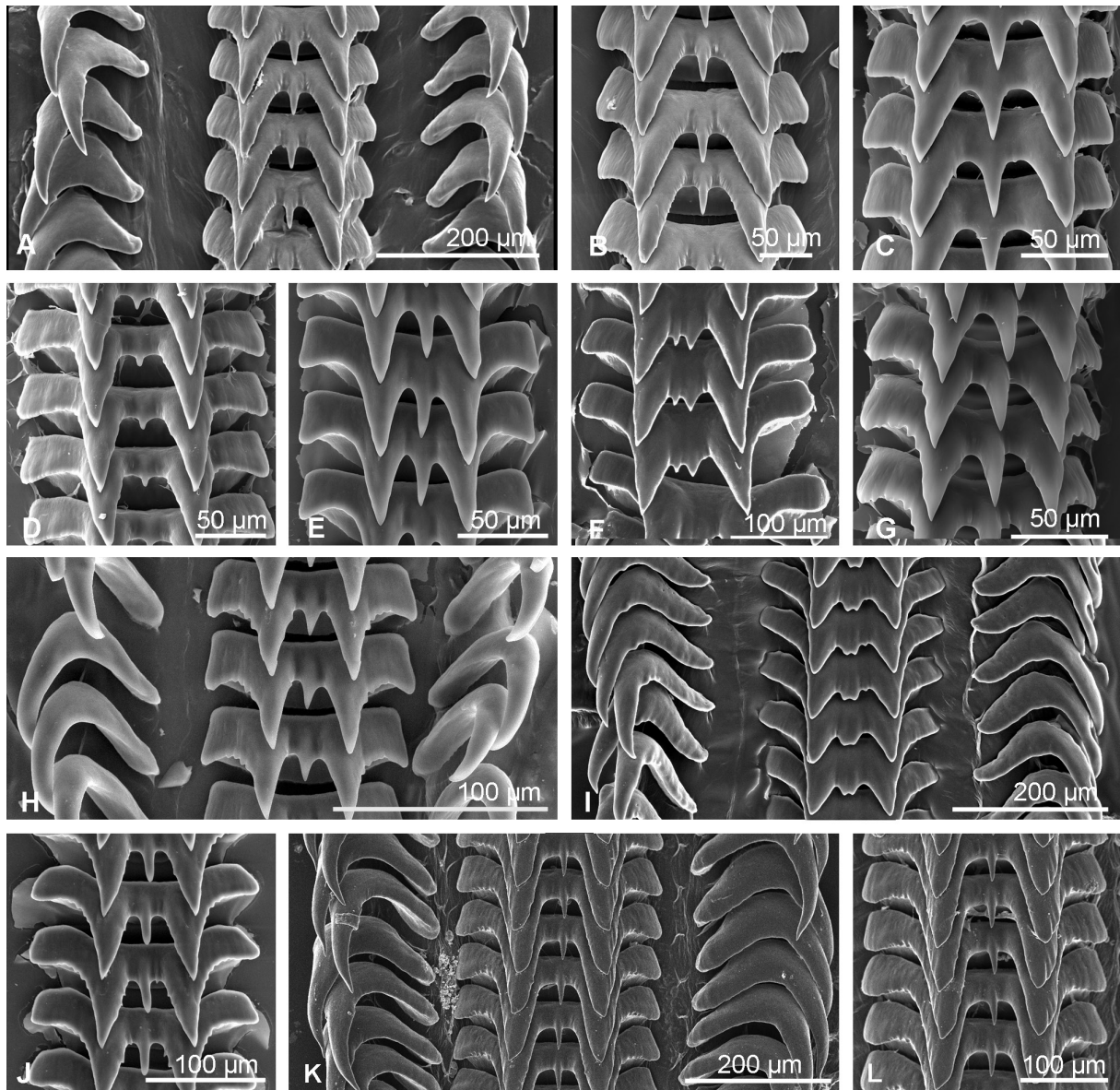


Fig. 7. Radulae of species of *Amalda* H. Adams & A. Adams, 1853. **A–G.** *A. hilgendorfi* (von Martens, 1897). **A–B.** MNHN IM-2019-621 (shell on Fig. 4D). **C.** MNHN IM-2009-11961 (shell on Fig. 4J). **D.** MNHN IM-2013-58045, Papua New Guinea. **E.** MNHN IM-2013-19909, Papua New Guinea. **F.** MNHN IM-2013-63430, southern New Caledonia. **G.** MNHN IM-2007-33312 (shell on Fig. 5F). **H.** *A. aureomarginata* Kilburn & Bouchet, 1988, MNHN IM-2013-63421, specimen not sequenced, southern New Caledonia. **I–J.** *A. miriky* sp. nov. **I.** Miriky, stn CP3210, specimen not sequenced, Madagascar. **J.** Miriky, stn DW3215 (shell on Fig. 10J). **K–L.** *A. cacao* sp. nov., holotype, MNHN IM-2000-35296 (shell on Fig. 11A–E).



Fig. 8. A–H. *Amalda aureomarginata* Kilburn & Bouchet, 1988, southern New Caledonia. A–C. Holotype, MNHN IM-2000-1345, SL 34.1 mm. D. MNHN IM-2007-43644, SL 26.6 mm. E. MNHN IM-2007-43655, SL 31.5 mm. F. MNHN IM-2007-43551, SL 30.5 mm. G–H. MNHN IM-2007-43654, SL 28.2 mm. I–J. *A. hilgendorfi* (von Martens, 1897), MNHN IM-2009-11968, northern New Caledonia, SL 31.6 mm. Shells at the same scale; H, J=enlarged upper part of the shell. Arrow on H points at dark brown line, bordering secondary spire callus.

Pins; 22°51' S, 167°12' E; 340–381 m deep; NORFOLK 1; stn DW1738 • ca 30 lv and dd; SW of Île des Pins; 22°51' S, 167°14' E; 404–448 m deep; NORFOLK 1; stn DW1739 • 1 dd, Île des Pins; 22°43' S, 167°16' E; 245–300 m deep; NORFOLK 2; stn DW2150 • 30 dd; Île des Pins; 22°52' S, 167°13' E; 453–

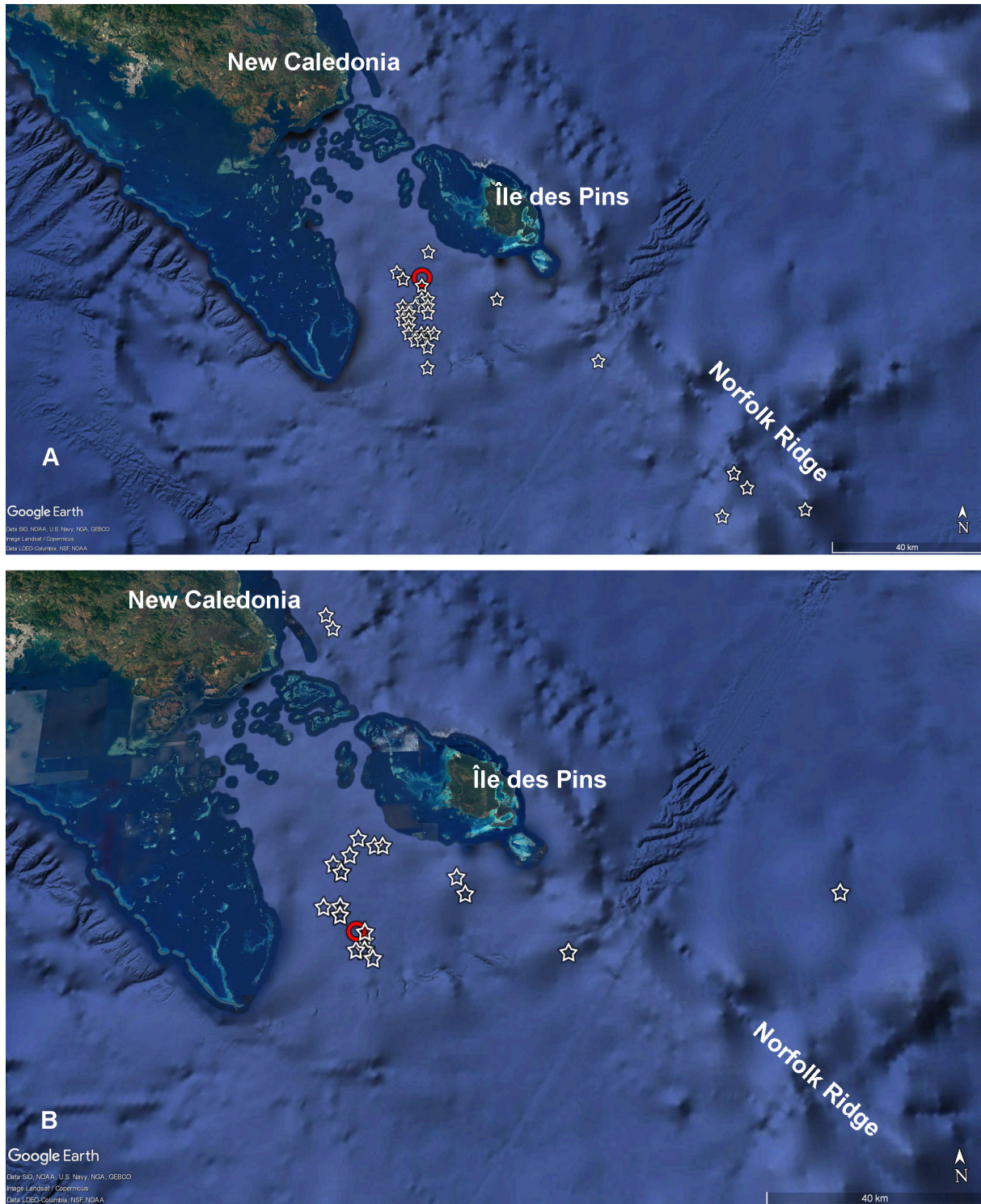


Fig. 9. Distribution map of *Amalda aureomarginata* Kilburn & Bouchet, 1988 (A) and *A. fuscolingua* Kilburn & Bouchet, 1988 (B) off southern New Caledonia. Red circles = the type localities; stars = indicate stations where the species were recovered.

455 m deep; NORFOLK 2; stn DW2155 • 1 lv juv; SW of Île des Pins; 22°48' S, 167°15' E; 449–465 m deep; KANACONO; stn DW4697 • 1 lv juv; S of Île des Pins; 22°59' S, 167°43' E; 494–508 m deep; KANACONO; stn DW4746; MNHN-IM-2013-63421.

Description

MEASUREMENTS. Small to medium-sized (SL up to 34.5 mm).

SHELL. Rather narrow, ovate-fusiform, with narrow base and high, acutely conical spire. First protoconch whorl diameter 0.88–0.94 mm (mean 0.91, n=5). Primary spire callus thick, covering all except protoconch and one or two teleoconch whorls, secondary callus forming fairly thin, linguiform pad, extending to second last suture. Plication plate with 4–7 ridges, sometimes bifid. Olivoid groove rather shallow, labral denticle very weak. Upper anterior band weakly convex, nearly flat, may be slightly thickened at rear edge of anterior band. Lower anterior band flat, smooth. Colour light yellowish-brown with paler olivoid band, spire callus with orange-yellow lower band, bordered abapically by narrow light line and creamy upper band with purple tint. Adapically primary callus with narrow but distinct brown borderline. Parietal callus thick, typically purplish-pink. Upper anterior band yellowish orange, lower anterior band and plication plate white.

RADULA (Fig. 7H). With simple rather thin hook-shaped lateral teeth and tricuspid central teeth with central cusp smallest. Outer lower edges of outer cusps serrated.

Remarks

The radula of a specimen illustrated by Kilburn & Bouchet (1988: figs 52–56) is rather similar to ours, but the lateral cusps of the central tooth with serrated inner edges as well.

Kilburn & Bouchet (1988) recognized three local forms: typical (south New Caledonia), Chesterfield (Coral Sea) and northern New Caledonia form, the latter two characterized by a broader oval shell and details of colouration. A molecular analysis, however, revealed that the specimens identified as these two latter forms are in fact subadults of *A. hilgendorfi* (see Fig. 8I). They differ from *A. aureomarginata* by the absence of a characteristic reddish-purple or purplish-pink upper part of the parietal callus and the median part of the primary spire callus. Another stable difference is that in *A. aureomarginata*, the upper limit of the secondary callus is bordered by a narrow distinct brown band (arrow on Fig. 8H), which is not present in *A. hilgendorfi*. The specimen of *Amalda* cf. *aureomarginata* from the Chesterfields illustrated by Gratecap (2014) is *A. hilgendorfi*.

Distribution

The confirmed distribution is confined to southern New Caledonia (Fig. 9A), in a limited area off Île des Pins approximately 40 × 30 km, with a few records from adjacent Norfolk Ridge localities. Depth range 305–541 m.

Amalda miriky sp. nov.

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Figs 7I–J, 10

“form or subspecies” of *A. hilgendorfi* occurring off Madagascar – Kilburn 1996: 25.

Amalda cf. *hilgendorfi* – Gratecap 2016b: 4, 12, fig. 5.

Diagnosis

Shell large, up to 53 mm, fusiform, with large dome-shaped protoconch (diameter of first whorl ca 1.25 mm). Primary and secondary calluses very densely and distinctly microshagreened. Olivoid groove very shallow and indistinct. Anterior band separated by distinct fasciolar ridge into upper and twice more narrow lower bands. Upper anterior band has distinct ridge rounded on top. Body whorl cloak from light yellow to light orange, olivoid band pale, upper anterior band orange-brown, lower anterior band and plication plate white. Primary callus orange-brown, spire whorls with slight bluish tint. Protoconch of same colour as primary callus.

Etymology

The species is named after the expedition, itself named after the fishery boat on which the survey was conducted. Used as a noun in apposition.

Type material

Holotype

MADAGASCAR • off NW Madagascar between Nosy-Be and Banc du Leven; 12°38' S, 48°14' E; 420–436 m deep; MIRIKY; stn CP3183; MNHN IM-2007-36868 (sequenced).

Material examined

Sequenced material

13 sequenced specimens (Table 1).

Not sequenced material

OFF NW MADAGASCAR • 5 lv; between Nosy-Be and Banc du Leven; 12°36' S, 48°16' E; 331–364 m deep; MIRIKY; stn CP3182; MNHN IM-2007-36899, MNHN IM-2007-36879, MNHN IM-2007-36852, MNHN IM-2007-36869, MNHN IM-2007-36857 • 38 lv, 10 dd; 12°38' S, 48°14' E; 420–436 m deep; MIRIKY; stn CP3183; 1 lv specimen with registration MNHN IM-2007-36881 • 2 lv; 1 dd; 12°40' S, 48°12' E; 492–524 m deep; MIRIKY; stn CP3184 • 8 lv; 12°31' S, 48°22' E; 298–301 m deep; MIRIKY; stn CP3188; 2 lv specimens with registration MNHN IM-2007-38032, MNHN IM-2007-36934 • 22 lv; 11 dd; 12°30' S, 48°18' E; 346–376 m deep; MIRIKY; stn CP3189 • 1 dd; 12°43' S, 48°14' E; 291–353 m deep; MIRIKY; stn CP3209 • 2 lv, 1 dd; 12°44' S, 48°12' E; 442–491 m deep; MIRIKY; stn CP3210 • 4 dd; 12°32' S, 47°52' E; 244–300 m deep; MIRIKY; stn DW3211 • 6 lv, 6 dd; 12°34' S, 47°54' E; 367–369 m deep; MIRIKY; stn DW3212; 2 lv with registration MNHN IM-2007-38051; MNHN IM-2007-36682 • 5 lv, 6 dd; 12°31' S, 47°52' E; 262–289 m deep; MIRIKY; stn DW3213 • 4 lv, 2 dd; 12°33' S, 47°52' E; 302–327 m deep; MIRIKY; stn DW3214 • 14 lv, 9 dd; 12°32' S, 47°54' E; 316–433 m deep; MIRIKY; stn DW3215 • 4 lv, 2 dd; 12°34' S, 47°52' E; 296–350 m deep; MIRIKY; stn DW3216; 3 lv; MNHN IM-2007-38073; MNHN IM-2007-38074; MNHN IM-2007-36669 • 2 lv, 1 dd; 12°33' S, 47°56' E; 391–438 m deep; MIRIKY; stn DW3217 • 1 lv; 12°46' S, 48°12' E; 355–380 m deep; MIRIKY; stn CP3224 • 4 lv; 12°55' S, 48°11' E; 260–319 m deep; MIRIKY; stn DW3228 • 1 dd; West of Cap d'Ambre; 12°08' S, 48°53' E; 496–501 m deep; MIRIKY; stn DW3195 • 6 dd; 12°07' S, 48°58' E; 362–431 m deep; MIRIKY; stn DW3197 • 1 dd; 12°06' S, 48°57' E; 527–652 m deep; MIRIKY; stn DW3199.

Description (holotype)

MEASUREMENTS. SL 39.6 mm, AL 19.2 mm, SW 14.9 mm.

SHELL. Shell fusiform with relatively broad base, SW/SL 0.37; body whorl evenly convex on right side, very slightly drawn in at olivoid groove, evenly convex on left side, greatest width of body whorl median. Protoconch (Fig. 10D–E) large, broadly domed, first 0.75 whorls with distinct impressed suture, further

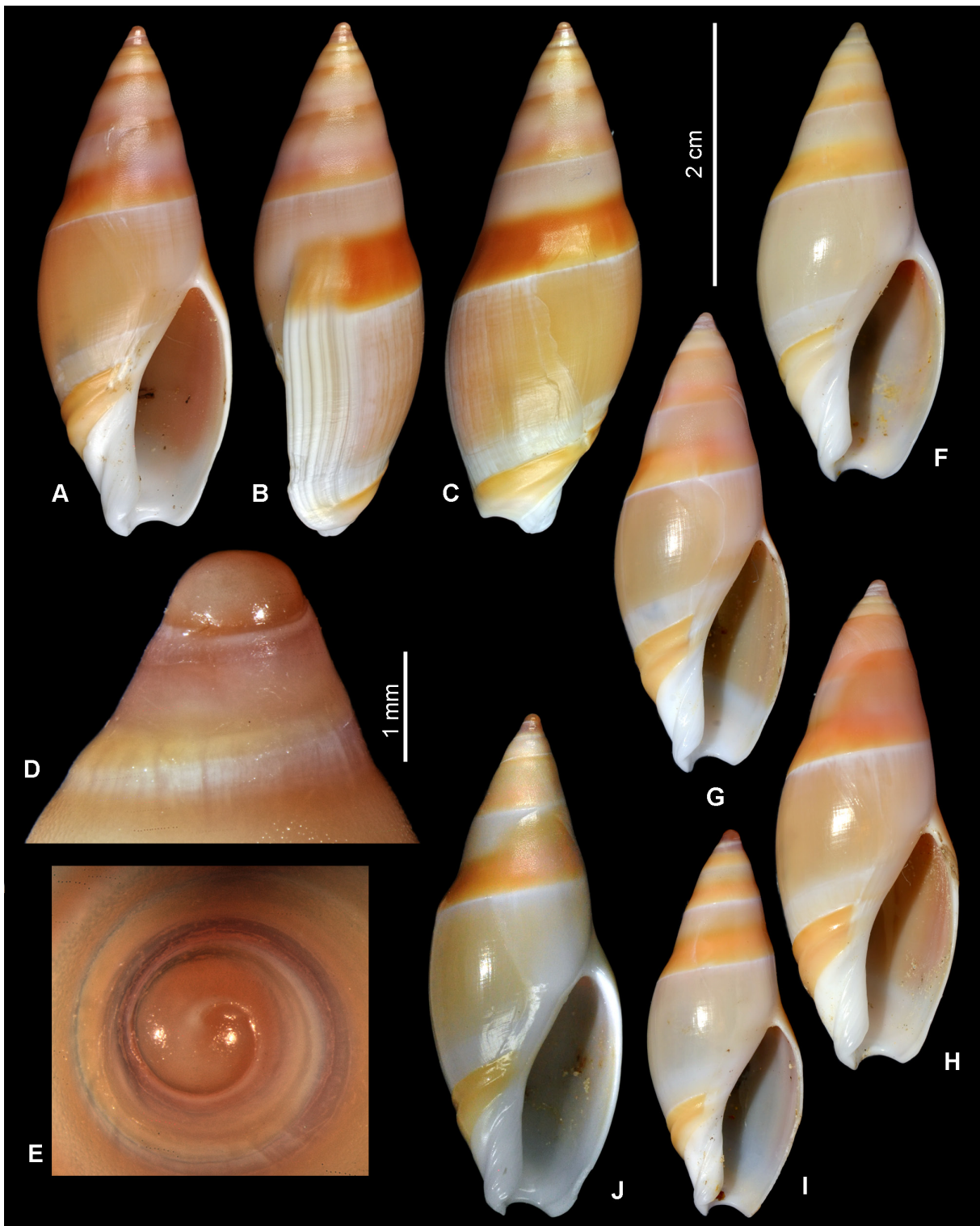


Fig. 10. *Amalda miriky* sp. nov., Madagascar. A–E. Holotype, MNHN IM-2007-36868, SL 39.6 mm (D–E=enlarged lateral and apical views of the protoconch). F. MNHN IM-2007-38073, SL 35.8 mm (specimen not sequenced). G. MNHN IM-2007-36842, SL 35.7 mm. H. MNHN IM-2007-36866, SL 37.9 mm. I. MNHN IM-2007-38064, SL 30 mm. J. Miriky, stn DW3215, between Nosy-Be and Banc du Leven, 12°32' S, 47°54' E, 316–433 m, SL 38.9 mm (specimen not sequenced, radula on Fig. 7J). Scale bars: A–C, F–J= 2 cm; D–E = 1 mm.

suture overlaid by callus. Protoconch borders indistinct, rendering whorl count impossible. Diameter of first whorl 1.23 mm. Spire high, conical; primary callus not thick and covering all whorls except protoconch, slightly impressed at sutures; surface of callus weakly glossy, very densely and distinctly microshagreened; secondary callus very thin, extending to right-ventral side of last whorl and continuing up as fairly thin, tongue-shaped pad, reaching suture of antepenultimate whorl. Surface of secondary callus very similar to that of primary one, borders indistinct. Body whorl cloak glossy, covered by microscopic, dense, wavy striae. Olivoid groove very shallow and indistinct, its presence detected by different colours of body whorl cloak and olivoid band rather than by actual depression of surface. Rear edge of anterior band very sharp and distinct. Anterior band strongly microshagreened, mat, and separated into upper (broader) and lower bands by distinct fasciolar ridge. Broader upper anterior band with distinct ridge rounded on top. Lower anterior band nearly flat, nearly twice narrower than upper band. Plication plate with deep and broad groove in upper third, separating adapical largest spiral ridge, followed by another deep groove and four spiral ridges progressively weakening abapically. Columella with indistinct spiral ridges visible as far as rear edge of anterior band. Aperture narrow oval, acute posteriorly, widest medially; outer lip rather thin, in side view very slightly opisthoclinal, nearly concave, with slight, blunt labral denticle not exactly corresponding to olivoid groove; siphonal notch shallow, symmetrically U-shaped. Body whorl cloak light orange, olivoid band light yellow, upper anterior band orange-brown, lower anterior band and plication plate white. Primary callus orange-brown, similar in tint, but slightly darker than anterior band, abapically to primary callus very narrow whitish spiral band, spire whorls with slight bluish tint. Protoconch of same colour as primary callus. Outer lip inside and lower part of aperture white, aperture inside light pinkish.

RADULA (n=2, not sequenced). Lateral teeth simple, thin, hook-shaped. Central teeth tricuspid, with central cusp much thinner and smaller than lateral ones (Fig. 7J). Lateral cusps with serrated sides. In one specimen central cusp subdivided into two very small cusplets (Fig. 7I), lateral cusps with smooth edge.

Remarks

The species, which may reach 53.4 mm, is variable in shell slenderness and colouration. The holotype is an average dark specimen, while some specimens are much lighter; some specimens may also have a distinct purplish tint on the secondary callus.

Molecular analysis clearly demonstrates that this is a separate species, although there is a morphological similarity with *A. hilgendorfi*. Both species are reliably distinguished by the protoconch: in *A. miriky* sp. nov. it is much larger (first protoconch whorl diameter of more than 1.2 mm vs 0.75–0.92 mm in *A. hilgendorfi*). Another somewhat similar species from the western Indian Ocean is *A. trippneri* Kilburn, 1996 from Saya de Malha Bank, depth unknown. The latter differs from *A. miriky* sp. nov. in its more narrow shell with much taller spire, the presence of the spiral lirae on the spire, as well as indistinct, rather deep, olivoid groove. In general outline and colour, *Amalda miriky* sp. nov. is also similar to *A. hayashii* Ninomiya, 1988, differing in exposed protoconch, not covered by callus, by a narrower olivoid band, by completely white plication plate and by more slender shell.

Distribution

North-western Madagascar, alive in 289–760 m.

Amalda cacao sp. nov.

[urn:lsid:zoobank.org:act:CE4694EC-3B8F-40C8-819D-F62DAFEF2AD9](https://doi.org/10.21203/rs.3.rs-1000000)

Figs 7K–L, 11

Amalda hilgendorfi richeri, partim – Kilburn & Bouchet 1988: 288, figs 23–24 (labelled as paratype, but not listed in text under type material).

Amalda cf. *hilgendorfi richeri* – Gratecap 2014: 14, 19, figs 24–25.

Diagnosis

Shell large, up to 75 mm, fusiform, with turreted whorls and small broadly dome shaped protoconch (diameter of first whorl ca 0.7 mm). Primary and secondary calluses distinctly microshagreened. Border between primary callus and cloak of body whorl very distinct with thin lighter line. Olivoid groove very shallow, obsolete on most part of last whorl. Anterior band separated by distinct fasciolar ridge into upper and slightly narrower lower bands. Upper anterior band with distinct triangular in section ridge. Body whorl cloak chestnut on apertural side and lighter on dorsal side, with axial lines alternating in colour; olivoid band and adjoining narrow zone of cloak of body whorl white, anterior band chestnut brown, plication plate white with weak yellowish spiral band. Primary and secondary calluses dark chocolate brown, parietal pad light, with bluish tint. Protoconch white.

Etymology

The species name refers to the chocolate colour of the shell. Used as a noun in apposition.

Type material

Holotype

CORAL SEA • Lord Howe Ridge, Nova Bank; 22°25' S, 159°13' E; 315 m deep; MUSORSTOM 5; stn CP320; not sequenced; MNHN IM-2000-35296.

Material examined

Sequenced material

CORAL SEA • 1 lv; Nova Bank; 22°17' S, 159°27' E; 360–370 m deep; EBISCO; stn DW2533; MNHN IM-2007-33287.

Not sequenced material

CORAL SEA • 1 dd; Kelso Bank; 24°06' S, 159°41' E; 295–310 m deep; EBISCO; stn DW2514 • 1 dd; Nova Bank; 22°07' S, 159°25' E; 487–610 m deep; MUSORSTOM 5; stn DW301 • 1 dd; Nova Bank; 22°10' S, 159°26' E; 385–420 m deep; MUSORSTOM 5; stn DW304 • 1 dd; Kelso Bank; 24°12' S, 159°41' E; 270–385 m deep; KANADEEP 1; stn DW4940 • 1 dd; Capel Bank; 25°29' S, 159°49' E; 310–320 m deep; KANADEEP 1; stn DW4951 • 1 dd; Argo Bank; 23°08' S, 159°31' E; 280 m deep; KANADEEP 1; stn DW4958.

SOUTHERN NEW CALEDONIA – **Norfolk Ridge** • 1 dd; Kaimon Maru Bank; 24°44' S, 168°09' E; 227–232 m deep; NORFOLK 1; stn CP1676 • 1 dd worn; 24°45' S, 168°08' E; 233 m deep; SMIB 3; stn DW08.

Description (holotype)

MEASUREMENTS. SL 74.9 mm, AL 40.0 mm, SW 29.3 mm.

SHELL. Shell fusiform with relatively narrow base, SW/SL 0.39; body whorl evenly convex on right side, evenly convex on periphery and shell base on left side, slightly concave subsuturally, greatest

width of body whorl median. Protoconch (Fig. 11D–E) small, broadly domed, first 1.5 whorls with distinct impressed suture, suture further overlaid by callus. Limit of protoconch indistinct, rendering whorl count impossible. Diameter of first whorl 0.68 mm. Spire high, turreted; primary callus not thick and covering all whorls except protoconch and uppermost teleoconch whorls, distinctly impressed on suture; surface of callus glossy, distinctly microshagreened, more dense in suture areas. Secondary callus very thin, forming distinct thickened pad on parietal wall, extending to right ventral side of last whorl and continuing up to form a fairly thin, tongue-shaped pad, reaching suture of antepenultimate

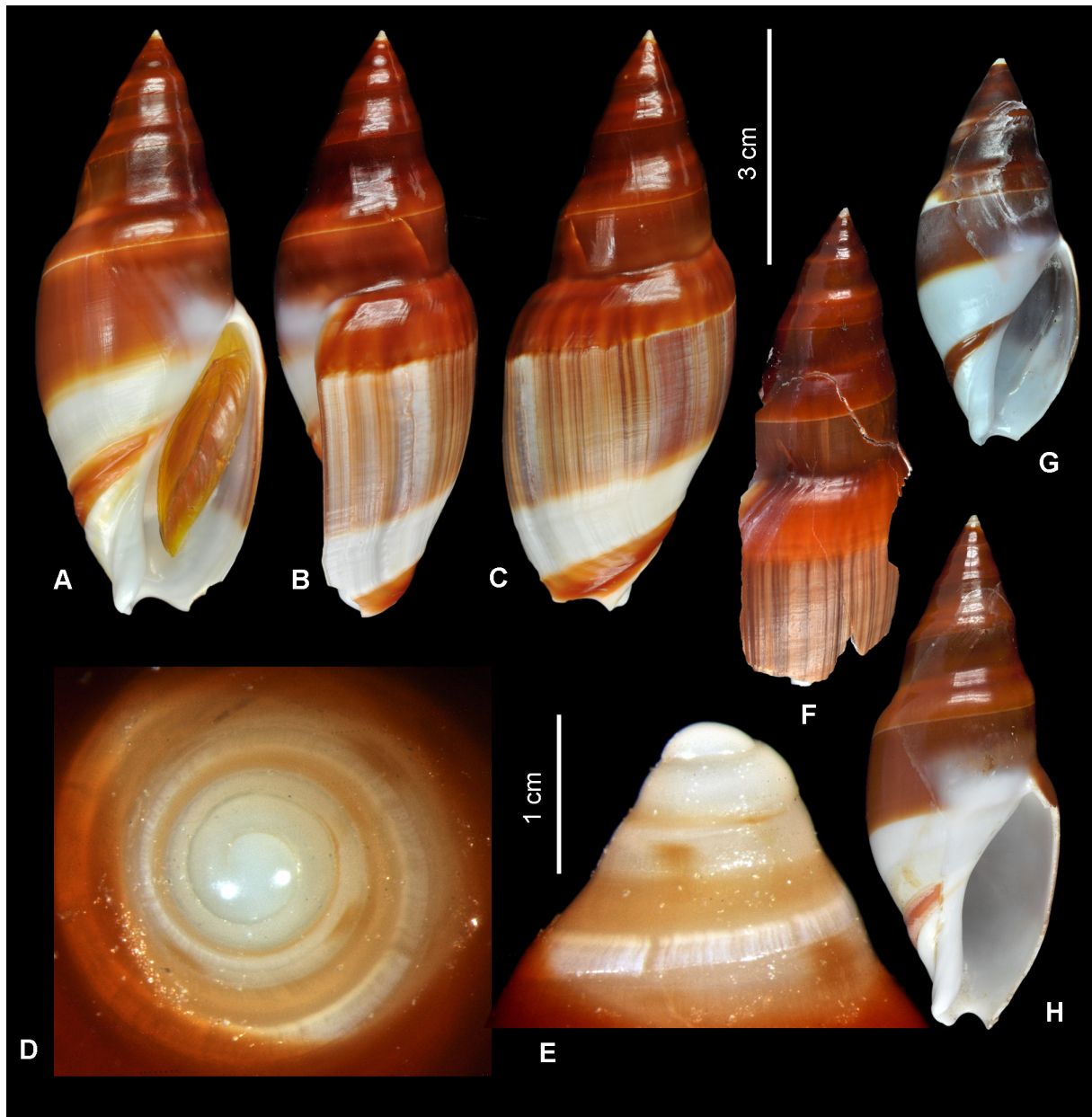


Fig. 11. *Amalda cacao* sp. nov. A–E. Holotype, MNHN IM-2000-35296, SL 74.9 mm (D–E=enlarged apical and lateral views of the protoconch), specimen not sequenced. F. MNHN IM-2007-33287, SL 61 mm, sequenced specimen. G. KANADEEP 1, stn DW4951, 25°29' S, 159°49' E, 310–320 m, Capel Bank, SL 50 mm, specimen not sequenced. H. NORFOLK 1, stn CP1676, 24°44' S, 168°09' E, 227–232 m, Norfolk Ridge, SL 67.1 mm, specimen not sequenced. Shells at the same scale.

whorl. Surface of secondary callus very similar to that of primary one, its borders indistinct. Body whorl cloak glossy, covered by indistinct spiral riblets of variable width. Olivoid groove very shallow, obsolete on most part of last whorl and present on last 1/3 whorl. Rear edge of anterior band very sharp and distinct near columella, becoming blurred and sinuous on dorsal side of last whorl towards aperture lip. Anterior band subdivided in upper and lower anterior bands by distinct, step-like, fasciolar ridge. Upper anterior band slightly broader, with distinct, nearly median, additional ridge, triangular in section. Lower anterior band nearly flat. Plication plate with shallow, rather broad, median groove. No ridges on plication plate and columella. Aperture narrow oval, acute posteriorly, widest in its lower third; outer lip thin, very slightly opisthoclinal in sideview, weakly concave, without visible labral denticle; siphonal notch shallow, symmetrically U-shaped. Body whorl cloak chestnut on apertural side and lighter on dorsal side, with axial lines alternating in colour, corresponding to growth lines; olivoid band and adjoining narrow zone of body whorl cloak white, anterior band chestnut brown, plication plate white with weak yellowish spiral band. Primary and secondary calluses dark chocolate brown, parietal pad light, with bluish tint. Protoconch white. Outer lip with broad spiral brownish band, corresponding to cloak, white deeper inside.

OPERCULUM. Large, spanning most of aperture, lanceolate, with subterminal nucleus near lower operculum edge.

RADULA (holotype) (Fig. 7K–L). Lateral teeth thick, hook-shaped. Central teeth strongly overlapping, tricuspid, with broad lateral flaps. Lateral cusps and lateral flaps with several distinct grooves on outer side, flattened and broad. Central cusp narrow, sharp, much shorter than lateral ones.

Remarks

This very distinct species differs from most other known species of *Amalda* in the combination of its dark brown colour and a rather broad shell with high turreted spire. In colour pattern, it resembles specimens of *Amalda raoulensis* Powell, 1967 illustrated by Hart (1995) from about 100 m depth on Colville Ridge off the North Island of New Zealand, but the latter differs in having a smaller (up to 56 mm) shell with a relatively lower spire. It should be mentioned that the holotype of *Amalda raoulensis* is a beach worn faded specimen with a very strong, callused, peripheral spiral keel which dominates the shell appearance (Powell 1967), and the conspecificity of the specimens illustrated by Hart (1995) with the types of *Amalda raoulensis* needs confirmation.

The shell of the only sequenced specimen of *A. cacao* sp. nov. is broken into pieces, but the intact upper teleoconch whorls (Fig. 11F) are identical to the holotype, leaving no doubt on their conspecificity. Kilburn & Bouchet (1988) considered it to be a colour variant of *Amalda hilgendorfi richeri*, but *Cox1* data clearly indicate that it is a separate species.

Distribution

Live collected in the Coral Sea; dead specimens also known from Kaimon Maru Bank on Norfolk Ridge. Depth range: alive at 315–360 m, empty shells at 227–487 m.

Amalda montrouzieri (Souverbie, 1860)

Figs 12, 13A–C, 14A–B, 17C–D

Ancillaria montrouzieri Souverbie, 1860a: 207.

Ancillaria montrouzieri – Souverbie 1860b: 324, pl. 11 fig. 3. — Reeve 1864: pl. 4 fig. 9.

Amalda montrouzieri – Kilburn & Bouchet 1988: 278–281, figs 1–8, 38–39, 51, 53. — Gratecap 2014: 13, 18, figs 1–4.

Type material

Syntypes

NEW CALEDONIA • 1 shell; “Insul. Lifu? (Loyalty). Insul. Art?” [Souverbie 1860a]; Île des Pins [Souverbie 1860b]; MNHN IM-2000-1367 • 3 shells; same collection data as for preceding; MNHN IM-2000-1475 (Fig. 12A–C).

Material examined

Sequenced material

SOUTHERN NEW CALEDONIA • 1 lv; Baie du Prony; 12–18 m deep; MNHN IM-2013-80199.

Not sequenced material

Material mentioned in Kilburn & Bouchet (1988), about 50 lots, 110 specimens.

Description

MEASUREMENTS. Shell medium in size (SL up to 41.5 mm, usually less than 30 mm).

SHELL. Ovate-fusiform, with a cyrtconoid spire. Primary spire callus thick, weakly microshagreened, covering all whorls, including most of protoconch rendering measurements inaccurate, and with weak spiral lirae (8–10 on penultimate whorl). Secondary callus medium thick, forming extensive pad on right side of spire. Plication plate with 2–4 (usually 3) ridges. Olivoid groove from shallow to rather deep, labral denticle weak, obtuse. Upper anterior band very weakly convex, nearly flat. Lower anterior band flat, smooth. Colour from uniformly white, to chestnut brown. In darker coloured specimens, primary spire callus and upper anterior band darker, olivoid band lighter than body whorl cloak, plication plate white.

RADULA (n=2, not sequenced) (Fig. 13A–C). Very similar in these two. Central tooth tricuspid, with central cusp $\frac{1}{3}$ smaller than lateral ones. All cusps, as well as lateral flaps of central tooth, with irregular distinct serration.

LIVE SPECIMENS (Fig. 14A–B). With truncated and notched posteriorly foot. Parapodia opaque, greyish, with scarce slightly darker speckles, can completely envelop shell. Propodium, anterior part of parapodia and siphon with more dense speckles.

Remarks

The species is quite variable in shell shape and particularly in colouration, with many specimens pure white or with lightly coloured secondary callus (e.g., Fig. 12F, I). The syntypes are the largest examined specimens. Kilburn & Bouchet (1988: 281) mentioned the existence of “a puzzling morph which is uniformly different in shape (although there are indications of intergradation in this regard) and in its faint ancillid (=olivoid) groove” at larger depths (175–420 m) (Fig. 12J–K). This morph differs from *A. montrouzieri* and *A. alabaster* sp. nov. in its narrower shell with taller spire. It may represent a peculiar morph of *A. alabaster* sp. nov. or a separate species.

Distribution

Southern New Caledonia. *Amalda montrouzieri* is normally distributed at depths of 10–70 m, with specimens occasionally collected down to 130 m; a few empty shells were collected at even larger depths, down to 280 m (SMIB 3, stn DW20). Kilburn & Bouchet (1988) cited some extralimital records, mostly on the basis of published records, namely the Loyalty Islands, Fiji, the Ryukyu Islands, and the Philippines. These records should be confirmed with molecular data.



Fig. 12. *Amalda montrouzieri* (Souverbie, 1860), southern New Caledonia. **A–C.** Syntype MNHN IM-2000-1475, SL 41.4 mm. **D–E.** MNHN IM-2013-80199, SL 18.7 mm (sequenced specimen). **F.** Secteur Île Ouen-Baie du Prony, LAGON, stn DW98, 22°35.7' S, 166°31.8' E, 15 m, SL 25.6 mm. **G.** Grand Récif Sud, LAGON, stn DW334, 22°38' S, 166°53.6' E, 47–48 m, SL 26.6 mm (illustrated by Kilburn & Bouchet 1988: fig. 14). **H.** Secteur de Nouméa. LAGON, stn DW51, 22°14.7' S, 166°11.1' E, 10 m, SL 27.6 mm. **I.** Grand Récif Sud, LAGON, stn DW544, 22°50.8' S, 166°48.5' E, 25 m, SL 25.4 mm. **J–K.** *A. cf. montrouzieri*. Deep-water morph, SMIB2, stn DW23, 22°31' S, 167°37' E, 410–420 m, SL 30.2 mm (specimen illustrated by Kilburn & Bouchet 1988: figs 5–6). All specimens except D–E not sequenced. Shells at the same scale.

Amalda alabaster sp. nov.

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Figs 13D–E, 15

Diagnosis

Shell small, up to 27 mm, ovate fusiform, with low broad conical spire and small low dome shaped protoconch (diameter of first whorl ca 0.8 mm). Primary callus smooth, shallowly impressed on left side at last whorl suture, secondary callus weakly microshagreened. Olivoid groove very shallow and indistinct. Anterior band separated by distinct fasciolar ridge into upper and slightly broader lower bands. Colour uniformly white.

Etymology

The specific epithet refers to the white and semitransparent shell. Used as a noun in apposition.

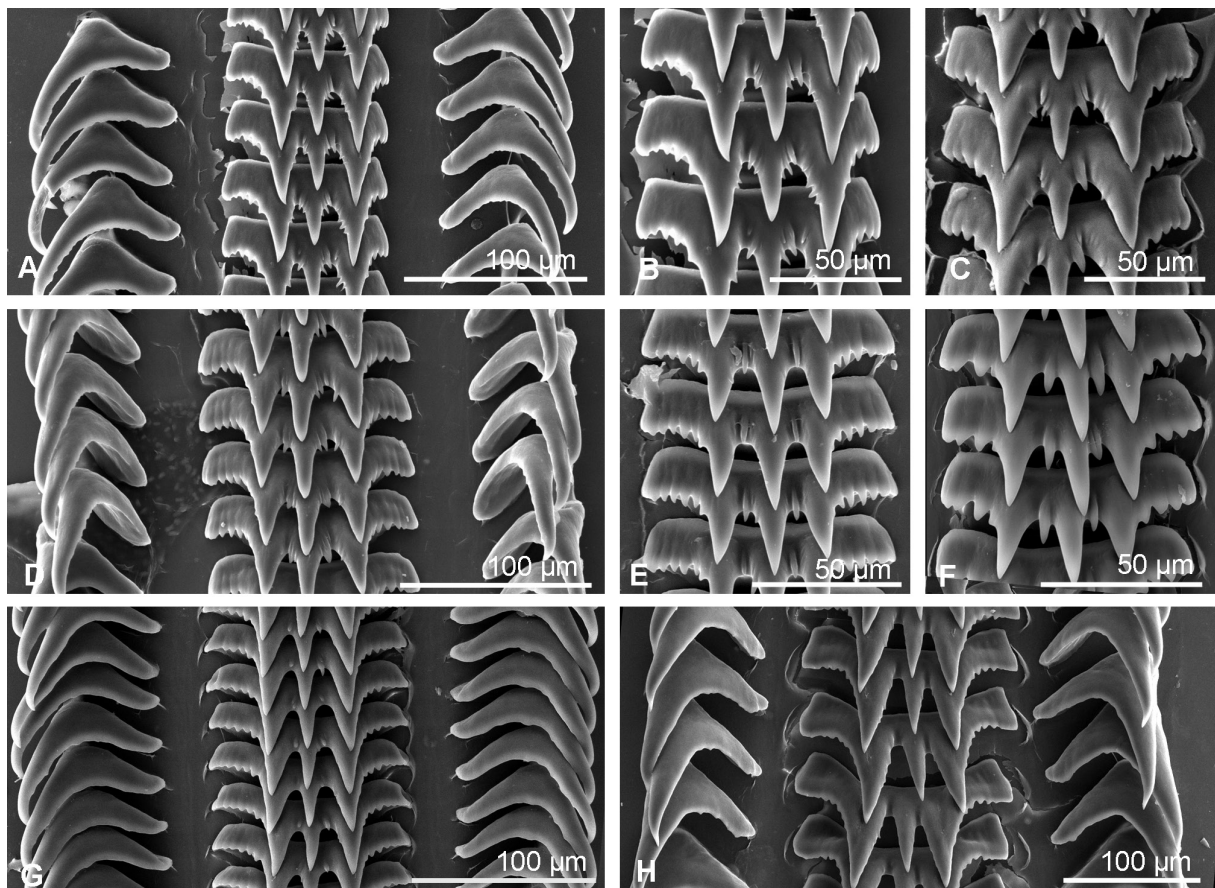


Fig. 13. Radulae of species of *Amalda* H. Adams & A. Adams, 1853. **A–C.** *A. montrouzieri* (Souverbie, 1860). **A–B.** Île Ouen – Baie du Prony, LAGON, stn DW239, 22°24.3' S, 166°57.8' E, 42–43 m, SL 20.2 mm. **C.** Grand Récif Sud, LAGON, stn DW544, 22°50.8' S, 166°48.5' E, 25 m, SL 25.4 mm (shell on Fig. 12I). **D–E.** *A. alabaster* sp. nov. **D.** Holotype, MNHN IM-2007-43627, SL 26.7 mm (shell on Fig. 15A–B). **E.** MNHN IM-2007-43636, SL 17.6 mm. **F.** *A. cf. alabaster*, MNHN IM-2013-63897, SL 18.1 mm (shell on Fig. 15H–I). **G.** *A. allaryi* Bozzetti, 2007, MNHN IM-2013-68272 (shell on Fig. 17A). **H.** *A. coriolis* Kilburn & Bouchet, 1988, MNHN IM-2013-63899 (shell on Fig. 18H–I).



Fig. 14. A–B. Live specimens of *Amalda montrouzieri* (Souverbie, 1860), Nouméa, 8 m. C–E. Shell and live specimen of *A. herberti* Cossignani, 2013, Nouméa, South Lagoon, about 250 m. Photos courtesy of David Massemin.

Type material

Holotype

SOUTHERN NEW CALEDONIA • 22°06' S, 167°03' E; 190–200 m deep; TERRASSES; stn DW3093; MNHN IM-2007-43627; sequenced.

Material examined

Sequenced material

9 sequenced specimens (Table 1).

Not sequenced material

NEW CALEDONIA • 1 lv; type locality; IM-2007-43633 • 3 lv; Bassin des Loyauté; 21°45' S, 166°37' E; 253–266 m deep; HALIPRO1; stn CP852 • 3 dd; 17 lv; 21°45' S, 166°37' E; 241–250 m deep; HALIPRO1; stn CP853 • 6 dd; east coast of mainland New Caledonia; 21°48' S, 166°41' E; 239–250 m deep; BATHUS 1; stn DW649 • 8 dd; 21°48' S, 166°41' E; 264–269 m deep; BATHUS 1; stn DW650 • 5 dd; 21°17' S, 165°57' E; 237–298 m deep; BATHUS 1; stn DW654 • 42 lv; 4 dd; 21°45' S, 166°37' E; 250 m deep; BATHUS 1; stn CP713.

Description (holotype)

MEASUREMENTS. SL 26.7 mm, AL 13.5 mm, SW 10.7 mm.

SHELL. Small, ovate fusiform with relatively broad base, SW/SL 0.40; body whorl evenly weakly convex on right side, and slightly bulging on left side due to strong callus, greatest width of body whorl median. Protoconch nearly completely covered by callus with part of first whorl exposed, low dome shaped. First protoconch whorl diameter 0.79 mm. Spire low, broadly conical; primary callus thick and covering all whorls except part of protoconch, shallowly impressed on left side at last whorl suture. Surface of callus glossy, smooth, with weak indistinct spiral ridges, secondary callus thick, with distinct anterior border, joining parietal callus without visible border, extending to right ventral side of last whorl and continuing up to form a thick, tongue-shaped pad that reaches suture of antepenultimate whorl. Surface of secondary callus weakly shagreened. Body whorl cloak weakly glossy, smooth, not microshagreened. Olivoid groove very shallow and indistinct, terminating in short, broadly triangular, labral denticle. Rear edge of anterior band very sharp and distinct. Anterior band subdivided into upper and lower parts by distinct fasciolar ridge. Both upper and lower bands very weakly evenly convex, nearly flat. Plication plate with deep and broad groove at upper third, separating adapical largest spiral ridge, and two slightly smaller ridges similar in size. Columella smooth. Aperture irregularly oval, rounded posteriorly due to callus, widest medially; outer lip medium thick, orthocline in side view, nearly straight, with slight, blunt labral denticle; siphonal notch shallow, symmetrically U-shaped. Colour uniformly white.

RADULA (n=3) (Fig. 13 D–F). Similar in all specimens. Central tooth tricuspid, with central cusp slightly longer than lateral ones. Cusps smooth, but lateral flaps strongly serrated and bearing longitudinal grooves between cusplets. 1–4 additional small cusplets between central and lateral major cusps.

Remarks

All sequenced specimens of *A. alabaster* sp. nov. are very similar to the holotype. In addition to pure white specimens, some are light ivory in colour of the upper teleoconch whorls or even of the entire shell (MNHN IM-2007-43583, Fig. 15C–D).

Conchologically *Amalda alabaster* sp. nov. is extremely similar to white specimens of *A. montrouzieri*. The slight differences may be the more regularly oval outline and the more cyrtocoid spire of *A. montrouzieri*, but those differences are very subtle. The new species is recorded at larger depths than

most of specimens of *A. montrouzieri* (180–210 versus 10–70 m), but *A. montrouzieri* can occasionally occur at the same depths as *A. alabaster* sp. nov.

Although *A. montrouzieri* and *A. alabaster* sp. nov. are closely related, a large genetic distance between them confirms their distinction. Furthermore, there appears to be a minor difference in the radula.



Fig. 15. *Amalda alabaster* sp. nov. **A–B.** Holotype, MNHN IM-2007-43627, SL 26.7 mm. **C–D.** MNHN IM-2007-43583, SL 24.8 mm. **E.** MNHN IM-2007-43621, SL 27.1 mm. **F.** MNHN IM-2007-43626, SL 22.2 mm, specimen not sequenced. **G.** MNHN IM-2007-43633, SL 22 mm, specimen not sequenced. **H–I.** *A. cf. alabaster*, MNHN IM-2013-63897, SL 18.1 mm. Shells at the same scale, all specimens except F–G sequenced.

In *A. montrouzieri* the central cusp of the central tooth is clearly shorter than the lateral ones, but in *A. alabaster* sp. nov. the situation is opposite – the central cusp is distinctly longer. The illustration of the radula of *A. montrouzieri* by Kilburn & Bouchet (1988: figs 51, 53) shows a central tooth with a morphology similar to that in our *A. alabaster* sp. nov. Regrettably, the authors did not present the station data of the specimen from which the radula was extracted and, therefore, it is not clear whether they indeed examined *A. montrouzieri*. All our sequenced specimens originated from only two stations off south and south-eastern New Caledonia at depths of 180–210 m, but numerous non-sequenced specimens (see Material) were collected in the depth range of 237–298 m. Some have a light yellowish spire callus and upper anterior band.

One specimen (MNHN IM-2013-63897, Fig. 15H–I) from a station more to the North on the east coast of New Caledonia is sister to *A. alabaster* sp. nov., with a very high support. Conchologically it differs from *A. alabaster* sp. nov. in having a stouter shell with thicker primary callus and a more pronounced colouration. It may represent a geographical morph (although it was collected very close to the type locality of *A. alabaster* sp. nov.) or even a separate species, but at the moment the lack of additional sequenced material does not allow to draw firmer conclusions. So, we refer to this and similar specimens as *A. cf. alabaster* sp. nov. The ABGD analysis also attributed *A. cf. alabaster* sp. nov. to the same PSH as *A. alabaster* sp. nov.

Distribution

South-eastern New Caledonia, in 180–280 m.

Amalda allaryi Bozzetti, 2007
Figs 13G, 16A–F, 17A–B

Amalda allaryi Bozzetti, 2007: 14, text-fig.

Amalda maritzae Bozzetti, 2007: 15–16, text-fig [possible synonym; see Remarks].

Amalda allaryi – Gratecap 2014: 14, 19, figs 26–27.

Type material

Holotype

NEW CALEDONIA • Holotype of *A. allaryi*; Île des Pins; 250–280 m deep; MNHN IM-2000-20532
• Holotype of *A. maritzae*; “Norol Récifs” [but see below]; 250–280 m deep; MNHN IM-2000-24475.

Material examined

Sequenced material

3 sequenced specimens (Table 1).

Not sequenced material

NEW CALEDONIA • 2 dd; Grand Récif Sud; 22°44' S, 167°19' E; 95–100 m deep; LAGON; stn DW580 • 3 dd; Canal de la Havannah; 22°13' S, 167°07' E; 264–273 m deep; EXBODI; stn CP3788 • 4 dd; Terrasses Sud Est; 22°28' S, 167°29' E; 300–420 m deep; TERRASSES, stn DW3079 • 3 dd; Terrasses Sud Est; 22°06' S, 167°03' E; 190–200 m deep; EXBODI; stn DW3093 • 1 dd; W of Île des Pins; 22°40' S, 167°12' E; 219–244 m deep; KANACONO; stn CP4656 • 1 dd; W of Île des Pins; 22°41' S, 167°02' E; 120–129 m deep; KANACONO; stn DW4727 • 1 dd; S of Île des Pins; 22°47' S, 167°27' E; 244–285 m deep; KANACONO; stn CP4673 • 2 dd; W of Île des Pins; 22°42' S, 167°13' E; 303–315 m deep; KANACONO; stn CP4658 • 1 dd; E of Île des Pins; 22°41' S, 167°41' E; 358–

393 m deep; KANACONO; stn CP4739 • 1 dd; W of Île des Pins; 22°41' S, 167°13' E; 225–250 m deep; KANACONO; stn DW4701 • 5 dd; 1 lv (MNHN IM-2013-68272); SW of Île des Pins; 22°47' S, 167°27' E; 200–290 m deep; KANACONO; stn DW4695 • 13 dd; S of Île des Pins; 22°48' S, 167°29' E; 311–302 m deep; KANACONO; stn CP4674.

Description

SHELL. Large (SL up to 65 mm), ovate-fusiform, with a cyrtocoid spire. Primary spire callus thick, weakly microshagreened, covering all whorls, except 1–1.5 protoconch whorls, thus rendering impossible the whorls count and measurements. First protoconch whorl diameter 0.84–1.02 mm (mean 0.92, n=3). Secondary callus thick, fusing without visible border with parietal callus, with distinct anterior border and reaching antepenultimate whorl. Plication plate with 2–3 ridges, lowest one the weakest, columella smooth. Olivoid groove very shallow, nearly obsolete, labral denticle very small, obtuse. Upper anterior band weakly convex, rear edge of anterior plate distinctly thickened, raised above the surface of upper anterior band, nearly flat. Lower anterior band nearly flat, smooth. Colour from very pale creamy to ivory. Primary callus from light to dark orange or brown, with strongly prosocline lighter axial lines. Secondary callus orange in upper part. Olivoid band slightly lighter than body whorl cloak, upper anterior band of the same colour as cloak, lower anterior band and plication plate white.

RADULA (MNHN IM-2013-68272, Fig. 13G). Central tooth tricuspid, with central cusp slightly narrower and shorter than lateral ones. Cusps smooth, broad lateral flaps strongly serrated and with shallow longitudinal grooves between cusplets. 0–2 additional small cusplets between central and lateral major cusps.

Remarks

Amalda allaryi is very similar to coloured specimens of *A. montrouzieri*, with which it can be sympatric where they bathymetrically overlap. The morphological differences between the two are very subtle and include the generally more obtuse shell apex in *A. allaryi*, reflecting its larger protoconch (Fig. 17A–B), and a more brightly coloured callus, which can be orange-pink (as in our studied specimens) with narrow, dense, strongly prosocline lighter axial lines. In the holotype, though, the callus is much paler, light yellowish-brown. Nevertheless the molecular data confirm the distinctiveness of the two species.

Based on shell characters, Gratecap (2014) considered *A. allaryi* to be a form of *A. montrouzieri*, a conclusion rejected by our molecular data. He also illustrated additional specimens (Gratecap 2014: figs 29 – no locality provided, 30 – Île des Pins at 450 m, 31 – no locality provided) as *A. maritzae*. The latter nominal species, which is known from the holotype only, is very similar to *A. allaryi* (Fig. 16G–H), differing in a larger and heavier shell and minor details of colouration. The stated type locality, “Norol reefs, northward of New Caledonia”, is problematic. The place name “Norol reefs” is absent in New Caledonia, and the handwritten label accompanying the holotype in fact reads “Nord Récifs d’Entrecasteaux”, to the north of New Caledonia, where we have not found *A. allaryi*. The holotype originated from a commercial source and the locality needs confirmation. It may represent a separate species or a disjunct population of *A. allaryi*. In the absence of molecular material, we conditionally synonymize the two species and as first revisers select *A. allaryi* as the valid name.

Distribution

Judging from sequenced and dead collected material, *Amalda allaryi* inhabits a narrow perimeter near Île des Pins at depths of 90 to 250–280 m (holotype) that lies completely within the range of *A. montrouzieri* (5–280 m).

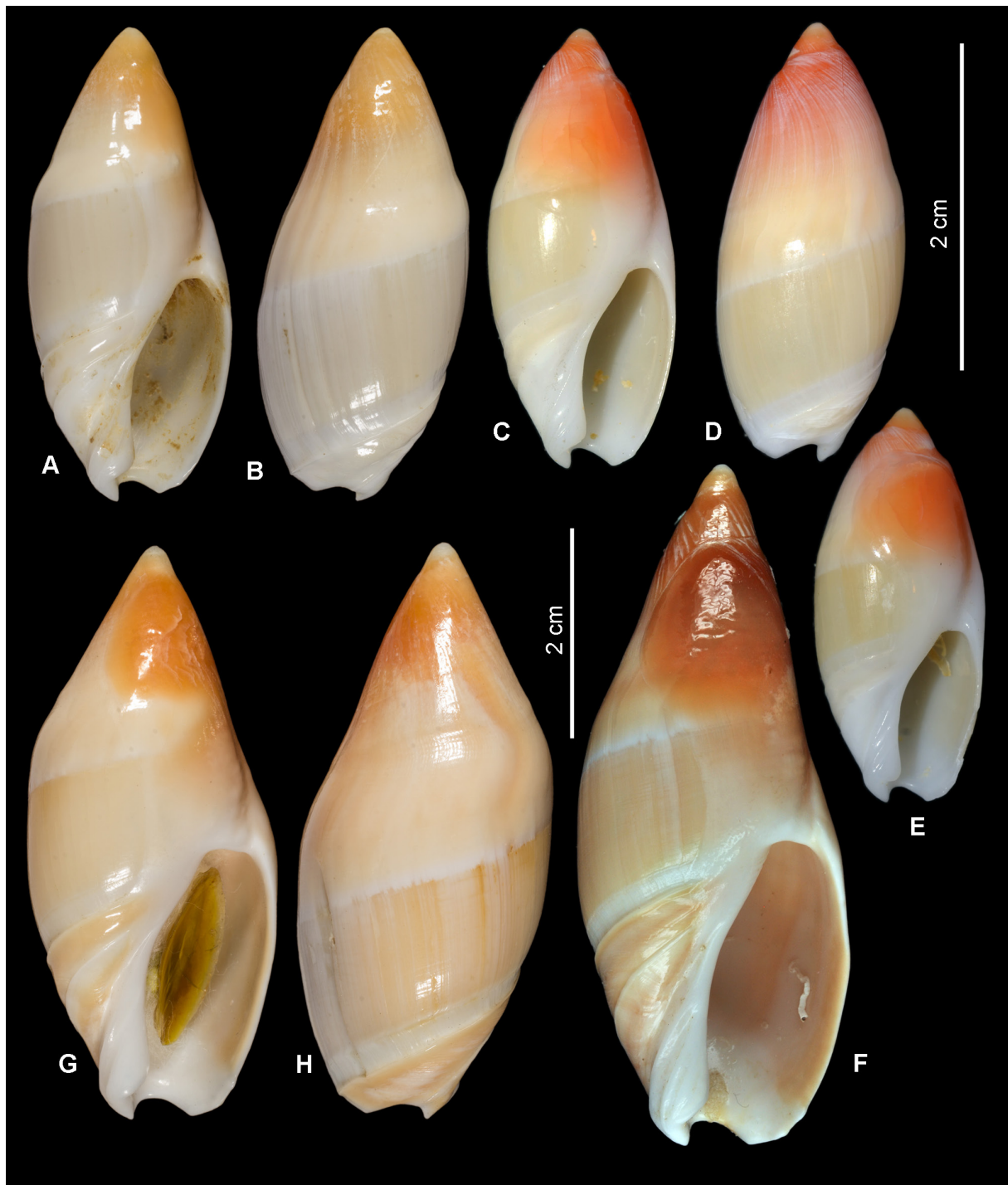


Fig. 16. A–F. *Amalda allaryi* Bozzetti, 2007. A–B. Holotype, MNHN IM-2000-20532, SL 29.4 mm. C–D. MNHN IM-2007-43630, SL 27.2 mm. E. MNHN IM-2007-43628, SL 24.4 mm. F. KANACONO, stn CP4656, 22°40' S, 167°12' E, 219–244 m, W of Île des Pins, SL 64.5 mm. G–H. *A. maritzae* Bozzetti, 2007, holotype, MNHN IM-2000-24475, SL 54.4 mm. A–E = at the same scale; F–H = at the same scale; C–E = sequenced specimens.

Amalda fuscolingua Kilburn & Bouchet, 1988
Fig. 9B, 18A–E

Amalda fuscolingua Kilburn & Bouchet, 1988: 288–289, figs 25–28, 40–41, 54.

Amalda fuscolingua – Gratecap 2014: 14, 18, figs 11–13.

Type material

Holotype

SOUTHERN NEW CALEDONIA • S of Île des Pins; 22°54' S, 167°14' E; 412–428 m deep; SMIB 2; stn DW03; MNHN IM-2000-1439.

Material examined

Sequenced material

8 sequenced specimens (Table 1).

Not sequenced material

SOUTHERN NEW CALEDONIA • material listed by Kilburn & Bouchet (1988) • 1 dd; SW of Île des Pins; 22°56' S, 167°15' E; 437 m deep; SMIB 3; stn DW25 • 1 dd; SW of Île des Pins; 22°46' S, 167°11' E; 394 m deep; SMIB 3; stn DW28 • 4 dd; SW of Île des Pins; 22°47' S, 167°12' E; 405 m deep; SMIB 3; stn DW29 • 1 lv; 3 dd; between Île des Pins and Grand Récif Sud; 22°56' S, 167°14' E; 400–420 m deep; SMIB 4; stn DW65 • 1 dd; between Île des Pins and Grand Récif Sud; 22°56' S, 167°15' E; 400–430 m deep; SMIB 4; stn DW66 • 1 dd; between Île des Pins and Grand Récif Sud; 22°55' S, 167°15' E; 395–405 m deep; SMIB 4; stn DW69 • 15 lv, dd; E of Île des Pins; 22°51' S–22°52' S, 168°12' E–168°13' E; 408–436 m deep; SMIB 8; stn DW197-199 • 15 lv, dd; SE slope of Passe de Dumbéa; 22°52' S, 167°12' E; 400 m deep; BATHUS 2; stn DW729 • 15 dd; S of Île des Pins; 22°44' S, 167°17' E; 350–393 m deep; BATHUS 2; stn DW717 • 3 dd; S of Île des Pins; 22°50' S, 167°27' E; 430–433 m deep; BATHUS 2; stn DW723 • 10 dd; S of Île des Pins; 22°48' S, 167°26' E; 344–358 m

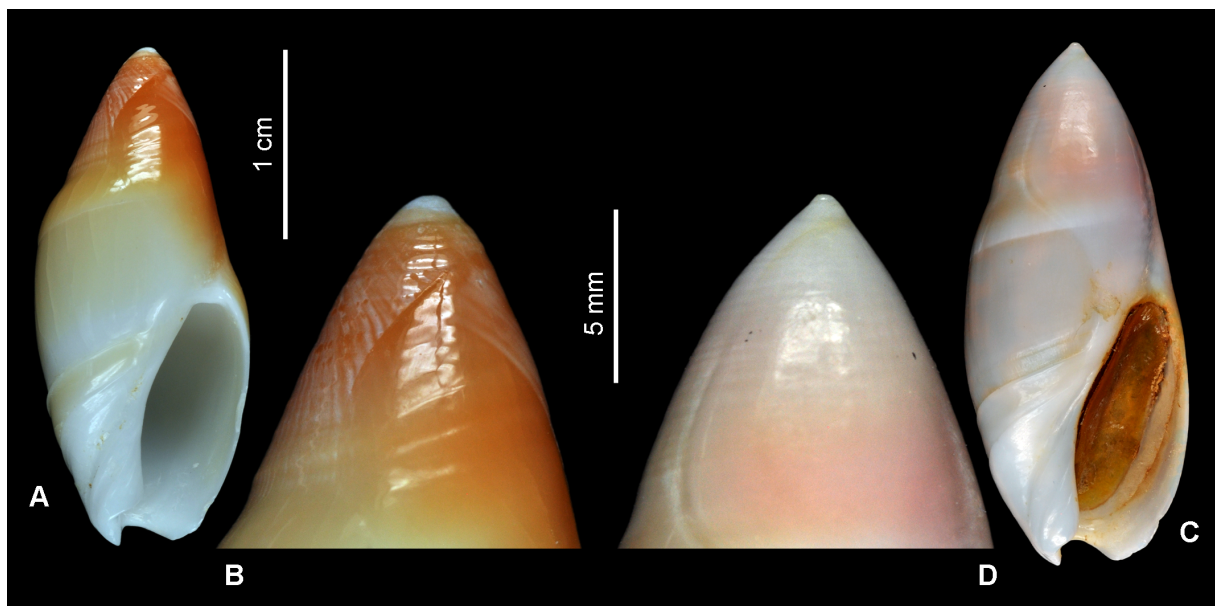


Fig. 17. Comparison of *Amalda allaryi* Bozzetti, 2007 with *A. montrouzieri* (Souverbie, 1860). **A–B.** *A. allaryi*, MNHN IM-2013-68272, SL 26.2 mm, specimen not sequenced. **C–D.** *A. montrouzieri*, LAGON, stn DW51, Nouméa Sector, 22°15' S, 166°11' E, 10 m, SL 27.6 mm, specimen not sequenced.

deep; BATHUS 2; stn DW724 • 6 dd; Canal de la Havannah; 22°13' S, 167°09' E; 353–365 m deep; EXBODI; stn DW3784 • 1 dd; Canal de la Havannah; 22°15' S, 167°10' E; 386–387 m deep; EXBODI; stn DW3785 • 7 dd; SW of Île des Pins; 22°57' S, 167°16' E; 427–433 m deep; NORFOLK 1; DW1733 • 15 lv, dd; SW of Île des Pins; 22°52' S, 167°12' E; 383–407 m deep; NORFOLK 1; stn DW1736 • ca 30 lv, dd; SW of Île des Pins; 22°51' S, 167°10' E; 400 m deep; NORFOLK 1; stn DW1737; • 15 dd; SW of Île des Pins; 22°51' S, 167°12' E; 340–381 m deep; NORFOLK 1; stn DW1738. – **Off Île des Pins** • 10 dd; 22°44' S, 167°16' E; 386–391 m deep; NORFOLK 2; stn DW2148 • 12 dd; 22°43' S, 167°14' E; 353–368 m deep; NORFOLK 2; stn DW2151 • 4 dd; 22°47' S, 167°12' E; 395–400 m deep; NORFOLK 2; stn CP2153 • 25 dd; 22°54' S, 167°15' E; 468–500 m deep; NORFOLK 2; stn DW2156 • 1 lv; 22°45' S, 167°13' E; 400–405 m deep; KANACONO; stn DW4660; MNHN IM-2013-68426 • 2 lv; 22°57' S, 167°39' E; 310–403 m deep; KANACONO; stn DW4745; MNHN IM-2013-63419; MNHN IM-2013-63425.

Description

MEASUREMENTS. Shell large (SL up to 57 mm).

SHELL. Ovate-fusiform, with blunt orthoconoid spire. Primary spire callus thick, microshagreened, covering all whorls, except 1–1.5 protoconch whorls. First protoconch whorl diameter 0.92–1.06 mm (mean 0.98, n=5). Secondary callus thick, fusing without visible border with parietal callus, with distinct anterior border, reaching suture of antepenultimate whorl. Plication plate with 3–6 ridges, all weak except outer 2, columella smooth. Olivoid groove very shallow to obsolete, labral denticle very small, obtuse to absent. Upper anterior band nearly flat except weak submedian low ridge. Lower anterior band nearly flat, microshagreened. Primary callus orange-brown in lower part, brown on spire with distinct, strongly prosocline, lighter axial lines. Secondary callus orange-brown. Body whorl cloak light yellowish-brown, olivoid band usually slightly lighter, anterior band orange brown with upper anterior band slightly darker, of the same colour as cloak, plication plate white.

Remarks

This distinct species poses no taxonomic problems due to its very characteristic colour pattern of primary spire callus with strongly prosocline lighter axial lines and brightly coloured thick orange-brown secondary callus. There is no species in New Caledonia resembling *A. fuscolingua*.

The radula, examined by Kilburn & Bouchet (1988: fig. 54), is similar to that of *A. montrouzieri* with central tooth with less serrated cusps.

Distribution

The species is confined to a narrow perimeter around Île des Pins (Fig. 9B), with a maximal extension of 150 × 60 km and a depth range of 300–500 m.

Amalda coriolis Kilburn & Bouchet, 1988
Figs 13H, 18F–J

Amalda coriolis Kilburn & Bouchet, 1988: 293, figs 33–37, 42–43, 58.

Amalda coriolis – Gratecap 2014: 14, 19, figs 14–15.

Type material

Holotype

CORAL SEA • Lord Howe Ridge, Kelso Bank; 24°10' S, 159°36' E; 270 m deep; MUSORSTOM 5; stn DW280; MNHN IM-2000-1393.

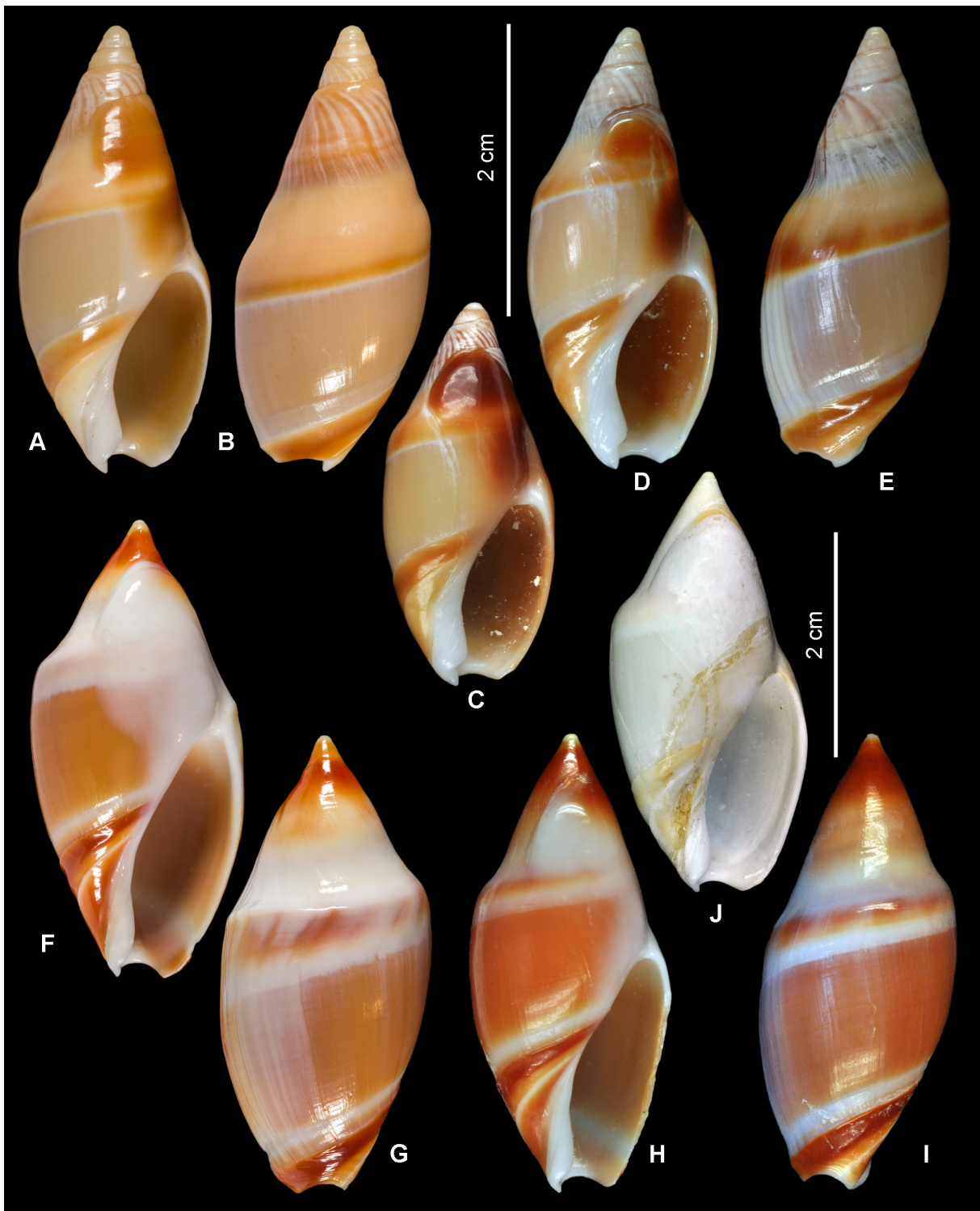


Fig. 18. A–E. *A. fuscolingua* Kilburn & Bouchet, 1988. A–B. Holotype, MNHN IM-2000-1439, SL 30.6 mm. C. MNHN IM-2007-43643, SL 26.6 mm (sequenced specimen). D–E. MNHN IM-2007-43649, SL 30.2 mm (sequenced specimen). F–J. *A. coriolis* Kilburn & Bouchet, 1988. F–G. Holotype, MNHN IM-2000-1393, SL 40.1 mm. H–I. MNHN IM-2013-63899, SL 40.4 mm (sequenced specimen). J. Coral Sea, Capel Bank, KANADEEP, stn DW4944, 25°21' S, 159°45' E, 235–242 m, SL 37.3 mm. A–E=at the same scale; F–J=at the same scale.

Material examined

Sequenced material

Two sequenced specimens (Table 1).

Not sequenced material

CORAL SEA • Material listed by Kilburn & Bouchet (1988) • 1 dd; Capel Bank; 25°08' S, 159°50' E; 270 m deep; KANADEEP 1; stn CP4928 • 9 dd; Capel Bank; 25°21' S, 159°45' E; 235–242 m deep; stn DW4944 • 2 dd; Kelso Bank; 24°08' S, 159°37' E; 275–276 m deep; stn CP4947 • 1 dd; Kelso Bank; 24°07' S, 159°40' E; 275 m deep; stn CP4948 • 1 dd subadult; Kelso Bank; 24°12' S, 159°41' E; 270–385 m deep; stn DW4951.

Description

MEASUREMENTS. Shell large (SL up to 48.9 mm).

SHELL. Biconic-ovate, with narrow base and high, acutely conical spire. Last whorl angulated just below suture. Primary spire callus thick, microshagreened, covering all whorls, except 1–1.5 protoconch whorls, with very weak spiral ridges. Protoconch large, low-dome shaped, first whorl diameter 0.95–1.13 mm (mean 1.06, n=5). Secondary callus very thick, fusing without visible border with parietal callus, with distinct anterior border, forming a strong pad reaching adapical suture of antepenultimate whorl. Plication plate with 1–4 ridges, all weak except adapical one, columella smooth. Olivoid groove distinct, labral denticle not pronounced. Upper anterior band weakly convex, with rounded and weak submedian low ridge. Lower anterior band nearly flat, microshagreened. Primary callus from very light yellowish to dark orange-brown in upper part, in the lower part with white to creamy spiral band. Secondary callus white to creamy. Body whorl cloak from white to orange, olivoid band nearly white, upper anterior band from yellowish to dark brown and lower anterior band from white to orange-brown, plication plate white.

RADULA (Fig. 13H). Examined in one specimen. Central tooth tricuspid, with broad lateral flaps, central cusp slightly narrower and shorter than lateral ones. Central cusp nearly smooth, lateral ones slightly serrated, broad lateral flaps strongly serrated with indistinct longitudinal grooves situated between cusplets.

Remarks

The radula illustrated by Kilburn & Bouchet (1988: fig. 58) is very similar to our specimen.

This very characteristic species is readily distinguished from all other species in New Caledonia by its shell shape. Although the holotype is dark coloured, most specimens are much lighter, sometimes even pure white (Fig. 18J). The upper anterior band is the last shell zone that loses colour.

Distribution

The species is a narrow endemic found only on Kelso and Capel banks in the Coral Sea at depths of 150–275 m.

Amalda sp.
Figs 19A–B, 20A

Material examined and sequenced

PAPUA NEW GUINEA • 1 lv; Manus I; 02°10' S, 147°16' E; 200–219 m deep; BIOPAPUA; stn DW3694; MNHN IM-2013-63891.

Remarks

Radula (n=1, Fig. 20A) with tricuspid central tooth, with medium broad lateral flaps, central cusp 1.5 times narrower and shorter than lateral ones. Cusps nearly smooth, while lateral flaps are strongly serrated with shallow longitudinal grooves situated between cusplets. 1–2 additional minute cusplets on both sides of central cusp.

In the molecular tree, this seemingly subadult specimen was recovered as sister to *Amalda cacao* sp. nov. In shell appearance it resembles a miniature *A. hilgendorfi*, although with thinner and uncarinated spire callus, which is much less microshagreened than in *A. hilgendorfi*. Judging from the molecular tree, this specimen clearly represents a new species, but we abstain from description pending the collection of additional material including adult specimens.

Amalda monilifera (Reeve, 1864)
Figs 19F–G, 20B, E

Ancillaria monilifera Reeve, 1864: pl. 10, sp. 36.

Gracilispira monilifera – Wilson 1994: 131, pl. 29, fig. 16 a–c.

Amalda (Gracilispira) monilifera – Gratecap 2016a: 6, 18, fig. 12.

Type material

Holotype (by monotypy)

WESTERN AUSTRALIA • Swan River; NHMUK 197933.

Material examined

One sequenced specimen (Table 1).

Description

MEASUREMENTS. Shell small (SL up to 18 mm).

SHELL. Ovate-fusiform, with conical spire with nearly straight sides. Primary spire callus thin, semi-transparent, smooth, covering all whorls, except protoconch. Protoconch rounded above, boundary with teleoconch indistinct, first whorl diameter 0.65 mm. Secondary callus medium thick on parietal wall and forming distinct parietal pad, extending only to penultimate whorl. Plication plate with 3 weak ridges and still two weaker on columella. Olivoid groove distinct but shallow, labral denticle prominent, narrow triangular. Upper anterior band weakly convex, with low median ridge, lower anterior band nearly flat, smooth. Colour of primary callus light orange, body whorl cloak creamy with light brown anastomosing pattern, subsuturally a row of large, irregular oval brown spots, seen through transparent callus on all teleoconch whorls, olivoid band and lower anterior band with row of brown spots, plication plate creamy.

RADULA (n=1, Fig. 20B, E). With broad, subtriangular lateral teeth with sharp, hook-shaped, curved tip. Central cusp multicuspid, with three major central cusps, median much narrower and slightly shorter than lateral ones, in addition medium long, irregularly shaped, 2–4 cusps between lateral and median cusps, also irregular-shaped fissures in median part of central tooth. Lateral flaps of central tooth dentated, with 3–5 triangular short cusplets.

Remarks

The radula of the species is studied here for the first time.

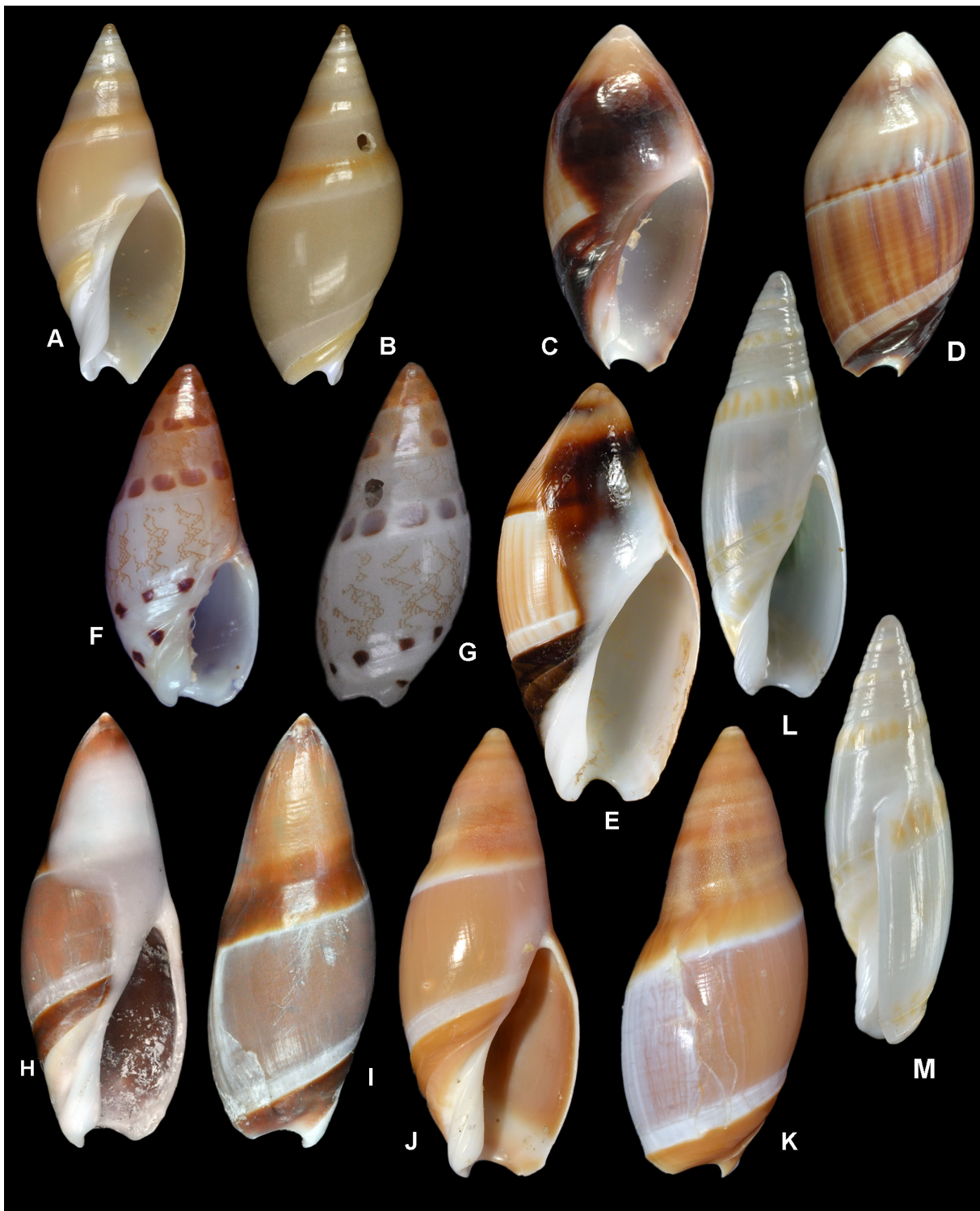


Fig. 19. Sequenced species of *Amalda* H. Adams & A. Adams, 1853. **A–B.** *Amalda* sp., MNHN IM-2013-63891, SL 20 mm. **C–D.** *A. contusa* (Reeve, 1864), MNHN IM-2009-22263, SL 24.9 mm. **E.** *A. optima* (G.B. Sowerby III, 1897), MNHN IM-2007-38287. **F–G.** *A. monilifera* (Reeve, 1864), MNHN IM-2013-63898, SL 11.7 mm. **H–I.** *A. hinomotoensis* (Yokoyama, 1922), MNHN IM-2019-618, SL 41.4 mm. **J–K.** *A. hayashii* Ninomiya, 1988, MNHN IM-2013-44413, SL 38.4 mm. **L–M.** *A. bellonarum* Kilburn & Bouchet, 1988, MNHN IM-2007-33273. Shells not to scale.

Ninomiya (1990) included this species in his new subgenus *Mundaspira* (type species *Amalda concinna* Ninomiya, 1990).

Distribution

The Recherche Archipelago in southern Western Australia (Gratecap 2016a), in 0–15 m.

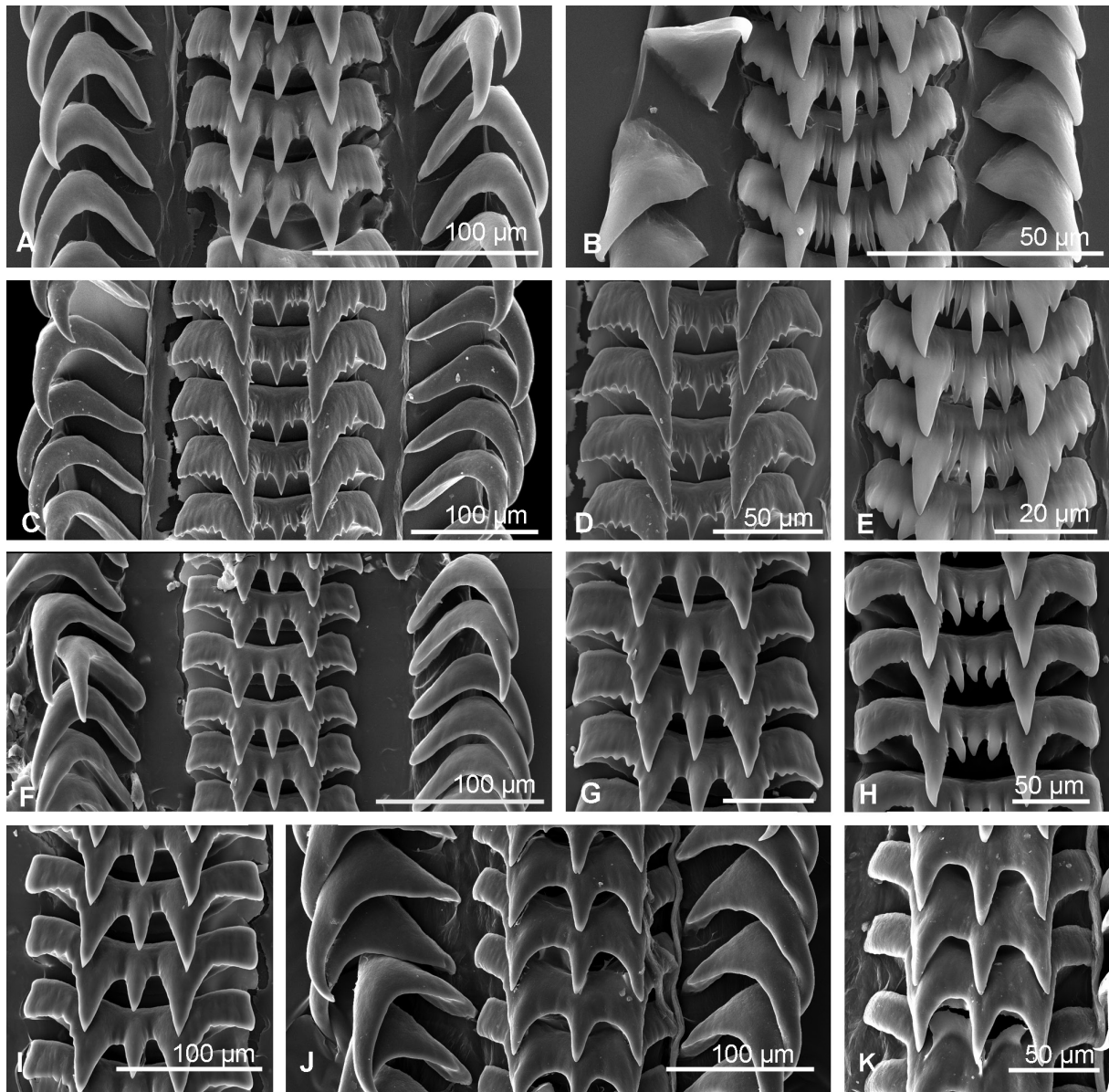


Fig. 20. Radulae of species of *Amalda* H. Adams & A. Adams, 1853. **A.** *Amalda* sp., MNHN IM-2013-63891 (shell on Fig. 19A–B). **B, E.** *A. monilifera* (Reeve, 1864), MNHN IM-2013-63898 (shell on Fig. 19F–G). **C–D.** *A. contusa*, MNHN IM-2009-22264, SL 22.7 mm. **F–I.** *A. hayashii* Ninomiya, 1988. **F–G.** MNHN IM-2013-44413 (shell on Fig. 19J–K). **H.** MNHN IM-2013-44432. **I.** MNHN IM-2013-44457, SL 38.2 mm. **J–K.** *A. hinomotoensis* (Yokoyama, 1922), MNHN IM-2019-619, SL 38.5 mm.

Amalda hinomotoensis (Yokoyama, 1922)
Figs 19H–I, 20J–K

Ancilla hinomotoensis Yokoyama, 1922: 48, pl. 2 fig. 5.

Ancilla hinomotoensis – Taki & Oyama 1954: pl. 22 figs 5–5a.

Baryspira urasima Is. Taki ms – Kira 1959: 63, pl. 31 fig. 3.

Amalda hinomotoensis – Tsuchida 2017: 332, pl. 288 fig. 5, 996. — Gratecap 2016b: 5, 13, figs 11–13.

Amalda urasima – Okutani 2000: 523, pl. 260 fig. 5.

Type material

Lectotype

JAPAN • lectotype of *Ancilla hinomotoensis* (designated by Taki & Oyama 1954); Pliocene of Shito; UMUT 20840.

Material examined

Two sequenced specimens (Table 1).

Description

MEASUREMENTS. Shell medium in size (SL exceeding 41 mm).

SHELL. Narrow to ovate-fusiform, with a weakly cyrtocoid spire. Primary spire callus thick, microshagreened, covering all whorls except protoconch tip, rendering measurements impossible. Secondary callus thick, strongly microshagreened and mat, fusing without visible border with parietal callus, with distinct anterior border and nearly reaching shell tip. Plication plate with up to 5 ridges subdivided by grooves, or nearly smooth, columella smooth. Olivoid groove shallow to very shallow, labral denticle very short, obtuse. Anterior band strongly microshagreened, upper anterior band very weakly convex, lower anterior band flat. Primary callus orange-brown in middle part, lighter abapically, bordered by very thin, light spiral line. Secondary callus white. Body whorl cloak light chestnut, olivoid band whitish, upper anterior band dark brown, lower anterior band creamy, plication plate white.

RADULA (n=1, Fig. 20J–K). With hook-shaped lateral teeth with broad bases. Central tooth tricuspid with subequal, large, triangular, smooth cusps and medium broad lateral flaps.

Remarks

The name *Baryspira urasima* was introduced by Kira (1959) without description and despite its use by Okutani (2000), it remains an unavailable name (ICZN art. 13.1.1).

Distribution

Japan, from Sagami Bay to Kyushu, in 200–350 m (Tsuchida 2017).

Amalda hayashii Ninomiya, 1988
Figs 19J–K, 20F–I

Amalda (Alcospira) hayashii Ninomiya, 1988: 145, pl. 1 figs 7–8.

Amalda hayashii – Okutani 2000: 523, pl. 260, fig. 3 (erroneously labelled as *A. hilgendorfi*). — Tsuchida 2017: atlas: 332, pl. 288 fig. 2, text: 995.

Type material

Holotype

SOUTHERN JAPAN • Amami-Oshima Island; Ninomiya collection [not seen].

Material examined

9 sequenced specimens (Table 1).

Description

MEASUREMENTS. Shell medium in size (SL up to 50 mm).

SHELL. Ovate-fusiform, with medium high, weakly cyrtocoid spire. Primary spire callus thick, strongly pustulose except smooth last whorl, covering all whorls, except tip of protoconch, rendering measurements impossible. Secondary callus rather thin, with indistinct borders, microshagreened, weakly glossy, fusing with parietal callus without visible border, and reaching antepenultimate whorl and merging into primary callus. Plication plate from nearly smooth to bearing up to 5 ridges, columella smooth or with traces of plicae. Olivoid groove shallow to very shallow, labral denticle short, obtuse, rounded. Anterior band microshagreened, upper anterior band weakly convex with median or shifted more abapically, obtuse ridge, lower anterior band flat. Primary callus yellow-brownish on spire and slightly darker abapically, also bordered by almost white, medium broad, band. Secondary callus whitish, translucent. Body whorl cloak light chestnut with slight purple tint, olivoid band whitish, anterior brown, lower anterior band lighter, plication plate creamy.

RADULA (n=3, sequenced, Fig. 20F–I). With simple, hook-shaped lateral teeth. Central teeth quite variable, from tridentate with large, smooth cusps, central smallest (Fig. 20I), with serrated cusps and lateral flaps (Fig. 20G), to multicuspid central with five smooth cusps, central three much smaller than lateral ones.

Distribution

From southern Japan to the South China Sea, in 250–310 m.

Amalda contusa (Reeve, 1864)

Figs 19C–D, 20C–D

Ancillaria contusa Reeve, 1864: pl. 9, species no. 31.

Amalda contusa – Gratecap 2012: 19, 27, figs 1–2 (holotype illustrated), 3–5.

Amalda cf. *contusa* – Gratecap 2012: figs 9–10.

Type Material

Holotype

Holotype by monotypy; locality unknown; NHMUK 197836.

Material examined

Three sequenced specimens (Table 1).

Description

MEASUREMENTS. Shell small (SL up to 25 mm).

SHELL. Broadly ovate, with narrow base and low conical spire. Primary spire callus very thick, smooth and glossy, covering all whorls, except tip of protoconch, rendering measurements impossible. Secondary callus rather thick, with distinct anterior border, smooth and glossy, fusing without visible border with parietal callus, and reaching shell apex. Plication plate smooth, separated from anterior band by broad and deep groove, columella smooth. Olivoid groove shallow but distinct, labral denticle short, obtuse. Anterior band smooth, upper and lower anterior bands weakly convex. Primary callus milky-caramel with irregularly positioned sinuous, brownish axial lines, abapically bordered by interrupted narrow spiral, brown and lighter narrow lines. Secondary callus dark brown, turning very light above aperture. Body whorl cloak background caramel with irregularly spaced, orthocone, brown axial bands of uneven width and lighter spiral colour lines, olivoid band much lighter than cloak, of same tint, anterior band very dark brown, light brown near columella, very light brownish abapically.

RADULA (n=1, sequenced, Fig. 20C–D). With rather short, hook-shaped lateral teeth. Central tooth broad, with broad lateral flaps, and three major cusps, median more than twice shorter and narrower than lateral ones. Lateral cusps serrated at their base as well as lateral flaps. 1–4 additional, smaller, irregularly shaped cusps between median and lateral major cusps.

Remarks

Our sequenced specimens correspond to what was treated and illustrated by Gratecap (2012: figs 9–10) as *A. cf. contusa*. This author also provided a lengthy discussion of the complex taxonomic history of *A. contusa* and concluded that there may be two similar but separate species, one in Natal, and the other in Mozambique and Natal. At present, the lack of comparative material does not allow us to clarify the situation and we provisionally consider our specimens to be the true *A. contusa*.

Distribution

KwaZulu Natal and Mozambique, in 15–20 m.

Amalda optima (G.B. Sowerby III, 1897)
Fig. 19E

Ancilla optima Sowerby III, 1897: 7, pl. 6 fig. 31.

Amalda optima – Gratecap 2012: 23, 29, fig. 23.

Type material

Possible syntype

SOUTH AFRICA • Durban; NHMUK 1899.4.14.648.

Material examined

One sequenced specimen (Table 1).

Description

MEASUREMENTS. Shell large (SL up to 55 mm).

SHELL. Broadly ovate, with narrow base and low conical spire. Primary spire callus very thick, smooth and glossy, covering all whorls, except tip of protoconch, rendering measurements impossible. Secondary callus rather thick, with distinct anterior border, smooth and glossy, fusing without visible border with parietal callus, and reaching the shell apex. Plication plate smooth, poorly separated from anterior band, columella smooth. Olivoid groove distinct, labral denticle very short, obtuse. Anterior band smooth,

upper anterior band nearly flat, lower anterior band weakly convex. Primary callus milky-caramel with distinct sinuous, narrow brown axial lines, particularly pronounced on last whorl, its narrow spiral brown line bordered abapically by lighter, narrow line. Secondary callus caramel to dark brown, turning very light, nearly white, above aperture. Body whorl cloak background light caramel with irregularly spaced, orthocline, brown axial bands of uneven width, olivoid band much lighter than cloak, creamy-coloured, anterior band very dark brown.

RADULA. Not studied.

Distribution

Natal to Mozambique.

Amalda bellonarum Kilburn & Bouchet, 1988
Fig. 19L–M

Amalda bellonarum Kilburn & Bouchet, 1988: 290, 292, figs 29–32, 48–49.

Amalda (Alocospira) bellonarum – Gratecap 2014: 14, 19, figs 17–18.

Type material

Holotype

CORAL SEA • Bellona Plateau; 21°25' S, 159°09' E; 60 m deep; CHALCAL; stn D56; MNHN IM-2000-1112.

Material examined

One sequenced specimen (Table 1).

Description

MEASUREMENTS. Shell small (SL up to 15 mm).

SHELL. Oblong-fusiform, with high spire. Primary spire callus not thick, glossy, covering all whorls, including most of protoconch rendering measurements inaccurate, and with distinct spiral lirae (6–7 on penultimate whorl). Secondary callus thin, with indistinct borders, narrow, nearly reaching antepenultimate whorl. Plication plate with 3–4 ridges. Olivoid groove deep and distinct, labral denticle weak, obtuse. Anterior band poorly separated in narrower upper anterior band and twice broader lower band, both nearly flat. Colour uniformly greyish-white with rows of faint yellow-orange spots, one subsutural and one on olivoid band and anterior band.

RADULA. Unknown.

Remarks

The only studied specimen from north Bellona Plateau, collected close to the type locality, differs from the types in having significantly more slender shell, although similar in other details. Besides, that specimen was collected at a significantly larger depth (324–330 m vs 45–240 m).

Distribution

Chesterfield-Bellona Plateau, Coral Sea, New Caledonia, at about 45–240 m.

Discussion

The new molecular data confirm the validity of most nominal taxa described from New Caledonia except the status of *Amalda hilgendorfi richeri*, while the status of *A. maritzae* remains doubtful. In addition to those treated herein, one seemingly valid species has been described from south-west of Caledonia (Passe de Kouaré) in depths of 250–400 m – *Amalda herberti* Cossignani, 2013. We did not have in our possession specimens of the species, but the photo of the shell and live animal were made available by David Massemin (Fig. 14C–E). When the two new species described herein are considered, the fauna of *Amalda* of New Caledonia and the Coral Sea thus now includes at least 10 species, all but one (*Amalda hilgendorfi*) endemic to this region (see, however, the remarks under *A. montrouzieri*). *Amalda cacao* sp. nov. and *A. hilgendorfi* are broadly distributed in the New Caledonia EEZ, while *A. bellonarum* and *A. coriolis* are found only in the Coral Sea, and *A. alabaster* sp. nov., *A. fuscolingua*, *A. allaryi*, *A. montrouzieri*, *A. herberti* and *A. aureomarginata* are confined to southern New Caledonia (the range of the latter species now restricted based on molecular data).

Most New Caledonian species of *Amalda* have a narrow distributional range, but may be common within their range (Fig. 9), such as *A. fuscolingua* and *A. aureomarginata* which are known from hundreds of specimens. By contrast, *A. hilgendorfi* exhibits a remarkably broad distribution now confirmed by molecular data, and is known from Japan, the Philippines, Papua New Guinea, the Solomon Islands, New Caledonia and probably northern Australia (Gratecap 2016a). It is not clear why this species in particular is so broadly distributed in comparison to the other species of the genus. Its protoconch is not much different from that of other species examined (Table 2) and is similar in size to the protoconch of the narrow range endemic *A. aureomarginata*, restricted to southern New Caledonia. Nothing is known about the egg cases and larval development of any deep-water *Amalda* species. Kilburn & Bouchet (1988: 298) speculated that, “the paucispiral protoconch in such cases reflects not holobenthic development with intracapsular metamorphosis, but lecithotrophic larval development with a short free-swimming larval phase”. Thirty years later, this hypothesis remains mere speculation. Our data on the protoconchs of different *Amalda* did not reveal any correlation between the distributional range and protoconch size (Table 2). In species with paucispiral protoconchs, the larger protoconch suggests a longer intracapsular development (or direct development) and as a result the absence of long living planktonic larvae. In species of *Amalda* with narrow and very narrow ranges, both largest (*A. miriky* sp. nov.) and smallest (*A. monilifera*) protoconchs were found. But it should also be emphasized that, since protoconchs are covered by the callus, we were able to measure the diameter of the first whorl only, which may not be a reliable proxy for actual protoconch size.

In general, species of *Amalda* (shallow and deep water), however, have rather narrow ranges, as reviewed by Gratecap for different parts of the Indo-Pacific, where local faunas are usually dominated by narrow endemics (especially that of South Africa and, to a lesser extent, Australia). Although there are species with broader distributions extending, e.g., from Japan to Taiwan (*A. hinomotoensis*) or Indonesia, the Strait of Malacca, Vietnam and the China Sea (*A. mamillata*) (Gratecap 2016b), such distributions should be taken with caution, as exemplified by *A. miriky* sp. nov., previously considered a form or subspecies of *A. hilgendorfi*, but shown by molecular data to be a distinct although morphologically similar, species.

With our dataset being very patchy and relying on a single genetic marker, having limited validity of phylogenetic inference at the supraspecific level, we did not address the validity of the subgenera recognized within *Amalda*. Nevertheless, our observations are in line with the conclusions made by Gemmel *et al.* (2020), who analyzed the *Amalda* from New Zealand and several Indo-Pacific locations based on the entire mitogenome and long nuclear rRNA gene cassette data. *Amalda australis* (type species of *Baryspira*) is the sister species to *A. novaezealandiae* (type species of *Gracilispira*), while other species, attributed to *Baryspira* (*A. mucronate*) and to *Gracilispira* (*A. benthicola*) form a polytomy. Thus we agree with Gemmel *et al.* (2020) that the status of at least these two subgenera is not resolved. Both

Table 2. Size of the protoconchs of the studied species.

Species	N° of studied specimens	First protoconch whorl diameter, mm	Distribution range
<i>Amalda hilgendorfi</i>		0.75–0.92 mm	Very broad
Japan morph	3	0.8–0.92 (mean 0.88)	
Coral Sea morph	5	0.75–0.92 (mean 0.82)	
Northern New Caledonia morph	5	0.80–0.84 (mean 0.83)	
Southern New Caledonia morph	5	0.84–0.90 (mean 0.86)	
<i>Amalda aureomarginata</i>	5	0.88–0.94 (mean 0.91)	Very narrow
<i>Amalda miriky</i> sp. nov.	3	1.15–1.25 (mean 1.23)	Narrow
<i>Amalda cacao</i> sp. nov.	1	0.68	Medium broad
<i>Amalda alabaster</i> sp. nov.	1	0.79	Narrow
<i>Amalda allaryi</i>	3	0.84–1.02 (mean 0.92)	Very narrow
<i>Amalda fuscolingua</i>	5	0.92–1.06 (0.98)	Very narrow
<i>Amalda coriolis</i>	5	0.95–1.13 (mean 1.06)	Very narrow
<i>Amalda monilifera</i>	1	0.65	Very narrow

in Gemmel *et al.* (2020) and our trees, *A. bellonarum* occupies a basal position in the first offshoot in the datasets analyzed. Kilburn & Bouchet (1988: 292) concluded that it “closely resembles (in miniature) its probable sister-species *A. rosea* (Macpherson, 1956) of the Queensland and New South Wales littoral” and that “*Amalda rosea*, together with a number of similar Australian species, is generally referred to [the] subgenus *Alocospira*, but probably belongs (with *A. bellonarum*) to an unnamed group”. The isolated position of the species as revealed by molecular data is concordant with this conclusion, but it is premature to propose any change to its subgeneric classification.

We have observed that radular morphology is poorly correlated with shell characters or with species phylogeny, and similar radulae can be found in distantly related species, as in *A. hilgendorfi* and *A. hayashii*. The intraspecific variability of the radula morphology can be high, as demonstrated for species in which multiple radulae have been examined, e. g., *A. hilgendorfi* (Fig. 7A–G) or *A. hayashii* (Fig. 20F–I).

The radula in species of *Amalda* (Figs 7, 13, 20) is not very variable in comparison with species of *Ancilla* (Kantor *et al.* 2017: fig. 13), a fact probably reflecting a lower genetic variability in *Amalda*. The lateral teeth are very similar in most species, simple hook-shaped, while central teeth are more variable. Ponder (1968) illustrated the radulae of a number of species of *Amalda*, including the type species of two nominal subgenera – *Baryspira* P. Fischer, 1883 (*Ancillaria australis* G.B. Sowerby I, 1830) and *Gracilispira* Olsson, 1956 (*Ancillaria novaezealandiae* G.B. Sowerby II, 1859). The type species of *Alocospira* Cossmann, 1899 (*Ancillaria papillata* Tate, 1889) is fossil, but the radulae of two Recent species, attributed to the subgenus by Ponder (1968) – *A. (Alocospira) marginata* (Lamarck, 1811) and *A. (Alocospira) oblonga* G.B. Sowerby I, 1830 – were also illustrated.

Among our species, *A. hilgendorfi*, *A. miriky* sp. nov. and *A. aureomarginata* form a supported molecular subclade and have radulae somewhat similar to those illustrated for *Baryspira* (Fig. 7A–J). The radulae of *Baryspira* and *Alocospira*, as illustrated by Ponder (1968), are also quite similar. The species forming the subclade that includes *A. alabaster* sp. nov., *A. fuscolingua*, *A. allaryi* and *A. montrouzieri* also possess rather similar radulae (Fig. 13). They are characterized by central teeth with rather narrow, strongly serrated lateral flaps and relatively large cusps, also usually with serrated edges. Kilburn & Bouchet (1988: 281) hypothesized that “The conspicuously cyrtoconoid spire (of *A. montrouzieri*),

which gives the shell an elongately pupiform shape, is characteristic of typical members of the subgenus *Alocospira* Cossmann, 1899". The radulae of *A. montrouzieri* and closely related species, however, differ markedly from representatives of *A. (Alocospira)* as illustrated by Ponder (1968: figs 26–27). Most divergent of all studied species is the radula of *A. monilifera* (Fig. 18B–E), which has practically multicuspid central teeth and differs from other species by its subtriangular, rather than hook-shaped, lateral teeth. Its radula is, however, similar to those illustrated for the type of *Gracilispira* (Ponder 1968: figs 24–25). *A. monilifera* was classified in *Amalda (Gracilispira)* by Gratecap (2016a).

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