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Research article

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Rare, deep-water and similar: revision of *Sibogasyrinx* (Conoidea: Cochlespiridae)

Yuri I. KANTOR^{1,*} & Nicolas PUILLANDRE²

¹A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences,
Leninski prospect 33, 119071 Moscow, Russian Federation.

^{1,2}Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'histoire naturelle, CNRS,
Sorbonne Université, EPHE, Université des Antilles, 57 rue Cuvier, 75005 Paris, France.

* Corresponding author: kantor.yuri1956@gmail.com

² Email: puillandre@mnhn.fr

¹ [urn:lsid:zoobank.org:author:48F89A50-4CAC-4143-9D8B-73BA82735EC9](https://zoobank.org/author:48F89A50-4CAC-4143-9D8B-73BA82735EC9)

² [urn:lsid:zoobank.org:author:00565F2A-C170-48A1-AAD9-16559C536E4F](https://zoobank.org/author:00565F2A-C170-48A1-AAD9-16559C536E4F)

Abstract. The genus *Sibogasyrinx* has to date included only four species of rare deep-water Conoidea, each known from few specimens. In shell characters it strongly resembles three distantly-related genera, two of which, *Comitas* and *Leucosyrinx*, belong to a different family, the Pseudomelatomidae. A molecular phylogenetic analysis of a large amount of material of Conoidea has revealed the existence of much additional undescribed diversity within *Sibogasyrinx* from the central Indo-Pacific and temperate Northern Pacific. Based on partial sequences of the mitochondrial *cox1* gene and morphological characters of 54 specimens, 10 species hypotheses are proposed, of which six are described as new species: *S. subula* sp. nov., *S. lolae* sp. nov., *S. maxime* sp. nov., *S. clausura* sp. nov., *S. pagodiformis* sp. nov. and *S. elbakyanae* Kantor, Puillandre & Bouchet sp. nov. One of the previously described species was absent in our material. Most of the new species are very similar and are compared to *Leucosyrinx* spp. Species of *Sibogasyrinx* are unique among Conoidea on account of the high intrageneric variability in radular morphology. Three distinct radula types are found within *Sibogasyrinx*, two of which are confined to highly supported subclades.

Keywords. *Sibogasyrinx pyramidalis* species complex, deep-water Conoidea, *cox-1*, integrative taxonomy, new species.

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Introduction

The superfamily Conoidea is well known for high levels of homoplasy in shell form. Molecular studies have revealed that very similar or nearly indistinguishable shell morphologies are found in distantly related lineages (Puillandre *et al.* 2011; Abdelkrim *et al.* 2018), thus rendering the attribution of species to genus and even family questionable, when based on shell characters alone.

Particularly striking examples of such homoplastic shells are found in the genera *Comitas* Finlay, 1926, *Leucosyrinx* Dall, 1889, *Sibogasyrinx* Powell, 1969 and, to some extent, *Comispira* Kantor, Fedosov & Puillandre, 2018, all of which possess rather similar fusiform shells with a long siphonal canal and axial ribs or nodules on a more or less angular shoulder. *Sibogasyrinx* was originally established as a subgenus of *Leucosyrinx*, at that time assigned to the Cochlespiridae (Powell 1966; Taylor *et al.* 1993). However, molecular data demonstrate that *Leucosyrinx* constitutes a sister group to the Pseudomelatomidae, albeit with low support, while *Sibogasyrinx* is clearly referable to the Cochlespiridae (Puillandre *et al.* 2011; Abdelkrim *et al.* 2018). Furthermore, species of *Sibogasyrinx* are characterized by a radula typical of Cochlespiridae – with paired marginal and well-defined central teeth, in contrast to *Leucosyrinx* spp. which possess only marginal teeth (Bouchet *et al.* 2011). Both radula type and phylogenetic analyses (Bouchet *et al.* 2011; Puillandre *et al.* 2011; Abdelkrim *et al.* 2018) confidently placed *Comitas* in the Pseudomelatomidae. Finally, the recently described *Comispira* is clearly referable to the Cochlespiridae, both on anatomical and molecular grounds.

The taxonomy and morphology of these genera were treated in detail by Kantor *et al.* (2018); however, although they can be reliably distinguished by the morphology of the radula, most of the species have never been examined in this respect. Consequently, the generic placement of the anatomically unknown species relies in most cases on shell characters only, even though generic diagnoses based on conchological features are still lacking. For example, *Sibogasyrinx* originally included two species with “peripheral angle right down at the lower suture” (Powell 1969: 343). Later it was found that this character is inconsistent and in *Sibogasyrinx sangeri* Kantor *et al.*, 2018 the angulation may be situated at mid-whorl (Kantor *et al.* 2018). Finally, many species are known from a very limited number of specimens, and their interspecific and intraspecific variability has not been evaluated.

A consequence of this taxonomic imprecision is that the generic placement of species is often doubtful. Most species are currently attributed to the pseudomelatomid genera *Leucosyrinx* and *Comitas*, with 26 and 53 valid Recent species, respectively (MolluscaBase), while the cochlespirid genera *Comispira* and *Sibogasyrinx* only include two and three species, respectively. Furthermore, while DNA sequences of only seven species of *Leucosyrinx* (four undescribed), three of *Comitas* (two undescribed), two of *Comispira* and two of *Sibogasyrinx* are available in GenBank, molecular data from Indo-Pacific material in the Muséum national d’histoire naturelle (MNHN) revealed the existence of numerous undescribed species of *Sibogasyrinx*, including several that cluster with the type species, *S. pyramidalis* (Schepman, 1913). The aim of this publication is the clarification of the diagnosis of *Sibogasyrinx* and a taxonomic revision of the genus based on molecular and morphological data.

Material and methods

Sampling

Samples were collected during several expeditions of the MNHN (expeditions.mnhn.fr): DongSha 2014 and NanHai 2014 in the South China Sea, AURORA 2007 and PANGLAO 2005 in the Philippines, SALOMON 2 and SALOMONBOA 3 in the Solomon Islands, BIOPAPUA, KAVIENG 2014, MADE EP and PAPUA NIUGINI in Papua New Guinea, BOA1 and SANTO 2006 in Vanuatu, EXBODI, KANADEEP and TERRASSES in New Caledonia, EBISCO in the Chesterfield Islands, MIRIKY in Madagascar and GUYANE 2014 in French Guiana. Full details on the stations of these expeditions, including dates, are available at the above-mentioned website. One additional sample was collected in New South Wales, Australia, during the IN2017_V03 expedition on R/V *Investigator*. Specimens processed before 2012 were anaesthetized using an isotonic solution of MgCl₂ before fixation in 96% ethanol. Specimens processed after 2012 were microwaved and fixed in 96% ethanol (Galindo *et al.* 2014). The samples are recorded in the BOLD database and the sequences have been deposited in GenBank (Table 1).

Table 1 (continued on next three pages). List of examined material included in molecular phylogenetic analysis. ABGD PSH = Automatic Barcode Gap Discovery, primary species hypothesis; BOLD = Barcode of Life Datasystem; GB = Genbank. New BOLD and GB sequences are highlighted in red.

Reg. no.	Expedition	Stn	Coordinates	Depth (m)	Family	Genus	ABGD PSHs	species	BOLD ID	GB ID
MNHN-IM-2007-42517	SALOMON 2	CP2276	08°41' S, 157°38' E	814–980	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO792-08	MZ379777
MNHN-IM-2007-42530	SALOMON 2	CP2187	08°17' S, 160°00' E	482–604	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO806-08	MZ364512
MNHN-IM-2007-42533	SALOMON 2	CP2194	08°25' S, 159°27' E	440–521	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO809-08	MZ364501
MNHN-IM-2009-13567	SALOMON 2	CP2184	08°17' S, 160°00' E	464–523	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO3220-21	MZ364503
MNHN-IM-2009-13568	SALOMON 2	CP2184	08°17' S, 160°00' E	464–523	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO3214-21	MZ364481
MNHN-IM-2009-17048	BIOPAPUA	CP3750	05°39' S, 153°59' E	654–660	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO3212-21	MZ364497
MNHN-IM-2013-58409	KAVIENG 2014	CP4448	02°13' S, 150°12' E	564–743	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO3229-21	MZ364494
MNHN-IM-2007-17701	BOA1	CP2432	15°00' S, 166°55' E	630–705	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO153-08	EU015646.1
MNHN-IM-2007-17702	BOA1	CP2432	15°00' S, 166°55' E	630–705	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO154-08	EU015647.1
MNHN-IM-2007-17703	BOA1	CP2432	15°00' S, 166°55' E	630–705	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO155-08	MN322452.1
MNHN-IM-2007-17704	BOA1	CP2432	15°00' S, 166°55' E	630–705	Cochlespiridae	<i>Sibogasyrinx</i>	3	<i>subula</i>	CONO156-08	MZ364507
MNHN-IM-2009-16972	BIOPAPUA	CP3689	02°16' S, 147°29' E	679–685	Cochlespiridae	<i>Sibogasyrinx</i>	1	cf. <i>pyramidalis</i> 2	CONO3208-21	MZ364518
MNHN-IM-2009-16973	BIOPAPUA	CP3689	02°16' S, 147°29' E	679–685	Cochlespiridae	<i>Sibogasyrinx</i>	1	cf. <i>pyramidalis</i> 2	CONO3211-21	MZ364511
MNHN-IM-2009-16988	BIOPAPUA	CP3671	04°04' S, 151°56' E	585–601	Cochlespiridae	<i>Sibogasyrinx</i>	1	cf. <i>pyramidalis</i> 2	CONO3209-21	MZ364492
MNHN-IM-2009-17000	BIOPAPUA	CP3672	04°04' S, 151°50' E	702–724	Cochlespiridae	<i>Sibogasyrinx</i>	1	cf. <i>pyramidalis</i> 2	CONO3210-21	MZ364486
MNHN-IM-2013-19716	PAPUA NIUGINI	CP3981	05°11' S, 147°03' E	688	Cochlespiridae	<i>Sibogasyrinx</i>	1	cf. <i>pyramidalis</i> 2	CONO3224-21	MZ364517
MNHN-IM-2013-19745	PAPUA NIUGINI	CP3982	05°10' S, 147°03' E	724	Cochlespiridae	<i>Sibogasyrinx</i>	1	cf. <i>pyramidalis</i> 2	CONO3227-21	MZ364499

Table 1 (continued). List of examined material included in molecular phylogenetic analysis.

Reg. no.	Expedition	Stn	Coordinates	Depth (m)	Family	Genus	ABGD PSHs	species	BOLD ID	GB ID
MNHN-IM-2013-19768	PAPUA NIUGINI	DW3983	05°12' S, 146°59' E	470–508	Cochlespiridae	<i>Sibogasyrinx</i>	1	<i>cf. pyramidalis</i> 2	CONO3226-21	MZ364519
MNHN-IM-2013-58845	KAVIENG 2014	CP4483	02°42' S, 150°02' E	827–966	Cochlespiridae	<i>Sibogasyrinx</i>	1	<i>cf. pyramidalis</i> 2	CONO3231-21	MZ364516
MNHN-IM-2009-13451	AURORA 2007	CP2729	15°20' N, 121°37' E	593–600	Cochlespiridae	<i>Sibogasyrinx</i>	2	<i>cf. pyramidalis</i> 1	CONO2061-18	MG968492.1
MNHN-IM-2013-44574	NanHai 2014	CP4118	20°01' N, 115°02' E	700–723	Cochlespiridae	<i>Sibogasyrinx</i>	2	<i>cf. pyramidalis</i> 1	CONO2095-18	MG968491.1
MNHN-IM-2013-44605	NanHai 2014	CP4118	20°01' N, 115°02' E	700–723	Cochlespiridae	<i>Sibogasyrinx</i>	2	<i>cf. pyramidalis</i> 1	CONO2096-18	MG968493.1
MNHN-IM-2013-50215	DongSha 2014	CP4129	20°29' N, 116°08' E	590–633	Cochlespiridae	<i>Sibogasyrinx</i>	2	<i>cf. pyramidalis</i> 1	CONO2097-18	MG968494.1
MNHN-IM-2009-11327	SANTO 2006	AT139	16°00' S, 167°38' E	1262–1285	Cochlespiridae	<i>Sibogasyrinx</i>	5	<i>pagodiformis</i>	CONO3206-21	MZ364502
MNHN-IM-2009-16825	SALOMONBOA 3	CP2789	08°28' S, 160°32' E	1250–1402	Cochlespiridae	<i>Sibogasyrinx</i>	5	<i>pagodiformis</i>	CONO3221-21	MZ364496
MNHN-IM-2009-16834	SALOMONBOA 3	CP2817	09°55' S, 161°33' E	1136–1750	Cochlespiridae	<i>Sibogasyrinx</i>	4	<i>elbakyanae</i>	CONO3219-21	MZ364498
MNHN-IM-2013-19752	PAPUA NIUGINI	CP3982	05°10' S, 147°03' E	724	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2080-18	MG968497.1
MNHN-IM-2013-52052	BIOPAPUA	CP3671	04°04' S, 151°56' E	585–601	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2088-18	MG968498.1
MNHN-IM-2009-17021	BIOPAPUA	CP3750	05°39' S, 153°59' E	654–660	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2058-18	MG968502.1
MNHN-IM-2009-16989	BIOPAPUA	CP3671	04°04' S, 151°56' E	585–601	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2079-18	MG968501.1
MNHN-IM-2009-16766	SALOMON 2	CP2181	08°47' S, 159°40' E	645–840	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2062-18	MG968505.1
MNHN-IM-2007-42523	SALOMON 2	CP2288	08°36' S, 157°27' E	509–520	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO799-08	MG968466.1
MNHN-IM-2009-16995	BIOPAPUA	CP3674	04°02' S, 151°50' E	788–805	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2057-18	MG968495.1
MNHN-IM-2009-17022	BIOPAPUA	CP3729	07°52' S, 148°03' E	575–655	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2059-18	MG968496.1
MNHN-IM-2009-17057	BIOPAPUA	CP3742	09°08' S, 152°19' E	448–470	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2060-18	MG968499.1

Table 1 (continued). List of examined material included in molecular phylogenetic analysis.

Reg. no.	Expedition	Stn	Coordinates	Depth (m)	Family	Genus	ABGD PSHs	species	BOLD ID	GB ID
MNHN-IM-2013-19961	PAPUA NIUGINI	CP4014	05°35' S, 148°13' E	630–870	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2082-18	MG968504.1
MNHN-IM-2009-13434	AURORA 2007	CP2663	15°45' N, 121°45' E	562	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2064-18	MG968500.1
MNHN-IM-2009-16779	SALOMON 2	CP2288	08°36' S, 157°27' E	509–520	Cochlespiridae	<i>Sibogasyrinx</i>	7	<i>sangeri</i>	CONO2063-18	MG968503.1
MNHN-IM-2007-42498	SALOMON 2	CP2227	06°37' S, 156°13' E	508–522	Cochlespiridae	<i>Sibogasyrinx</i>	6	<i>filosa</i>	CONO772-08	MZ364480
MNHN-IM-2013-59044	KAVIENG 2014	DW4500	02°33' S, 150°45' E	150–170	Cochlespiridae	<i>Sibogasyrinx</i>	6	<i>filosa</i>	CONO3230-21	MZ364489
MNHN-IM-2009-16831	SALOMONBOA 3	CP2767	09°19' S, 160°06' E	416–425	Cochlespiridae	<i>Sibogasyrinx</i>	6	<i>filosa</i>	CONO3218-21	MZ364482
MNHN-IM-2009-29230	EXBODI	CP3864	22°22' S, 168°57' E	460–708	Cochlespiridae	<i>Sibogasyrinx</i>	8	<i>lolae</i>	CONO3222-21	MZ364514
MNHN-IM-2009-29311	TERRASSES	CP3098	21°58' S, 167°07' E	511–1050	Cochlespiridae	<i>Sibogasyrinx</i>	8	<i>lolae</i>	CONO3223-21	MZ364500
MNHN-IM-2013-48156	KANADEEP	CP4923	21°39' S, 162°42' E	787	Cochlespiridae	<i>Sibogasyrinx</i>	8	<i>lolae</i>	CONO3233-21	MZ364491
MNHN-IM-2007-42537	SALOMONBOA 3	CP2839	10°26' S, 161°20' E	506–567	Cochlespiridae	<i>Sibogasyrinx</i>	8	<i>lolae</i>	CONO820-08	MZ364485
MNHN-IM-2013-45883	MADEEP	DW4323	08°38' S, 151°46' E	720	Cochlespiridae	<i>Sibogasyrinx</i>	9	<i>maximei</i>	CONO3228-21	MZ364490
MNHN-IM-2009-16763	SALOMON 2	CP2182	08°47' S, 159°38' E	762–1060	Cochlespiridae	<i>Sibogasyrinx</i>	10	<i>clausura</i>	CONO3215-21	MZ364484
MNHN-IM-2013-48167	KANADEEP	CP4966	21°10' S, 157°46' E	975–980	Cochlespiridae	<i>Sibogasyrinx</i>	10	<i>clausura</i>	CONO3234-21	MZ364509
MNHN-IM-2013-48169	KANADEEP	CP4965	21°20' S, 157°50' E	961	Cochlespiridae	<i>Sibogasyrinx</i>	10	<i>clausura</i>	CONO3235-21	MZ364487
MNHN-IM-2013-48256	KANADEEP	CP4964	21°20' S, 157°55' E	963–970	Cochlespiridae	<i>Sibogasyrinx</i>	10	<i>clausura</i>	CONO3236-21	MZ364510
MNHN-IM-2013-48258	KANADEEP	CP4965	21°20' S, 157°50' E	961	Cochlespiridae	<i>Sibogasyrinx</i>	10	<i>clausura</i>	CONO3237-21	MZ364504
MNHN-IM-2013-48244	KANADEEP	CP4963	21°21' S, 158°00' E	978–1000	Cochlespiridae	<i>Sibogasyrinx</i>	10	<i>clausura</i>	CONO3238-21	MZ364495
MNHN-IM-2013-48144	KANADEEP	CP4965	21°20' S, 157°50' E	961	Cochlespiridae	<i>Sibogasyrinx</i>	10	<i>clausura</i>	CONO3232-21	MZ364515

Table 1 (continued). List of examined material included in molecular phylogenetic analysis.

Reg. no.	Expedition	Stn	Coordinates	Depth (m)	Family	Genus	ABGD PSHs	species	BOLD ID	GB ID
AMS C.519344	IN2017_V03	–	28°03' S, 154°05' E	999–1013	Cochlespiridae	<i>Sibogasyrinx</i>	10	<i>clausura</i>	–	MZ345688
MNHN-IM- 2013-19689	PAPUA NIUGINI	CP3979	4°44' S, 146°11' E	540–580	Pseudomelatomidae	<i>Leucosyrinx</i>	–	G	CONO3225-21	MZ364479
MNHN-IM- 2009-17089	BIOPAPUA	DW3748	5°37' S; 154°01' E	398–399	Pseudomelatomidae	<i>Leucosyrinx</i>	–	G	CONO3213-21	MZ364505
MNHN-IM- 2007-17846	EBISCO	CP2600	19°39' S, 158°45' E	603–630	Pseudomelatomidae	<i>Leucosyrinx</i>	–	F	CONO189-08	EU015655.1
MNHN-IM- 2009-16897	MIRIKY	CP3250	15°22' S, 46°00' E	493–662	Pseudomelatomidae	<i>Leucosyrinx</i>	–	E	CONO3207-21	MZ364493
MNHN-IM- 2007-42503	SALOMON 2	CP2219	7°58' S, 157°34' E	650–836	Pseudomelatomidae	<i>Leucosyrinx</i>	–	C	CONO777-08	MZ364513
MNHN-IM- 2009-16769	SALOMON 2	CP2217	7°49' S, 157°41' E	1045–1118	Pseudomelatomidae	<i>Leucosyrinx</i>	–	D	CONO3217-21	MZ364508
MNHN-IM- 2007-42445	PANGLAO 2005	CP2360	8°49' N, 123°38' E	357–372	Pseudomelatomidae	<i>Leucosyrinx</i>	–	A	CONO716-08	MZ364488
MNHN-IM- 2009-16764	SALOMON 2	CP2182	08°47' S, 159°38' E	762–1060	Pseudomelatomidae	<i>Leucosyrinx</i>	–	B	CONO3216-21	MZ364483
MNHN-IM- 2013-56288	GUYANE 2014	CP4367	07°09' N, 53°01' W	351–354	Pseudomelatomidae	<i>Leucosyrinx</i>	–	<i>verillii</i>	CONO2101-18	MG968474.1
MNHN-IM- 2013-56840	GUYANE 2015	CP4407	06°53' N, 52°33' W	495–502	Pseudomelatomidae	<i>Leucosyrinx</i>	–	<i>verillii</i>	CONO2109-18	MG968470.1
MNHN-IM- 2009-8188	CEAMARC	87EV524	65°29' S, 139°19' E	397–411	Cochlespiridae	<i>Aforia</i>	–	sp.	CONO1120-10	KT448835.1
MNHN-IM- 2007-17919	PANGLAO 2005	CP2340	9°29' N, 123°44' E	271–318	Cochlespiridae	<i>Cochlespira</i>	–	sp.	CONO294-08	EU015719.1
MNHN-IM- 2013-59407	ZhongSha 2015	CP4157	19°48' N, 116°29' E	1205–1389	Cochlespiridae	<i>Comispira</i>	–	sp.	CONO2119-18	MG968463.1
MNHN-IM- 2007-42554	SANTO 2006	FR11	15°36'52" S, 167°10'29" E	6–33	Pseudomelatomidae	<i>Crassispira</i>	–	sp.	CONO871-08	KX051344.1
MNHN-IM- 2007-17916	PANGLAO 2005	CP2385	8°51' N, 123°10' E	982–989	Pseudomelatomidae	<i>Comitas</i>	–	sp.	CONO321-08	EU015731.1

DNA sequencing

DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the manufacturer's recommendations. The barcode fragment (658 bp) of the mitochondrial *cox1* gene was amplified using the universal primers LCO1490/HCO2198 (Folmer *et al.* 1994). Polymerase chain reactions (PCRs) were performed using a previously well-established protocol (Puillandre *et al.* 2017). The PCR products were purified and sequenced by the Eurofins sequencing facility.

Species delimitation

The *cox1* sequences were aligned manually (no gaps were inferred). The Automatic Barcode Gap Discovery (ABGD; Puillandre *et al.* 2012a) and Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al.* 2021) methods were used to propose primary species hypotheses (PSH), using the web versions (<https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html> and <https://bioinfo.mnhn.fr/abi/public/asap/>) with default parameters. Both methods use genetic distances only. ABDG automatically detects the gap (the so-called 'barcode gap') between intra- and interspecific distances, which is then used to propose species hypotheses. ASAP screens all the genetic distances from the lowest to the highest and merges sequences into 'groups' that are successively further merged until all sequences form a single group. At each merging step, the partition is evaluated and given a score. At the end of the analyses, the 10 partitions with the lowest scores are provided (the lower the ASAP-score, the better the partition).

The robustness of the PSHs proposed by ABGD and ASAP was then evaluated by checking whether they correspond to highly supported clades, whether they are conchologically and anatomically diagnosable, and whether they are geographically and/or bathymetrically isolated, and in so doing they were converted into secondary species hypotheses (SSH), following the methodology described in Puillandre *et al.* (2012b).

Phylogenetic analyses

Phylogenetic trees were reconstructed using the *cox1* alignment containing the *Sibogasyrinx* sequences, plus *Leucosyrinx*, *Comitas* and *Comispira* sequences for comparison, and outgroups from the respective families of the four genera (Cochlespiridae and Pseudomelatomidae) (Table 1). Maximum Likelihood (ML) and Bayesian Approach (BA) were used to infer phylogenetic trees. ML was performed using the IQ-Tree webserver (<http://iqtree.cibiv.univie.ac.at/>) (Trifinopoulos *et al.* 2016), and robustness of the tree was estimated using ultrafast bootstrapping (1000 replicates) (Minh *et al.* 2013). BA was performed using MrBayes 3.2. (Ronquist *et al.* 2012), as implemented on the Cipres Science Gateway (MrBayes ver. 3.2.2 on XSEDE; <http://www.phylo.org/portal2>), with two parallel analyses consisting each of 8 Markov chains for 30 000 000 generations with 5 swaps at each generation, a sampling frequency of one tree each 10 000 generations, a chain temperature of 0.02 and the parameters of the substitution model estimated during the analysis. Convergence of each analysis was evaluated using Tracer ver. 1.4.1 (Rambaut *et al.* 2014) by checking that ESS values all exceeded 200, and a consensus tree was reconstructed after removing trees from the burn-in phase (first 25% of the trees). For the ML, the best substitution model for each codon position was estimated during the analysis. For the BA, a substitution model with six substitution categories, a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites was used for each codon position independently.

Morphological studies

Protoconchs were measured in standard position and the number of whorls counted according to Bouchet & Kantor (2004). Foregut anatomy was examined by dissections. Radulae were prepared by standard methods (Kantor & Puillandre 2012) and examined by scanning electron microscopy (TeScan TS5130MM) at the Institute of Ecology and Evolution of the Russian Academy of Sciences (IEE RAS).

Abbreviations

AL	=	aperture length
IEE RAS	=	A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russian Federation
I.	=	island
Is.	=	islands
lv	=	live collected specimen
MNHN	=	Muséum national d'histoire naturelle, Paris, France
PSH	=	primary species hypothesis
SL	=	shell length
SSH	=	secondary species hypothesis
stn	=	station
SW	=	shell width
USNM	=	National Museum of Natural History, Smithsonian Institution, Washington DC, USA
ZMA	=	Naturalis Biodiversity Center, Leiden, the Netherlands

Results

Phylogenetic analysis

ABGD and ASAP partitions

ABGD consistently returned a partition with 10 PSHs, numbered from PSH 1 to PSH 10 (Fig. 1). The best ASAP partition includes 9 PSHs, with the ABGD PSHs 4 and 5 grouped into a single PSH. The second best ASAP partition includes 10 PSHs, identical to the ABGD PSHs. The third best ASAP partition includes 11 PSHs, splitting the ABGD PSH 2 into two PSHs, one including the single specimen from the Philippines, the other including the three specimens from Taiwan. The remaining ASAP partitions have a much higher score and will not be discussed further.

From PSHs to SSHs

All the ABGD PSHs are morphologically distinct, although PSHs 1 and 2 exhibit considerable similarity (see below – Taxonomy). All the studied *Sibogasyrinx* have a protoconch suggestive of non-planktotropic development, thus suggesting limited dispersal abilities. All the ABGD PSHs including more than one sample correspond to supported (Posterior Probabilities $PP > 0.95$ and Bootstraps $BS > 90$) or highly supported ($PP > 0.98$ and $BS > 95$) clades. Three main lineages can be recognized, all highly supported. The first one includes PSH 1, 2 and 3, of which PSH 1 and 2 are morphologically very similar; the former is from Papua New Guinea, the latter from Taiwan and the Philippines. They are thus allopatric, but they are not sister taxa, PSH 2 being sister to the morphologically distinct PSH 3 from Papua New Guinea (together with the PSH 1, but not from the same station), but also occurring in the Solomon Islands and Vanuatu. These three PSHs have overlapping bathymetric distributions, between 500 and 1000 m deep (Fig. 2). Because of their *cox-1* distinctiveness and the morphological differentiation between the two most closely related PSHs, we convert these 3 PSHs into 3 SSHs. The split of PSH 2 into two PSHs in the third ASAP partition is interpreted as resulting from genetic distances between allopatric populations within a single species, potentially linked to the limited dispersal abilities of the species.

The second main lineage includes PSH 4 and 5, represented by only one and two samples, respectively. Both are found at similar depths (1200–1700 m), thus deeper than the PSH from the first lineage, and both are found in the Solomon Islands (PSH 5 also occurring in Vanuatu) (Fig. 2). They are easily distinguished morphologically, and we convert these two PSHs into 2 SSHs, thus contradicting the hypothesis proposed in the first partition of ASAP.

The third main lineage includes five PSHs (6 to 10). Except for PSH 9, represented by a single specimen, all these PSHs are found in at least two localities, and all of them have at least one representative from the Solomon Islands, but never from the same station (although sometimes from geographically very close stations). Three PSHs (6, 7 and 9) are found in Papua New Guinea, and again never at the same station. PSHs 8 and 10 are both present in New Caledonia, likewise from different stations. PSH 6 is found in relatively shallow water (between 150 and 500 m), whereas PSHs 7, 8 and 9 are found at depths between 500 and 800 m, and PSH 10 is found even deeper, between 900 and 1000 m. In contrast

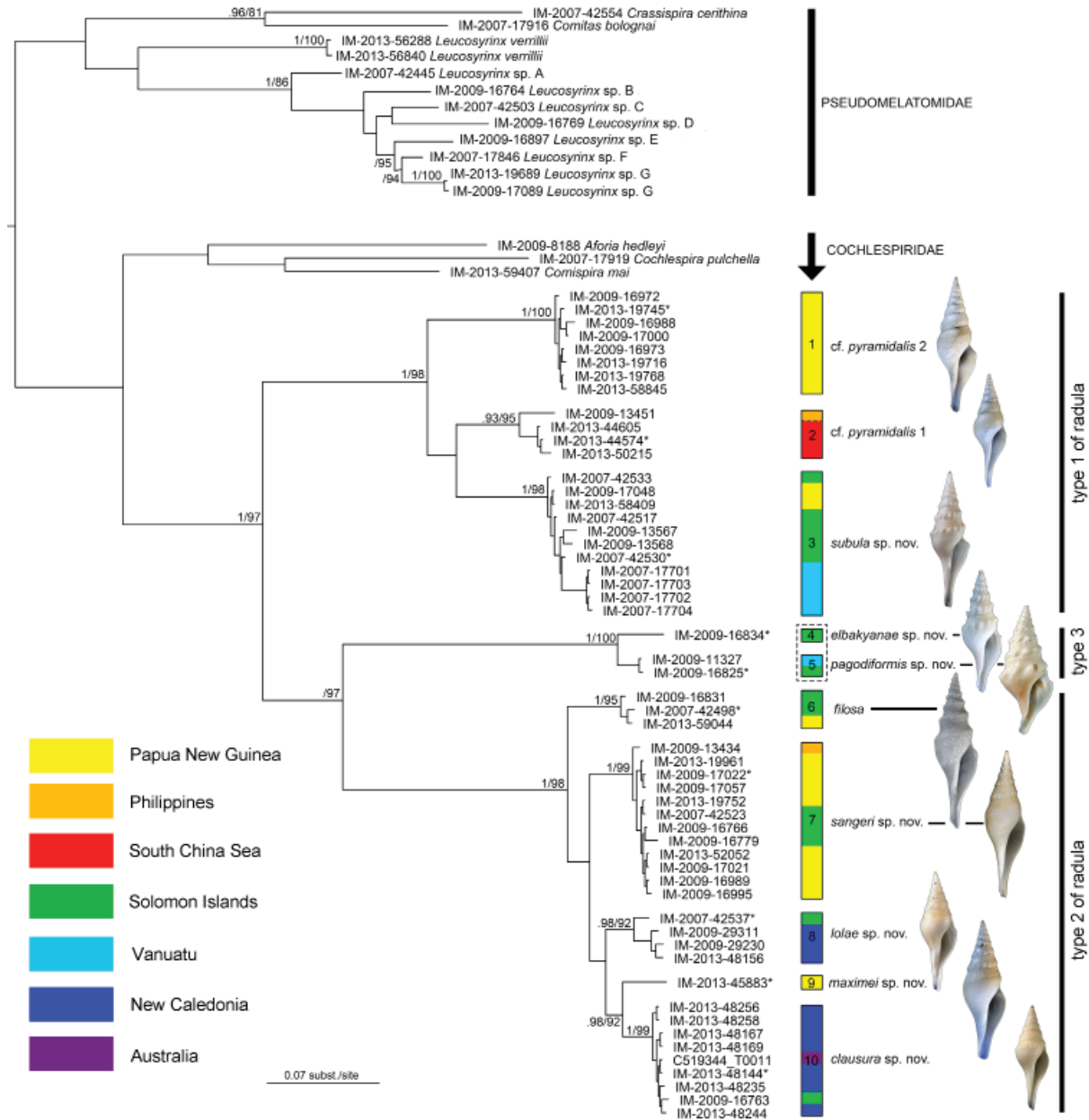


Fig. 1. Bayesian phylogenetic tree obtained with the *cox1* dataset. Posterior probabilities (>0.95) and bootstraps (>90) are shown for each node. The boxes in front of the lineages of *Sibogasyrinx* Powell, 1969 represent the ABGD PSHs, numbered from 1 to 10. Alternative PSH partitions obtained in the second and third-best ASAP partitions are shown with dashed lines. The colors refer to the locality; * = illustrated shells.

to the first two main lineages, the PSHs in the third main lineage tend to be bathymetrically structured, with the shallowest species sister to the four others, and the three intermediate ones in paraphyly and including the deepest one. Finally, diagnostic morphological characters have been found to distinguish these five PSHs. The *cox-1* and morphological distinctiveness together with sympatric distributions sometimes associated with bathymetric partitions, potentially correlated to ecological distinctiveness, are interpreted as arguments supporting the conversion of these five PSHs into SSHs.

The three main lineages recovered (PSH 1–3/PSH 4–5/PSH 6–10), although not distinguishable by shell characters, are characterized by different radula morphologies (see Taxonomy section below; Fig. 1). Furthermore, the *cox-1* distances among these lineages are similar to the distances between genera of Cochlespiridae. For these reasons, they could have been recognized as (sub)genera. However,

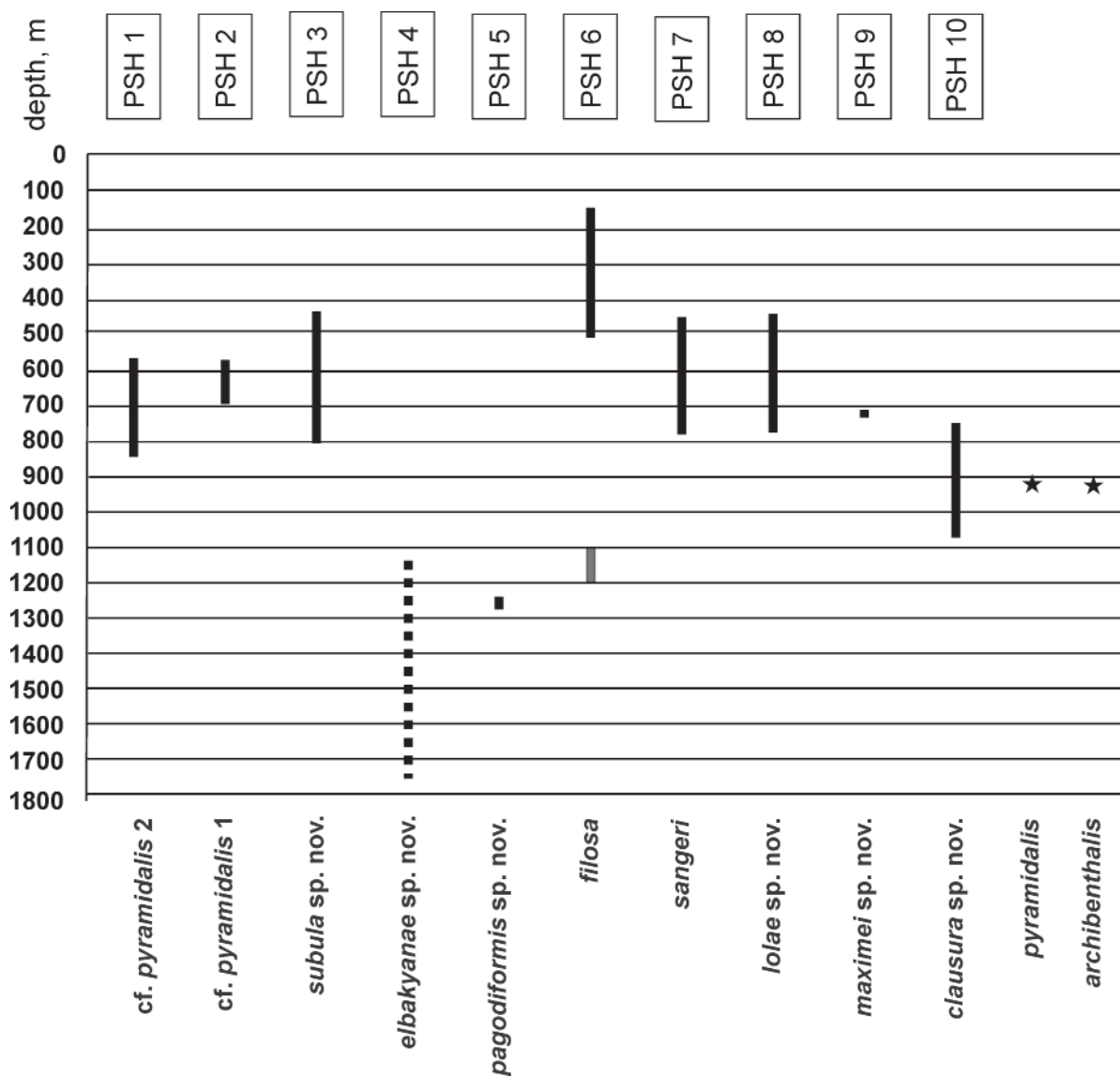


Fig. 2. Bathymetric ranges of species of *Sibogasyrinx* Powell, 1969. The dashed bar for PSH 4 (*S. elbakyanae* sp. nov.) marks the range of the trawl haul in which a single specimen was collected. The grey bar for PSH 6 (*S. filosa* Ardovini, 2021) indicates the depths of occurrence of the type material. Stars indicate the depths of collection of the holotypes of non-sequenced species.

because of their morphological similarity, and, more importantly, because of the lack of DNA sequence data for the type species of the genus (see Taxonomy section below), attributing the name *Sibogasyrinx* to any of the three lineages (and thus new names for the two others) would be untimely, and we thus abstain from naming them.

From SSH to named species

Both PSH 1 and 2 resemble the type of *S. pyramidalis* and we refer to them as *S. cf. pyramidalis* 1 and *S. cf. pyramidalis* 2 (see below – Taxonomy – for more discussion). The specimens of PSH 6 are very similar to the type material of *S. filosa* Ardovali, 2021 and we apply this name to it. PSH 7 contains the holotype of *S. sangeri*, and this name has thus been applied to this PSH. We were not able either to link the name *archibenthalis* (Powell, 1969) or any names proposed in other genera to any of the remaining PSHs (PSHs 3–5 and 8–10), and they are thus described as new species: *S. subula* sp. nov. (= PSH 3), *S. elbakyanae* sp. nov. (= PSH 4), *S. pagodiformis* sp. nov. (= PSH 5), *S. lolae* sp. nov. (= PSH 8), *S. maxime* sp. nov. (= PSH 9) and *S. clausura* sp. nov. (= PSH 10). *Sibogasyrinx archibenthalis* is thus the only species of the genus not represented in the molecular phylogeny.

For comparative purposes, we included several specimens of the distantly related genus *Leucosyrinx* that bear a strong conchological resemblance to the species of *Sibogasyrinx* treated herein. All but one, *L. verrillii* (Dall, 1881) (the type species of the genus), represent still unnamed species that are marked on the tree as *Leucosyrinx* sp. A to *Leucosyrinx* sp. G (Fig. 1). The included specimens represent a subsample of the sequenced material for the corresponding species and therefore we abstain from describing the new species pending a general revision of the genus.

Taxonomy

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Neogastropoda Wenz, 1938
Superfamily Conoidea Fleming, 1822
Family Cochlespiridae Powell, 1942

Genus *Sibogasyrinx* Powell, 1969

Leucosyrinx (*Sibogasyrinx*) Powell, 1969: 343.

Type species

Surcula pyramidalis Schepman, 1913 (original designation).

Diagnosis

Shell small to large, adult length from 27 to 65 mm, narrowly fusiform, rarely pagodiform, with concave to nearly flat subsutural ramp. Spiral sculpture variously developed, always present below shoulder, comprising narrow, close-set cords, often also on subsutural ramp, Shoulder with a row of strong nodules, often obsolete on last whorl.

Venom gland does not pass through nerve ring and opens into oesophagus within or posterior to nerve ring. Radula usually with central tooth, absent in one species, marginal tooth morphology variable, folded longitudinally.

Sibogasyrinx pyramidalis (Schepman, 1913) complex

Sibogasyrinx pyramidalis (Schepman, 1913)

Fig. 3H–I

Surcula pyramidalis Schepman, 1913: 423, pl. 27, fig. 10a–b.

Leucosyrinx (*Sibogasyrinx*) *pyramidalis* – Powell 1969: 343 (23–411), pl. 264 figs 1–5. — Shuto 1970: 171, pl. 11 figs 10–13. — Medinskaya 1999: 176–177, figs 3, 16d–e.

Sibogasyrinx pyramidalis – Kantor *et al.* 2018: 57–58, figs 5e–n, 6c–d.

Material examined

Holotype

TIMOR SEA • 10°48.6' S, 123°23.1' E; depth 918 m; ZMA.MOLL.136836.

Remarks

Kantor *et al.* (2018) provided illustrations of shells and radulae of sequenced specimens of what they considered to be *S. pyramidalis*. The specimens studied were collected off Luzon Island (Philippines) and in the central South China Sea (= PSH 2, *S. cf. pyramidalis* 1). The shell outline of these specimens of this generally variable species matched the illustration of the holotype, which was not examined. The present molecular analysis revealed that there are two molecularly distinct but morphologically cryptic species that match the description and illustrations of the holotype of *S. pyramidalis* (Schepman 1913: fig. 10a–b; Shuto 1970: pl. 11, figs 10–13; Fig. 3H–I herein). The second species, not discussed in Kantor *et al.* (2018), was collected in the Bismarck Sea and also displays significant shell variability (= PSH 1, *S. cf. pyramidalis* 2). The geographic ranges of these two PSHs do not include the type locality of *S. pyramidalis* (Timor Sea, Pulau Rote Island). There are two possible explanations for this: one of our species represents the true *S. pyramidalis*, or *S. pyramidalis* is a third species and both of ours are new to science. Unfortunately, this can only be resolved by sequencing topotypic material from the Timor Sea. In order to not add to the taxonomic ambiguity, we presently refrain from taking any taxonomic decision, but for the sake of convenience refer here to our molecular species as *S. cf. pyramidalis* 1 (= *S. pyramidalis* sensu Kantor *et al.* 2018) and *S. cf. pyramidalis* 2.

Medinskaya (1999: fig. 16d–e) illustrated the radula of a specimen from Indonesia (Tanimbar I., 08°36' S, 131°33' E, 699–676 m) collected close to the type locality. Unfortunately, the shell was not illustrated and the identification of the specimen cannot be confirmed. Its radula is identical to that of *S. cf. pyramidalis* 1 and *S. cf. pyramidalis* 2 (Kantor *et al.* 2018: figs 5c–d, 6a–b; Fig. 4A–D herein).

Sibogasyrinx cf. pyramidalis (Schepman, 1913) 1 (= PSH 2)

Figs 3A–G, 4A–B

Material examined (all sequenced)

PHILIPPINES • 1 lv; 15°20' N, 121°37' E; depth 593–600 m; AURORA 2007, stn CP2729; MNHN-IM-2009-13451.

SOUTH CHINA SEA • 2 lv; 20°01' N, 115°02' E; depth 700–723 m; NanHai 2014, stn CP4118; MNHN-IM-2013-44574, MNHN-IM-2013-44605 • 1 lv; 20°29' N, 116°08' E; depth 590–633 m; DongSha 2014, stn CP4129; MNHN-IM-2013-50215.

Description

MEASUREMENTS (largest specimen). SL 65.2 mm, AL (with canal) 35.1 mm, AL (without canal) 21.0 mm, SW 18.5 mm.

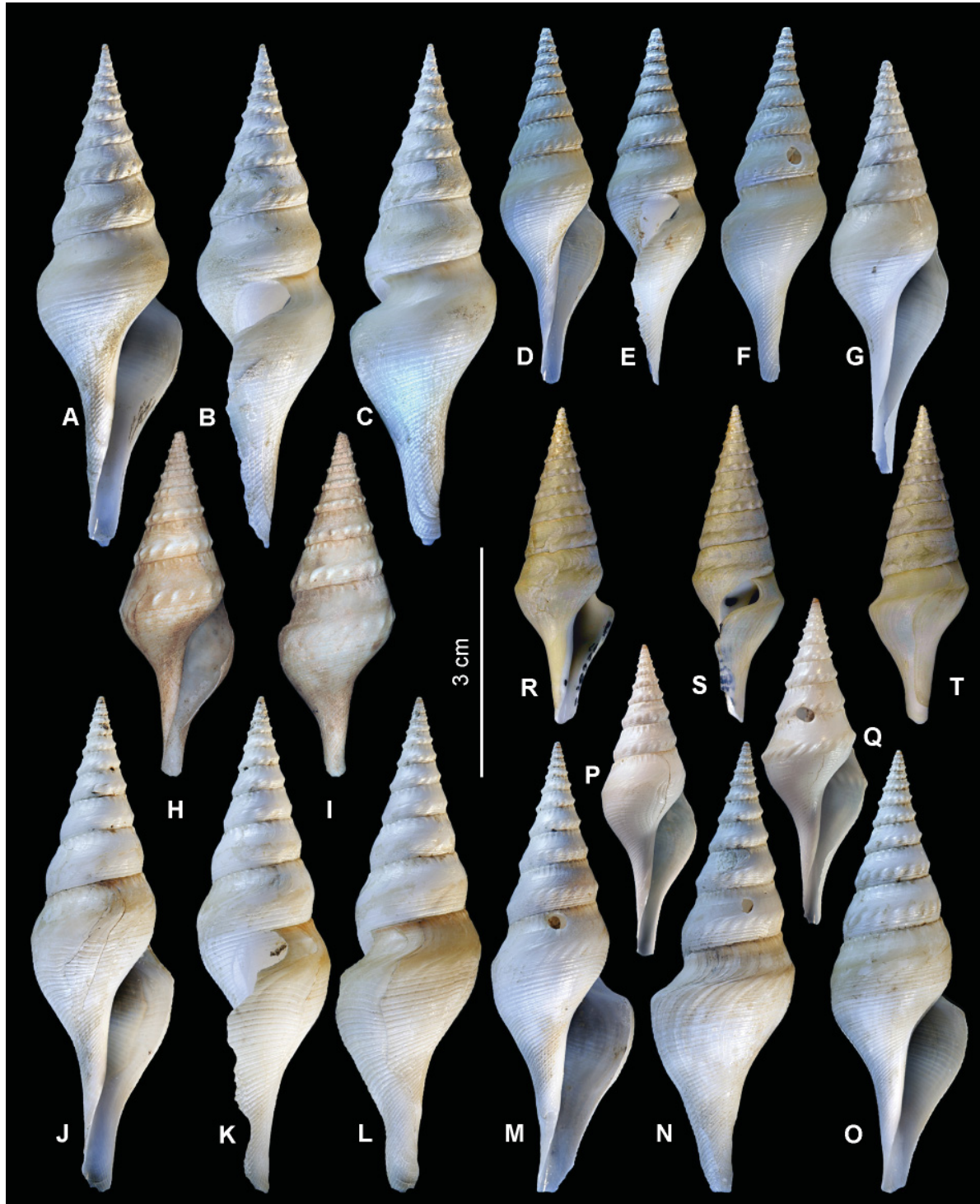


Fig. 3. *Sibogasyrinx pyramidalis* (Schepman, 1913) complex. **A–G.** *Sibogasyrinx* cf. *pyramidalis* 1. **A–C.** South China Sea, MNHN-IM-2013-44605, SL 65.2 mm. **D–F.** Philippines, MNHN-IM-2009-13451, SL 46.8 mm. **G.** South China Sea, MNHN-IM-2013-44574, SL 53.9 mm. **H–I.** *Surcula pyramidalis* Schepman, 1913, holotype, ZMA.MOLL.136836, SL 45 mm (photos by K. Hasegawa, copyright Naturalis, Leiden). **J–Q.** *Sibogasyrinx* cf. *pyramidalis* 2, Papua New Guinea. **J–L.** MNHN-IM-2013-19745, SL 65.2 mm. **M–O.** MNHN-IM-2009-17000, SL 59.2 mm. **P.** MNHN-IM-2009-16973, SL 41 mm. **Q.** MNHN-IM-2009-16988, SL 43 mm. **R–T.** *Sibogasyrinx archibenthalis* (Powell, 1969), holotype, USNM 238773, SL 41.8 mm. All shells to same scale.

SHELL. Moderately thick, strong except for fragile outer aperture lip, fusiform, with high spire and long, narrow, straight siphonal canal. Protoconch small, globose, of about 1.5 strongly convex, microshagreened whorls, eroded or missing in all specimens. Early teleoconch whorls weakly to moderately angular at shoulder. Largest available specimen (SL 65.2 mm) of 10.3 teleoconch whorls. Suture shallowly impressed, subsutural ramp broad, weakly concave to flat. All teleoconch whorls with a subsutural row of nodules, corresponding in shape to upper parts of thickened growth lines. Nodules more distinct on upper whorls, increasing in number, up to 30 on penultimate whorl and 37 on last whorl in largest specimen. Subsutural ramp may be completely smooth, or sometimes with very weak spiral striation or dendritic lines. Shoulder with pronounced thickened and rounded nodules, reaching lower suture, weakly opisthocline on upper whorls and more strongly inclined and confluent with growth lines on lower whorls. Nodules evanesce on last and even penultimate whorls at SL over 50 mm and shoulder becomes evenly rounded; their number increase with size from 14–15 on upper whorls to 21–22 on lower whorls. Spiral sculpture of 3–6 moderately pronounced, closely spaced narrow cords on shoulder, crossing shoulder nodules on spire whorls. Last whorl below shoulder with 40–45 cords varying in width, their intervals 0.5–2 times width of cords, also distinct on canal. Shell base gradually narrowing towards long, narrow, nearly straight siphonal canal. Aperture narrow, constricted posteriorly, with narrow and thin parietal callus, outer lip with rounded angle at shoulder, weakly convex below shoulder and weakly concave at transition to canal. Anal sinus moderately deep, subsutural, broadly arcuate, confluent with large forward extension of outer lip. Shell off-white with very light yellowish subsutural band, protoconch pale tan. Periostracum persists on part of shell, light yellowish.

ANATOMY. Foregut similar to that of *Sibogasyrinx* cf. *pyramidalis* 2 (see below), except for presence of a large oval accessory salivary gland, adjoining oesophagus, with rather thick duct, entering proboscis and following along its wall.

RADULA (n = 2; MNHN-IM-2009-13451, MNHN-IM-2013-50215). Comprising approximately 40 rows of teeth, 15 nascent, short, length ca 2.5 mm (15% of AL without canal). Radula width up to 530 µm (3.3% of AL without canal). Central tooth with broad, subrectangular basal plate and anteriorly broadly concave, borders distinct and with narrow but rather long, sharply pointed cusp. Marginal teeth with strongly thickened posterior edges, folded longitudinally. When immature, teeth nearly flat with elevated posterior edge, on developing part of radular tooth folding clearly visible (on Fig. 4A not fully folded teeth are marked by white arrows), bringing posterior and anterior edges close together. During tooth maturation the edges, particularly posterior one, progressively thicken, so that fully formed tooth appears duplex (Fig. 4B).

Distribution

The confirmed distribution is the South China Sea and the Philippines Sea, at 590–700 m.

Sibogasyrinx cf. *pyramidalis* (Schepman, 1913) 2 (= PSH 1)
Figs 3J–Q, 4C–D, 5

Material examined (all sequenced)

PAPUA NEW GUINEA • 2 lv; off Manus I.; 02°16' S, 147°29' E; depth 679–685 m; BIOPAPUA, stn CP3689; MNHN-IM-2009-16972, MNHN-IM-2009-16973 • 1 lv; N of Rabaul; 04°04' S, 151°56' E; depth 585–601 m; BIOPAPUA, stn CP3671; MNHN-IM-2009-16988 • 1 lv; N of Rabaul; 04°04' S, 151°50' E; depth 702–724 m; BIOPAPUA, stn CP3672; MNHN-IM-2009-17000 • 1 lv; Bismarck Sea, N of Long I.; 05°11' S, 147°03' E; depth 688 m; PAPUA NIUGINI, stn CP3981; MNHN-IM-2013-19716 • 1 lv; Bismarck Sea, N of Long I.; 05°10' S, 147°03' E; depth 724 m; PAPUA NIUGINI, stn CP3982; MNHN-IM-2013-19745 • 1 lv; Bismarck Sea, NW of Long I.; 05°12' S, 146°59' E; depth 470–508 m;

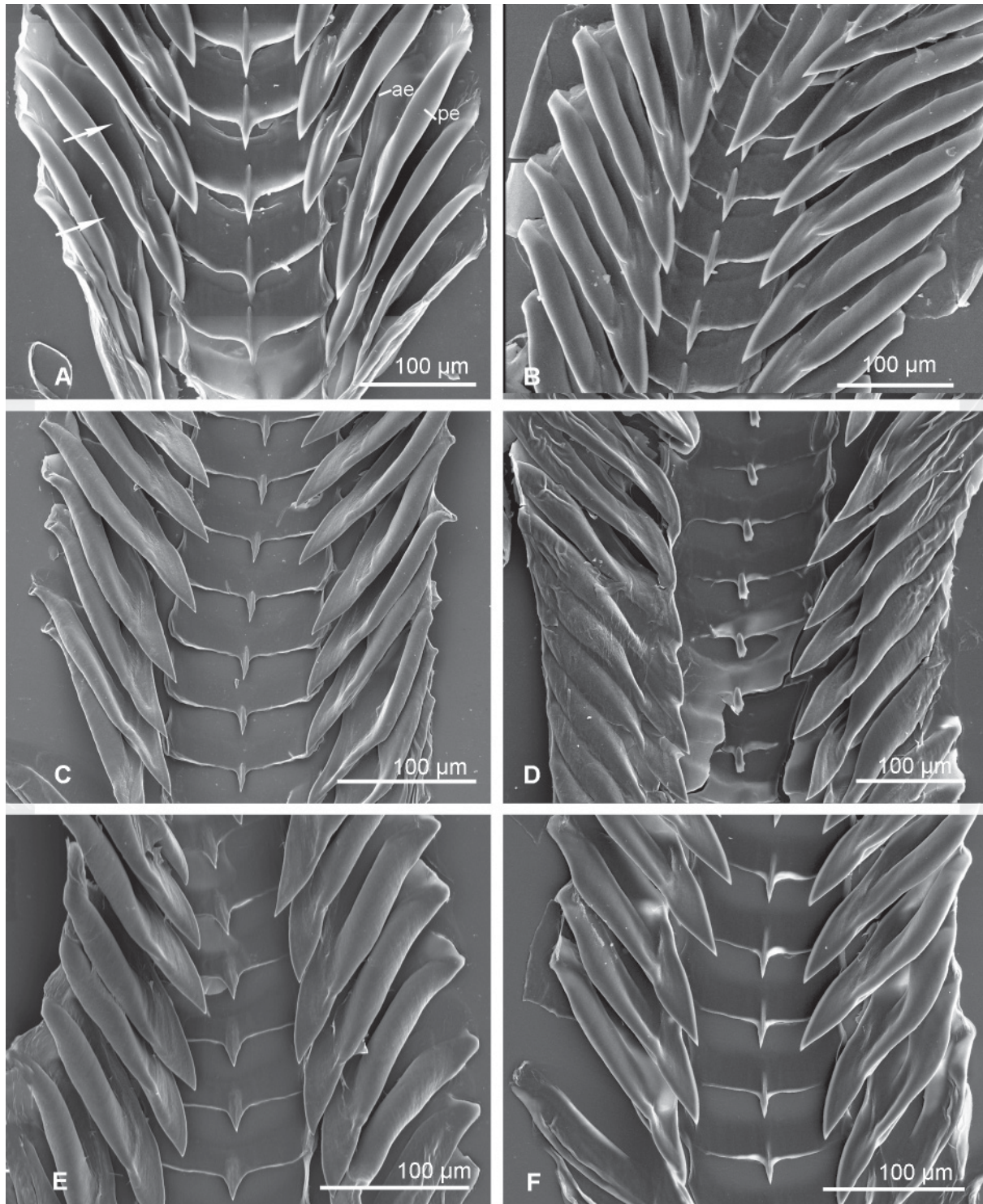


Fig. 4. Radulae of species of *Sibogasyrinx* Powell, 1969. **A–B.** *S. cf. pyramidalis* (Schepman, 1913) 1, MNHN-IM-2009-13451 (shell seen on Fig. 3D–F). **A.** Part of radula with marginal teeth not fully formed; white arrows indicate teeth that are not fully folded longitudinally (ae = anterior tooth edge; pe = posterior tooth edge). **B.** Part of radula with fully formed marginal teeth. **C.** *S. cf. pyramidalis* 2, MNHN-IM-2009-16972. **D.** *S. cf. pyramidalis* 2, MNHN-IM-2009-17000 (shell seen on Fig. 3M–O). **E.** *S. subula* sp. nov., MNHN-IM-2007-17703. **F.** *S. subula* sp. nov., MNHN-IM-2009-13568 (shell seen on Fig. 6H–I).

PAPUA NIUGINI, stn DW3983; MNHN-IM-2013-19768 • 1 lv; New Ireland, 02°42' S, 150°02' E; depth 827–966 m; KAVIENG 2014, stn CP4483; MNHN-IM-2013-58845.

Description

MEASUREMENTS (largest specimen). SL 65.2 mm, AL (with canal) 34.7 mm, AL without canal 22.9 mm, SW 18.0 mm.

SHELL. Extremely similar to that of *Sibogasyrinx* cf. *pyramidalis* 1. The only slight difference is the larger number of spiral cords crossing the shoulder nodules. Penultimate whorl of *S.* cf. *pyramidalis* 1 with 5–6 cords (increasing with SL), 6–8 in *S.* cf. *pyramidalis* 2.

ANATOMY (n = 2, MNHN-IM-2009-16972, MNHN-IM-2009-17000). Head with long, cylindrical tentacles, rounded on tips with closely spaced bases, eyes absent. One specimen (MNHN-IM-2009-17000) male, with long penis with obliquely truncated tip. Seminal papilla occupies entire tip and is surrounded by circular fold. Proboscis long, coiled, with broad conical base, occupied by large bulbous buccal mass, spanning posterior ¼ of proboscis and protruding backwards from proboscis. Proboscis sheath with very thin transparent walls. Remaining anterior part of proboscis narrow, gradually diminishing in diameter towards its tip. Proboscis retractors well defined, powerful and numerous, attached to posteriormost edge of rhynchodeum. Radular sac and short oval odontophore situated on right side of buccal mass, posterior to rear of proboscis. Oesophagus adjoining buccal mass slightly constricted and forming a moderately long loop before passing through nerve ring. Salivary glands irregularly shaped, covering dorsal portion of nerve ring. Accessory salivary gland not traced. Venom gland thick, long, strongly convoluted, opens dorsally into oesophagus, immediately posterior to nerve ring (Fig. 5B). Muscular bulb oval, of moderate size, situated to the right of oesophagus.

RADULA (n = 2; MNHN-IM-2009-16972, MNHN-IM-2009-17000). Comprising approximately 40 rows of teeth, 15 nascent, short, length (measured only in MNHN-IM-2009-16972) ca 1.7 mm (14% of AL without canal). Radula width up to 300 µm (2.5% of AL without canal). Shape of teeth very similar to that of *Sibogasyrinx* cf. *pyramidalis* 1, central tooth has less rounded posterior margin and in one specimen (MNHN-IM-2009-17000, Fig. 4D) the cusp is obtuse.

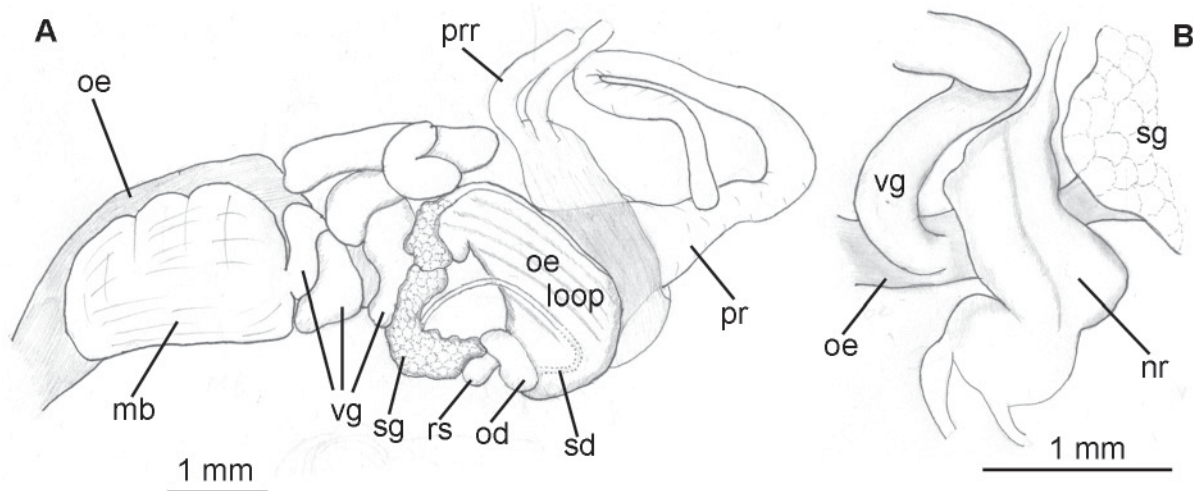


Fig. 5. Anterior foregut of *Sibogasyrinx* cf. *pyramidalis* (Schepman, 1913) 2, MNHN-IM-2009-16972. **A.** Right latero-dorsal view. **B.** Dorsal view of the nerve ring and opening of the venom gland. Abbreviations: mb = muscular bulb of the venom gland; nr = circumoesophageal nerve ring; od = odontophore; oe = oesophagus; pr = proboscis; prr = proboscis retractors; rs = radular sac; sd = salivary duct; sg = salivary gland; vg = venom gland.

Remarks

Despite the similarities in shell and radular morphology, *Sibogasyrinx* cf. *pyramidalis* 1 and *Sibogasyrinx* cf. *pyramidalis* 2 are clearly distinct from a molecular perspective. One morphological character of the foregut that separates the two species is the presence of an accessory salivary gland in the former.

Distribution

The confirmed distribution is Papua New Guinea, at 585–827 m.

Sibogasyrinx archibenthalis (Powell, 1969) Fig. 3R–T

Leucosyrinx (*Sibogasyrinx*) *archibenthalis* Powell, 1969: 344, pl. 264 figs 6–7.

Material examined

Holotype

PHILIPPINES • Mindanao I., Iligan Bay, Tabu Point; 08°16'45" N, 124°02'49" E; depth 924 m; R/V *Albatross*, stn 5513; USNM 238773.

Description

MEASUREMENTS (holotype). SL 41.8 mm.

SHELL. Fusiform, narrow, with high, very narrow, flat-sided spire and relatively short, almost straight, un-notched siphonal canal. Protoconch small, globose, of 1.5 smooth whorls. Teleoconch of 12 whorls. Spire whorl profile quite straight and descending steeply to a narrowly rounded, flange-like, peripheral carina, abutting lower suture. Last whorl distinctly angled by peripheral carina, and base rapidly contracting toward moderately long anterior canal. Axial sculpture of rounded peripheral nodules, about 13 per whorl, but these become obsolete on last two whorls; subsutural nodules or folds lacking. Spiral sculpture of dense well defined and regular spiral cords, 11–12 on subsutural ramp. Anal sinus moderately deep, subsutural, broadly arcuate, confluent with large forward extension of outer lip. Colour opaque white, covered by a thin pale buff periostracum.

Remarks

The species is known only from the holotype. In shell shape it is most similar to *S. pyramidalis*. The differences are most obvious when comparing specimens of the same size (e.g., Fig. 3 D–F and 3R); the last whorl is lower and the canal is proportionally much shorter in *S. archibenthalis*, while the spiral cords on the subsutural ramp are more pronounced and are of the same strength as on the remaining part of the last whorl. The last whorl is more angular in *S. archibenthalis* and the shell has a higher number of teleoconch whorls; in the holotype of *S. archibenthalis* the number of teleoconch whorls is 12 (SL 43 mm), compared with 9.5 (SL 46.8 mm) in samples of *S. cf. pyramidalis* 1 from the Philippines of similar shell size. Therefore, at present we consider *S. archibenthalis* to be a valid species.

Sibogasyrinx subula sp. nov. (= PSH 3) [urn:lsid:zoobank.org:act:6A992BBF-7C62-4F15-BFCC-AD9F347ED379](https://zoobank.org/act:6A992BBF-7C62-4F15-BFCC-AD9F347ED379) Figs 4E–F, 6

Sibogasyrinx sp. – Bouchet *et al.* 2011: figs 11b, 12b–c.

Diagnosis

Shell large, reaching 57 mm in length, narrowly fusiform, with concave, nearly smooth subsutural ramp with darker subsutural band on posterior half of last whorl and strong nodules on shoulder. Spiral sculpture of distinct, closely spaced cords below subsutural ramp. Radula with central tooth and duplex marginal teeth.

Etymology

Latin '*subula*' (noun in apposition), meaning 'awl', with reference to the general appearance of the spire.

Material examined

Holotype

SOLOMON ISLANDS • SE of Sta Isabel I.; 08°17' S, 160°00' E; depth 482–604 m; SALOMON 2, stn CP2187; MNHN-IM-2007-42530.

Other material (all sequenced)

PAPUA NEW GUINEA • 1 lv; 05°39' S, 153°59' E; depth 654–660 m; BIOPAPUA, stn CP3750; MNHN-IM-2009-17048 • 1 lv; New Ireland; 02°13' S, 150°12' E; depth 564–743 m; KAVIENG 2014, stn CP4448; MNHN-IM-2013-58409.

SOLOMON ISLANDS • 2 lv; SE of Sta Isabel I.; 08°17' S, 160°00' E; depth 464–523 m; SALOMON 2, stn CP2184; MNHN-IM-2009-13567, MNHN-IM-2009-13568 • 1 lv; SW of Sta Isabel I.; 08°25' S, 159°27' E; depth 440–521 m; SALOMON 2, stn CP2194; MNHN-IM-2007-42533 • 1 lv; 08°41' S, 157°38' E; depth 814–980 m; SALOMON 2, stn CP2276; MNHN-IM-2007-42517.

VANUATU • 4 lv; 15°00' S, 166°55' E; depth 630–705 m; BOA1, stn CP2432; MNHN-IM-2007-17701 to IM-2007-17704.

Description

MEASUREMENTS (holotype). SL 55 mm, AL (with canal) 31 mm, AL (without canal) 17.5 mm, SW 15.6 mm.

SHELL (holotype). Moderately thick, strong except for fragile outer lip of aperture, fusiform, with high spire and long, narrow, straight siphonal canal. Protoconch small, globose, of about 1.5 strongly convex, microshagreened whorls. Protoconch/teleoconch transition marked by arcuate axial rib and appearance of definitive sculpture. Protoconch diameter 1.0 mm, height 0.79 mm. Teleoconch whorls angular at shoulder. Teleoconch comprising just under 10 whorls in total. Suture shallowly impressed, subsutural ramp broad, strongly concave. Subsutural region with a row of distinct sigmoidal nodules that correspond in shape to upper parts of thickened growth lines, about 20 on first whorl, 17–19 on second–fourth whorls, 32 on penultimate and 30 on last whorl. Subsutural ramp smooth except for subsutural row of nodules, few thickened growth lines and 3–4 very weak spiral threads on last and penultimate whorls. Shoulder with pronounced thickened and rounded nodules, weakly opisthoclinal on upper whorls, but more strongly inclined and confluent with growth lines on last whorl; 17 on penultimate and antepenultimate whorls and 19 on last whorl. Spiral sculpture of 4–5 moderately pronounced, narrow cords on shoulder, seen both on nodules and in their intervals, and rather distinct, weakly rounded cords below shoulder, some flattened. Single cord appears on 3rd whorl, two cords on other whorls, including penultimate one. On last whorl cords occupy entire shell below shoulder, varying in width, their intervals 1–2 times width of cords, in total 48 cords on last whorl, of which 28 on canal. Shell base gradually narrowing towards long, narrow, nearly straight siphonal canal. Aperture narrow, constricted posteriorly, with very narrow and thin parietal callus, outer lip partially broken, with rounded angle at shoulder, weakly convex below shoulder and weakly concave at transition to canal. Anal sinus moderately deep, subsutural, broadly

arcuate, confluent with large forward extension of outer lip. Shell off-white, with very light yellowish subsutural band and darker subsutural band on posterior half of last whorl, protoconch light tan.

ANATOMY (n = 1, MNHN-IM-2009-13568). Head with long cylindrical tentacles, rounded on tips with closely spaced bases, eyes absent. Specimen male, with long penis with obliquely truncated tip. Seminal

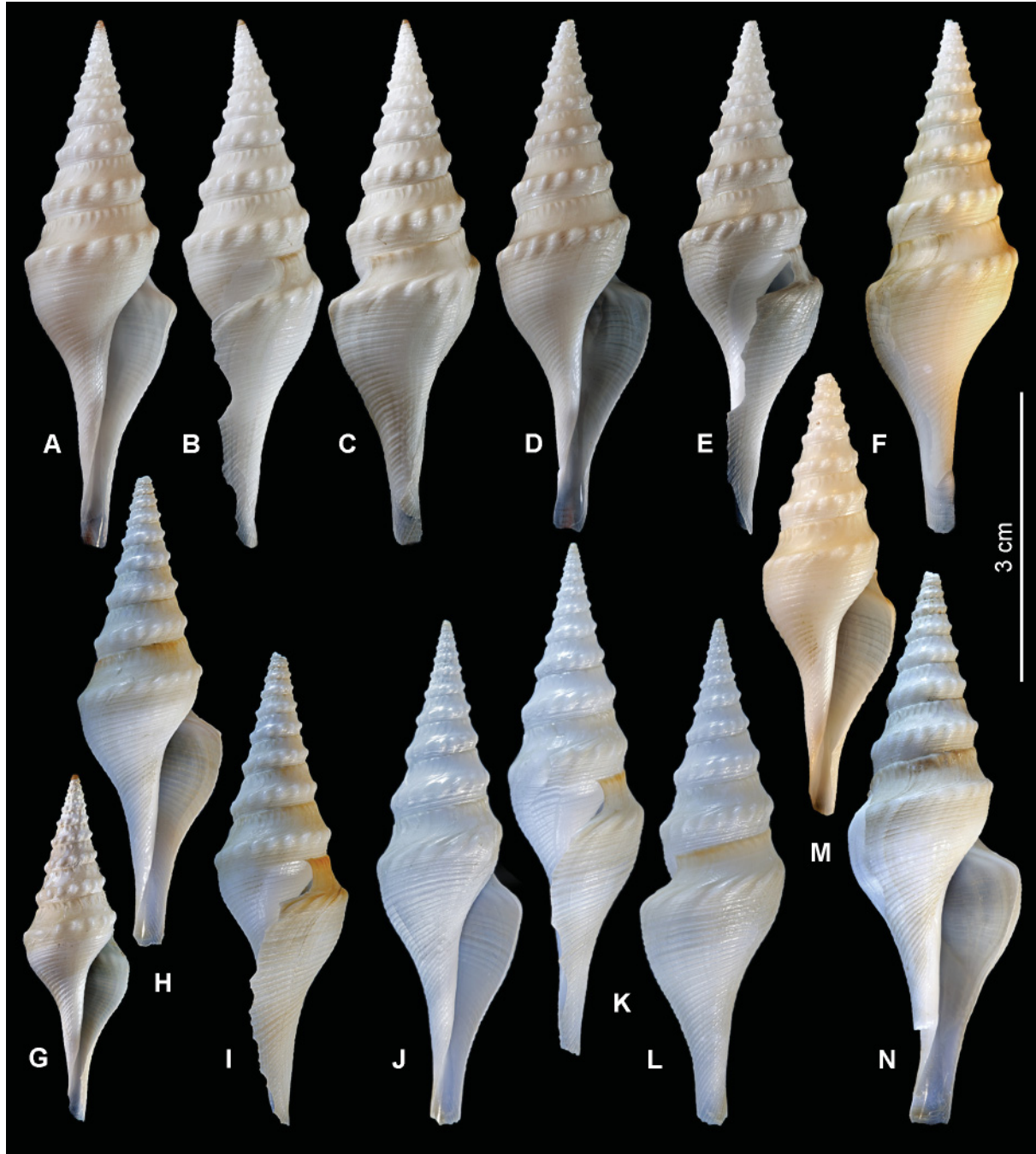


Fig. 6. *Sibogasyrinx subula* sp. nov. **A–C.** Solomon Islands, holotype, MNHN-IM-2007-42530, SL 55 mm. **D–F.** Solomon Islands, MNHN-IM-2007-42533, SL 53.6 mm. **G.** Papua New Guinea, MNHN-IM-2013-58409, SL 36.3 mm. **H–I.** Solomon Islands, MNHN-IM-2009-13568, SL 49.4 mm (radula seen on Fig. 4F). **J–L.** Vanuatu, MNHN-IM-2007-17704, SL 53 mm. **M.** Vanuatu, MNHN-IM-2007-17701, SL 46.0 mm. **N.** Solomon Islands, MNHN-IM-2009-13567, SL 57.4 mm. All shells to same scale.

papilla occupies entire tip and is surrounded by circular fold. Proboscis conical, with broad base, but very narrow along most of its length. Proboscis retractors large, arranged in two bundles attached to proboscis base. Buccal mass very large and broad, nearly as long as proboscis, oesophagus forming short loop before nerve ring. Venom gland thick, medium-long and convoluted, opening dorsally into oesophagus just posterior to nerve ring. Muscular bulb very large.

RADULA (n = 3; MNHN-IM-2007-17701, MNHN-IM-2007-17703, MNHN-IM-2009-13568). All specimens with similar radular morphology, radula comprising 38–40 rows of teeth, 11–17 nascent, short, length ca 1.8 mm (11% of AL without canal). Radula width up to 310 µm (1.9% of AL without canal). Central tooth with broad, subrectangular basal plate, anteriorly overlapped by preceding tooth, borders distinct, with narrow, sharply pointed cusp. Marginal teeth with strongly thickened posterior edges, folded longitudinally (Fig. 4E–F), in all details similar to those of *Sibogasyrinx* cf. *pyramidalis* 1.

Remarks

Largest specimen attains an SL of 57.4 mm.

The other specimens are rather similar to the holotype in shell shape and sculpture. The entire subsutural ramp may be pale yellowish on the last whorl, but the subsutural zone of the posterior part of last whorl in larger specimens is always more darkly coloured than the rest of the shell. The subsutural ramp may be completely smooth or with indistinct spiral threads, the shoulder angulation on the last whorl is sometimes less distinct than in the holotype, as may be the cords below the shoulder on the penultimate whorl (up to 4).

In shell outline, the new species resembles its congener *Sibogasyrinx filosa*, but differs in having much less distinct spiral sculpture on the subsutural ramp, as well as in its larger size (maximal SL 57.4 mm in *S. subula* sp. nov. and 52 mm in *S. filosa*) and radular morphology. The shell shape of the new species also strongly resembles that of some species of *Leucosyrinx*, particularly *L. verrillii* (Dall, 1881) (Fig. 13A–C) and to a lesser extent the smaller specimens of *Leucosyrinx* sp. B and *Leucosyrinx* sp. G (Fig. 13D and 13I, respectively). All these species of *Leucosyrinx*, however, have a different radular morphology, shorter siphonal canal and, according to the molecular tree (Fig. 1) and other published Conoidea phylogenies (Puillandre *et al.* 2011; Abdelkrim *et al.* 2018), belong to a different family.

Distribution

This species is known from the Solomon Islands, Papua New Guinea and Vanuatu, and has a relatively broad bathymetric range, from 440 to 814 m.

Sibogasyrinx sangeri Kantor, Fedosov & Puillandre, 2018 (= PSH 7)
Figs 7, 8A–B

Sibogasyrinx sangeri Kantor, Fedosov & Puillandre, 2018: 58, figs 5e–n, 6c–d.

Material examined

Holotype

PAPUA NEW GUINEA • 07°52' S, 148°03' E; depth 575–655 m; BIOPAPUA, stn CP3729; MNHN-IM-2009-17022 (sequenced).

Other material (all sequenced)

PAPUA NEW GUINEA • 2 lv; 04°04' S, 151°56' E; depth 585–601 m; BIOPAPUA, stn CP3671; MNHN-IM-2009-16989, MNHN-IM-2013-52052 • 1 lv; 04°24' S, 151°50' E; depth 788–805 m;

BIOPAPUA, stn CP3674; MNHN-IM-2009-16995 • 1 lv; off Woodlark Is.; 09°08' S, 152°19' E; depth 448–470 m; BIOPAPUA, stn CP3742; MNHN-IM-2009-17057 • 1 lv; 05°39' S, 153°59' E; depth 654–660 m; BIOPAPUA, stn CP3750; MNHN-IM-2009-17021 • 1 lv; N of Long I.; 05°10' S, 147°03' E; depth 724 m; PAPUA NIUGINI, stn CP3982; MNHN-IM-2013-19752 • 1 lv; Dampier Strait, E of Umboi I.; 05°35' S, 148°13' E; depth 630–870 m; PAPUA NIUGINI, stn CP4014; MNHN-IM-2013-19961.

PHILIPPINES • 1 lv; 15°45' N, 121°45' E; depth 562 m; AURORA 2007, stn CP2663; MNHN-IM-2009-13434.

SOLOMON ISLANDS • 1 lv; Sta Isabel I.; 08°47' S, 159°40' E; depth 645–840 m; SALOMON 2, stn CP2181; MNHN-IM-2009-16766 • 2 lv; Rendova I.; 08°36' S, 157°27' E; depth 509–520 m; SALOMON 2, stn CP2288; MNHN-IM-2007-42523, MNHN-IM-2009-16779.

Description

MEASUREMENTS. Holotype: SL 54.1 mm, AL (with canal) 31.3 mm, AL (without canal) 16.4 mm, SW 14.1 mm. Largest available specimen attains SL 55.8 mm (MNHN-IM-2009-16779; Fig. 7D–E).

SHELL. Thin, fragile, variable in shape, from narrowly fusiform to moderately broad (SW/SL ratio from 0.22 to 0.27), with rather high spire and long, narrow, straight siphonal canal. Protoconch small, globose, of 1.75 strongly convex, microshagreened whorls. Protoconch/teleoconch transition indistinct. Protoconch diameter about 1.1 mm, height 1.2 mm. Early teleoconch whorls angular, usually in lower part just above suture, but sometimes at mid-whorl; last whorl strongly to very weakly angled or evenly rounded, even in specimens of the same size. Teleoconch comprising up to 10 whorls. Suture shallow, subsutural ramp with a row of distinct, closely spaced nodules, 10 on first whorl, 14 on second whorl, becoming more broadly spaced and less discernible on later whorls, sometimes obsolete on last whorl of largest specimens. Subsutural zone very weakly concave, nearly straight on penultimate and last whorls, smooth except for a few irregularly spaced and indistinct spiral threads (sometimes oblique), or several rather pronounced flattened spiral cords (Fig. 7J; MNHN-IM-2009-13434). Lower part of whorls with a row of larger, more pronounced nodules, just above suture in upper whorls or sometimes nearer mid-whorl. In some specimens nodules absent on last whorl. Last whorl may bear low carina at periphery (in specimens with nodules absent), giving it very weakly angled outline. Below periphery 2–3 distinct spiral cords on penultimate whorl and about 30 cords below carina on last whorl and 20 on canal. Shell base gradually narrowing towards long, nearly straight siphonal canal. Aperture narrow, constricted posteriorly with broad, very thin parietal callus, outer lip partially broken, convex and weakly angled in upper part and slightly convex below shoulder, and shallowly concave at transition to canal. Anal sinus moderately deep, subsutural, broadly arcuate, growth lines confluent with large forward extension of outer lip. Growth lines thin but distinct. Shell uniformly off-white, protoconch light tan.

ANATOMY (n = 1, MNHN-IM-2009-16995). Proboscis of moderate length in contracted stage, buccal mass situated outside proboscis. Oesophagus very broad, forming short loop before passing through nerve ring. Venom gland opening into oesophagus ventrally and immediately posterior to nerve ring.

RADULA (n = 1, MNHN-IM-2009-16995) (Fig. 8A–B). Relatively short, comprising ca 40 rows of teeth, with long nascent part (15–16 rows). Radula length 2.2 mm (16% of AL without canal), width up to 365 µm (2.7% of AL without canal). Central tooth with subrectangular basal plate, very shallowly arcuate anteriorly, with distinct borders and weak cusp. Marginal teeth flat when formed, becoming trough-shaped during maturation, folded longitudinally when fully formed. On developing part of radula, folding of teeth occurs abruptly, within one subsequent row (on Fig. 8B white arrow indicates last still unfolded tooth, while black arrow with white outline indicate the first folded tooth). Folding

evident at 17th row in radula studied. Resulting folded tooth moderately broad, with sharp pointed tip, formed by overlapping of both thickened margins (on Fig. 8A these overlapping parts are marked by hollow white arrows).

Distribution

This species is known from the Solomon Islands, Papua New Guinea and the Philippines, over a relatively broad bathymetric range, from 448 to 788 m.

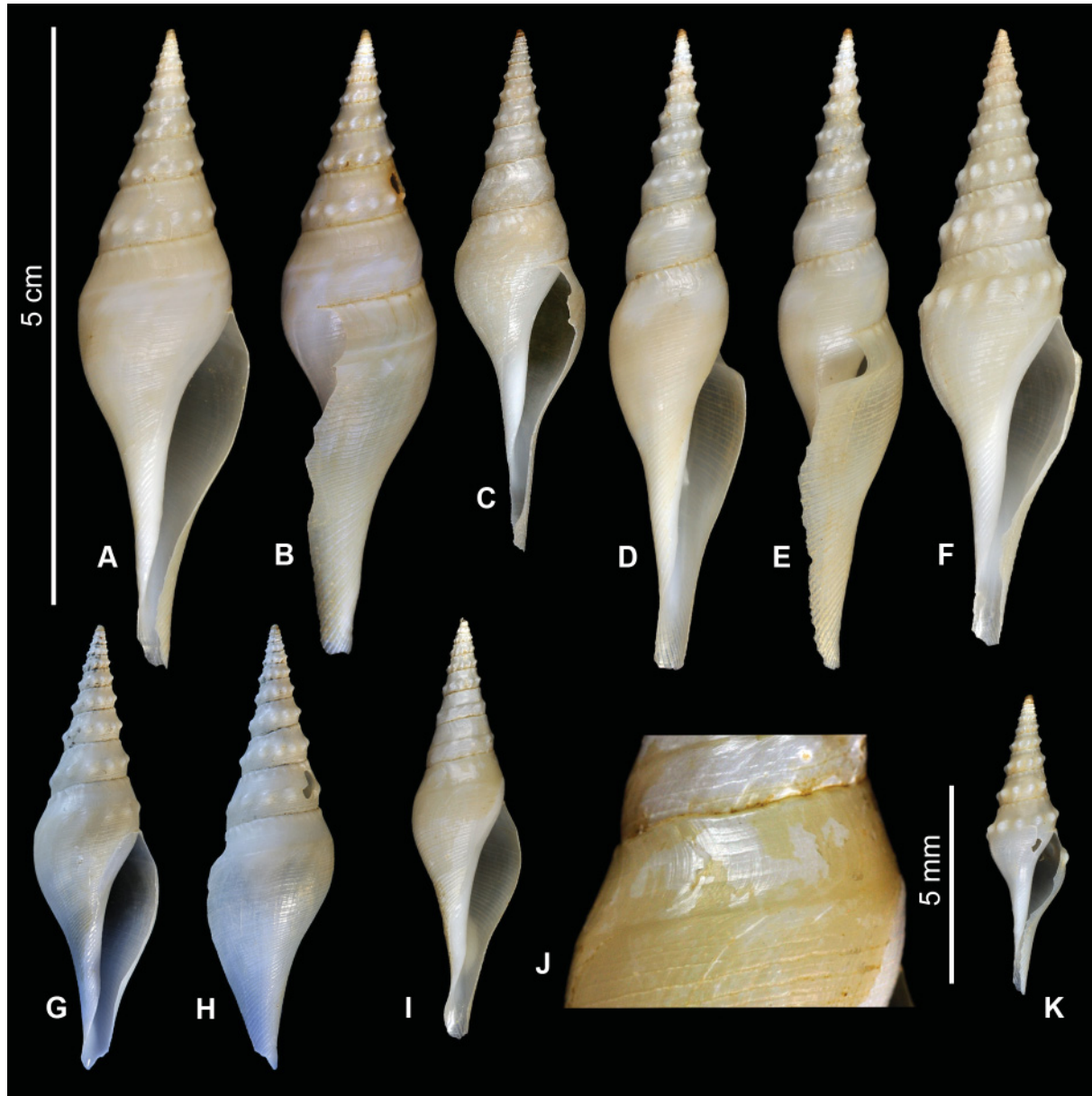


Fig. 7. *Sibogasyrinx sangeri* Kantor, Fedosov & Puillandre, 2018. **A–B.** Holotype, Papua New Guinea, MNHN-IM-2009-17022, SL 54.1 mm. **C.** Papua New Guinea, MNHN-IM-2009-16995, SL 47.7 mm (radula seen on Fig. 8A–B). **D–E.** Solomon Islands, MNHN-IM-2009-16779, SL 55.8 mm. **F.** Papua New Guinea, MNHN-IM-2009-17021, SL 53.7 mm. **G–H.** Papua New Guinea, MNHN-IM-2009-17057, SL 38.8 mm. **I–J.** Philippines, MNHN-IM-2009-13434, SL 36.9 mm. **K.** Solomon Islands, MNHN-IM-2009-16766, SL 26.3 mm. All shells to the same scale.

Sibogasyrinx filosa Ardovini, 2021 (= PSH 6)
Figs 8C, 9A–H

Sibogasyrinx filosus Ardovini, 2021: 5–6, textfigs (erroneous gender agreement of specific epithet).

Material examined

Holotype

PAPUA NEW GUINEA • 1v; NE of Bougainville I.; 04°30' S, 157°20' E; depth 1100–1200 m; MNHN-IM-2000-37629 (originally R. Ardovini collection).

Paratype

PAPUA NEW GUINEA • 1 lv; same collection data as for holotype; R. Ardovini collection.

Other material (all sequenced)

PAPUA NEW GUINEA • 1 lv; New Ireland; 02°33' S, 150°45' E; depth 150–170 m; KAVIENG 2014, stn DW4500; MNHN-IM-2013-59044.

SOLOMON ISLANDS • 1 lv; off Choiseul I., Papua New Guinea Exclusive Economic Zone; 06°37' S, 156°13' E, depth 508–522 m; SALOMON 2, stn CP2227; MNHN-IM-2007-42498 • 1 lv; Guadalcanal I.; 09°19' S, 160°06' E; depth 416–425 m; SALOMONBOA 3, stn CP2767; MNHN-IM-2009-16831.

Description

MEASUREMENTS. Largest available specimen (MNHN-IM-2007-42498): SL 49.9 mm, AL (with canal) 28 mm, AL (without canal) 16.7 mm, SW 13.5 mm. Holotype has SL 52 mm.

SHELL. Moderately thick, strong except for fragile and often partially broken outer aperture lip, narrowly fusiform, with high spire and long, narrow, straight siphonal canal. Protoconch small, globose, of just over 1.5 strongly convex, microshagreened whorls (MNHN-IM-2009-16831). Protoconch/teleoconch transition indistinct, marked by appearance of shoulder carina. Protoconch diameter 0.89 mm, height 0.72 mm. Spire whorls strongly angled at shoulder, last whorl with more rounded shoulder. Total teleoconch whorls just under 9 in largest specimen. Suture shallowly impressed on last whorl and rather deep on spire ones, subsutural ramp moderately broad, strongly concave. Subsutural region with a row of distinct narrow axial ribs, confluent with growth lines and forming small nodules at intersections with spiral cords, absent on most of first teleoconch whorl, about 20 on second–third whorls, about 35 on penultimate and 45 on last whorl. Subsutural ramp with spiral cords, first visible on second whorl and distinct on fourth whorl. Last, penultimate and antepenultimate whorls with 4–5 distinct cords on subsutural ramp, their intervals equal to width of cords, followed below shoulder by 5–7 more narrow, closely spaced cords. Shoulder with row of pronounced rounded nodules, more distinct on upper teleoconch whorls and absent on last whorl, 15–17 on penultimate and antepenultimate whorls. Spiral sculpture in addition to cords on subsutural ramp of distinct narrow cords, covering entire shell surface, including shoulder nodules. On last whorl about 45 cords below shoulder, 25 of which on canal. Cords weakly rounded or flat on top, their intervals mostly narrower than cords themselves, rarely equal to or even slightly wider than cords. Shell base gradually narrowing towards long, narrow, almost straight siphonal canal. Aperture narrow, constricted posteriorly, with very narrow and thin parietal callus, outer lip with rounded angle at shoulder, weakly convex below shoulder, weakly concave at transition to canal. Anal sinus moderately deep, subsutural, broadly arcuate, confluent with large forward extension of outer lip. Shell light orange with lighter middle part of last whorl, in sequenced specimens off-white, with very light yellowish subsutural ramp and irregular darker blotches on subsutural ramp. Protoconch light tan.

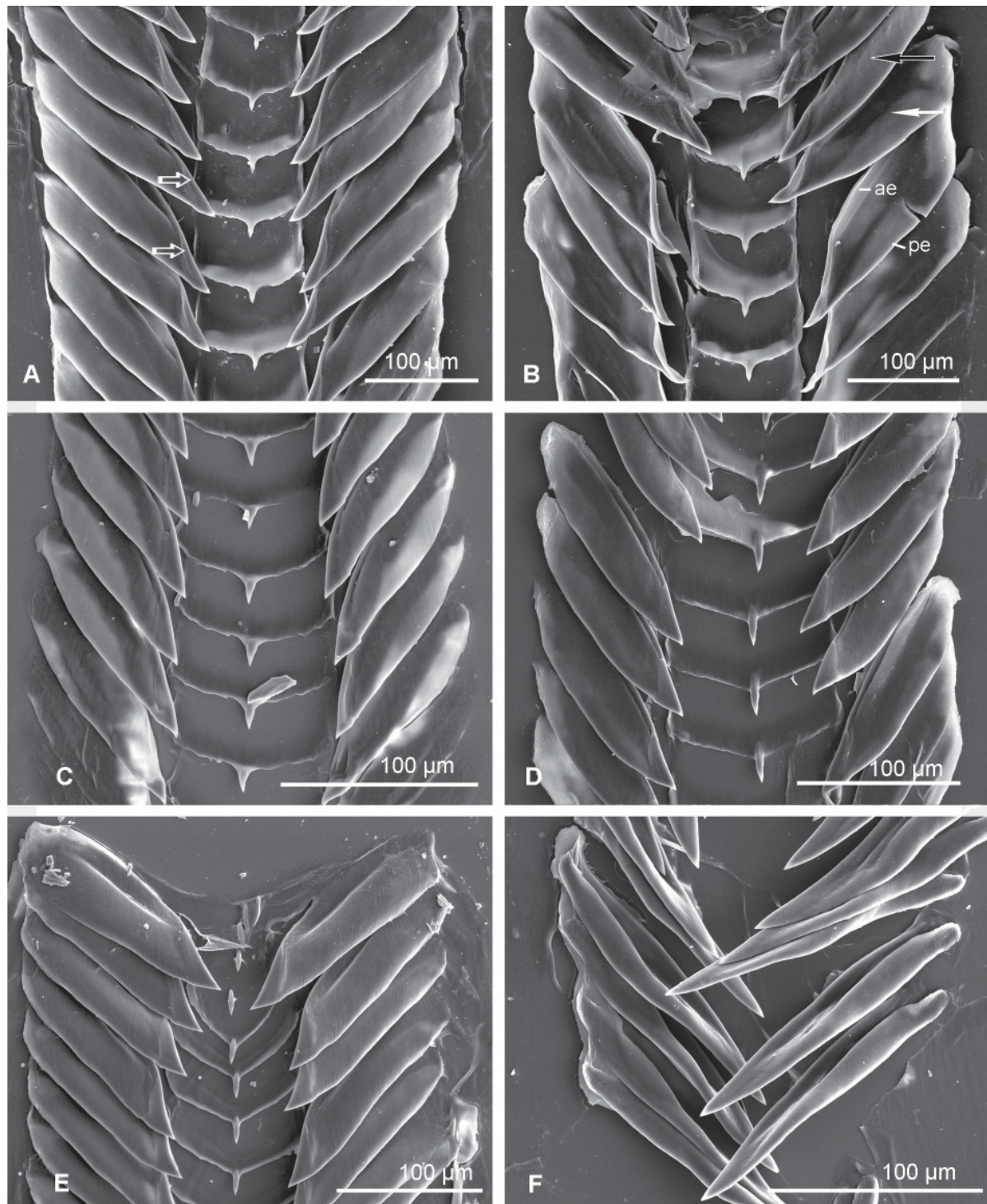


Fig. 8. Radulae of species of *Sibogasyrinx* Powell, 1969. **A–B.** *Sibogasyrinx sangeri* Kantor, Fedosov & Puillandre, 2018, MNHN-IM-2009-16995 (shell seen on Fig. 7C). **A.** Part of radula with fully formed marginal teeth; white hollow arrow indicates overlapping edges of the tooth at its tip. **B.** Part of radula showing transition between unfolded (white arrow) and completely longitudinally folded (black arrow) marginal teeth (ae = anterior tooth edge; pe = posterior tooth edge). **C.** *Sibogasyrinx filosa* Ardovini, 2021, Solomon Islands, MNHN-IM-2009-16831 (shell seen Fig. 9E–F). **D.** *Sibogasyrinx lolae* sp. nov., MNHN-IM-2009-29311. **E.** *Sibogasyrinx maximei* sp. nov., holotype, MNHN-IM-2013-45883, anterior end of radula. **F.** *Sibogasyrinx pagodiformis* sp. nov., MNHN-IM-2009-11327.

ANATOMY (n = 1; MNHN-IM-2009-16831). Head with moderately long, conical tentacles, rounded on tips and with closely spaced bases, large eyes situated on small lobes at tentacle base. Proboscis conical, moderately long, with broad base, rapidly narrowing towards tip. Proboscis retractors not defined, entire posterior part of very thin proboscis sheath base weakly muscular. Buccal mass very large and broad, posterior to proboscis base, constituting about half of proboscis length, oesophagus forming a very short loop before nerve ring. Radular sac with small odontophore, opening dorso-laterally at right side of buccal mass. Venom gland thick, moderately long and convoluted, opening into oesophagus within nerve ring. Muscular bulb moderately large, elongated and folded in posterior part. Salivary glands fused, relatively large, of irregular shape, acinous. Small ovate accessory salivary gland situated dorsally at nerve ring.

RADULA (n = 1; MNHN-IM-2009-16831) (Fig. 8C). Relatively short, consisting of 41 rows of teeth, 15 nascent. Radula length 1.55 mm (12% of AL without canal), width up to 225 μ m (1.8% of AL without canal). Central tooth with subrectangular basal plate, having distinct borders and moderately long cusp. Anterior margin overlapped by preceding row, posterior margin evenly and weakly rounded. Marginal teeth flat when formed, becoming trough-shaped with weakly thickened edges during maturation, folded longitudinally when fully formed, with both margins overlapping at tooth tip. Resulting folded tooth moderately broad, with sharp pointed tip, anterior edge with a narrow slit between folded tooth margins.

Remarks

Our specimens are very similar to the holotype and paratype (except lighter shells) and were collected close to the type locality. Our specimens were collected at much shallower depths (150–508 m) as compared to the holotype and paratype (1100 m). Nevertheless, the strong similarity of the shell shape and sculpture, especially obvious when comparing the holotype with sequenced specimen of the same size (Fig. 9A–B and C–D) suggests the conspecificity of our and the type specimens. Ardovini (2021) himself considered the specimen MNHN-IM-2007-42498 as belonging to his newly described species based on the photograph on the MNHN website. Smaller specimens (SL 34.4 and 29.9 mm) retain smooth, flaking, yellowish periostracum, better preserved in interspaces between cords.

This species is most similar to *Sibogasyrinx subula* sp. nov., but differs in having more strongly developed spiral cords on the subsutural ramp, a relatively narrower ramp resulting in a higher shoulder position on the spire whorls, a different radula and the presence of eyes. In shell outline the new species resembles some species of *Leucosyrinx*, particularly *Leucosyrinx* sp. A (Fig. 13H), but the shell is broader with more numerous nodules on the shoulder. Compared to *Leucosyrinx* sp. F (Fig. 13K), the shell of *S. filosa* is larger, broader and has a coarser sculpture.

Distribution

This species is found off the Solomon Islands Archipelago and New Ireland, at a broad depth range of 150–1100 m.

Sibogasyrinx lolae sp. nov. (= PSH 8)

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Figs 8D, 9I–Q

Diagnosis

Shell medium-sized, reaching 43 mm in length, fusiform, with weakly concave, nearly smooth subsutural ramp and nodules on shoulder of upper teleoconch whorls, absent on later whorls of large specimens. Spiral sculpture weak, of closely spaced cords covering entire shell except subsutural ramp in some specimens. Radula with central tooth and longitudinally folded marginal teeth with weakly thickened edges.

Etymology

The species is named after Lola, the daughter of the second author.

Material examined

Holotype

SOLOMON ISLANDS • W of San Cristobal I.; 10°26' S, 161°20' E; depth 506–567 m; SALOMONBOA 3, stn CP2839; MNHN-IM-2007-42537.

Other material (all sequenced)

NEW CALEDONIA • 1 lv; Bank de L'Orne/Walpole; 22°22' S, 168°57' E; depth 460–708 m; EXBODI, stn CP3864; MNHN-IM-2009-29230 • 1 lv; 21°58' S, 167°07' E; depth 511–1050 m; TERRASSES, stn CP3098; MNHN-IM-2009-29311 • 1 lv; Fairway Ridge; 21°39' S, 162°42' E; depth 787 m; KANADEEP, stn CP4923; MNHN-IM-2013-48156.

Description

MEASUREMENTS (holotype). SL 37.3 mm, AL (with canal) 22.9 mm, AL (without canal) 14.5 mm, SW 11.3 mm.

SHELL (holotype). Moderately thick, glossy, strong except for very fragile and partially broken outer aperture lip, narrowly fusiform, with high spire and long, narrow, straight siphonal canal. Protoconch small, globose, corroded, of about 1.5 whorls. Protoconch preserved in other juvenile specimen (MNHN-IM-2013-48156), comprising just over 1.5 strongly convex, microshagreened whorls. Protoconch/teleoconch transition indistinct, marked by appearance of axial ribs. Protoconch diameter 1.0 mm, height 0.74 mm. Spire whorls angled at shoulder, last whorl with less angular shoulder. Total teleoconch whorls just under 8. Suture shallowly impressed on last whorl and rather deep on spire whorls, subsutural ramp moderately broad, weakly concave on upper teleoconch whorls and nearly flat on penultimate and last whorls. Subsutural ramp with distinct prosocline axial wrinkles, extending from suture to upper $\frac{2}{3}$ of ramp, 22–23 on first and second whorls, 24 on penultimate and 31 on last whorl, and without spiral sculpture on upper four whorls and later with indistinct spiral cords, three on last whorl. Shoulder of teleoconch whorls (except last one) with a row of distinct, opisthoclinely elongated nodules, intersected by weak spiral cords. Seventeen nodules on first teleoconch whorl, 18 on antepenultimate and penultimate whorls. Weak spiral cords on and below shoulder, starting from 3rd teleoconch whorls, about twice as wide below shoulder. Penultimate whorl with four cords on shoulder and four below shoulder. Shoulder smooth on last whorl, but with about 55 cords below shoulder, of which 25 on canal. Cords weak, slightly wavy and closely spaced, their intervals about half the width of cords. Shell base gradually narrowing towards long, narrow, nearly straight siphonal canal. Aperture narrow, constricted posteriorly, with narrow, very thin parietal callus, outer lip badly broken, distinctly impressed at shoulder, weakly convex below shoulder and shallowly concave at transition to canal. Anal sinus judging from growth lines shallow, subsutural, broadly arcuate, confluent with forward extension of outer lip. Shell very light yellowish, protoconch very light tan (in holotype) and light brown in MNHN-IM-2013-48156.

ANATOMY (n = 1; MNHN-IM-2009-29311). Male. Penis tip obliquely truncated, with long and very narrow papilla, surrounded by circular fold, much larger in diameter than papilla itself. Proboscis conical, moderately long, with broad base, anterior half rapidly narrowing towards tip. Proboscis retractors distinct, arranged in two symmetrical lateral bundles, attached to inner proboscis walls at border of its posterior third. Buccal mass with small radular sac, odontophore situated within proboscis in its broader posterior part; elongate oval, occupying slightly less than half of proboscis length. Single small accessory salivary gland present. Salivary glands separate, acinous, irregular in shape. Venom gland long, moderately thick and convoluted, opening into oesophagus within the nerve ring.

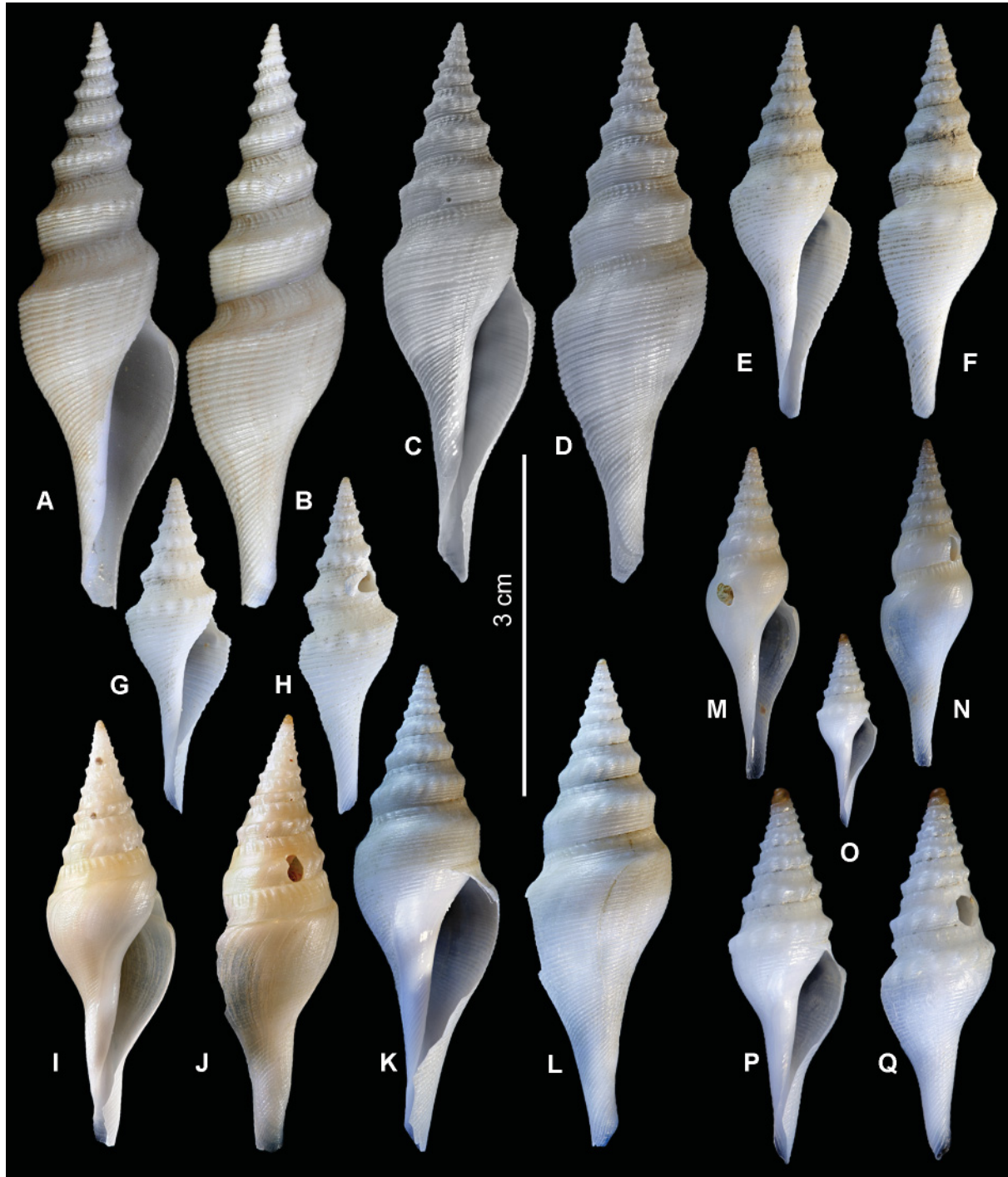


Fig. 9. A–H. *Sibogasyrinx filosa* Ardovini, 2021. A–B. Holotype, Solomon Islands (MNHN-IM-2000-37629), SL 52 mm. C–D. Solomon Islands, MNHN-IM-2007-42498, SL 49.9 mm. E–F. Solomon Islands, MNHN-IM-2009-16831, SL 34.4 mm (radula seen on Fig. 8C). G–H. Papua New Guinea, MNHN-IM-2013-59044, SL 29.9 mm. I–Q. *Sibogasyrinx lolae* sp. nov. I–J. Solomon Islands, holotype, MNHN-IM-42537, SL 37.3 mm. K–L. New Caledonia, MNHN-IM-2009-29230, SL 43.1 mm. M–N. New Caledonia, MNHN-IM-2009-29311, SL 29.1 mm. O–Q. New Caledonia, MNHN-IM-2013-48156, SL 17.1 mm (O at the same scale as the other specimens, P–Q enlarged). All shells (except P–Q) to same scale.

RADULA (n = 1; MNHN-IM-2009-29311) (Fig. 8D). Short, comprising 28 rows of teeth, 13 nascent. Radula length 1.15 mm (7.9% of AL without canal), width up to 255 µm (1.8% of AL without canal), tooth length 160 µm (1.10% of AL without canal). Central tooth with subrectangular basal plate, having distinct borders and long, narrow, sharp cusp. Anterior margin overlapped by preceding row, posterior margin formed by two straight sections meeting at obtuse angle in midline. Marginal teeth flat when formed, becoming trough-shaped with weakly thickened edges during maturation, folded longitudinally when fully formed, with both margins overlapping at tooth tip. Resulting folded tooth moderately broad, with sharp pointed tip, anterior edge with a narrow slit between tooth margins. Tooth folding occurring within 15th row of teeth.

Remarks

The largest specimen attains 43.1 mm.

Other specimens are similar to the holotype in shell shape, although some have much more pronounced spiral sculpture, especially MNHN-IM-2009-29230, which also retains spiral cords on the shoulder of the last whorl.

In shell shape and sculpture the new species is most similar to *Sibogasyrinx filosa*, some specimens being almost indistinguishable (e.g., holotype of *S. filosa* and MNHN-IM-2009-29230). *Sibogasyrinx lolae* sp. nov. can be distinguished from *S. filosa* due to its generally less distinct spiral sculpture and less concave, nearly flat subsutural ramp. Other conchologically similar species are *S. cf. pyramidalis* 1 and 2, but these differ in their radular morphology. In both these species and *S. lolae* sp. nov., the nodules on the shoulder become less pronounced or disappear on later whorls. Nevertheless, the nodules are still pronounced on the shoulder of the last whorl in specimens of *S. cf. pyramidalis* 1 and 2 of the same size as specimens of *S. lolae* sp. nov. which already lack nodules on the last whorl.

Distribution

This species is recorded from the Solomon Islands, the Coral Sea and southern New Caledonia, at depths of 460–787 m.

Sibogasyrinx maximei sp. nov. (= PSH 9)

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Figs 8E, 10A–C

Diagnosis

Shell medium-sized, reaching 41.6 mm in length, fusiform, subsutural ramp weakly concave on early teleoconch whorls, flat on later ones. It is nearly smooth (except for axial riblets). Shoulder of teleoconch whorls with nodules, absent on last whorl. Spiral sculpture weak, of indistinct closely spaced cords on and below shoulder. Radula with central tooth and longitudinally folded marginal teeth with weakly thickened edges.

Etymology

This species is named after Maxime, the son of the second author.

Material examined

Holotype

SOLOMON SEA • off Marshall Bennett I.; 08°38' S, 151°46' E; depth 720 m; MADEEP, stn DW4323; MNHN-IM-2013-45883.

Description (holotype)

MEASUREMENTS. SL 41.6 mm, AL (with canal) 23.2 mm, AL (without canal) 15.7 mm, SW 12.4 mm.

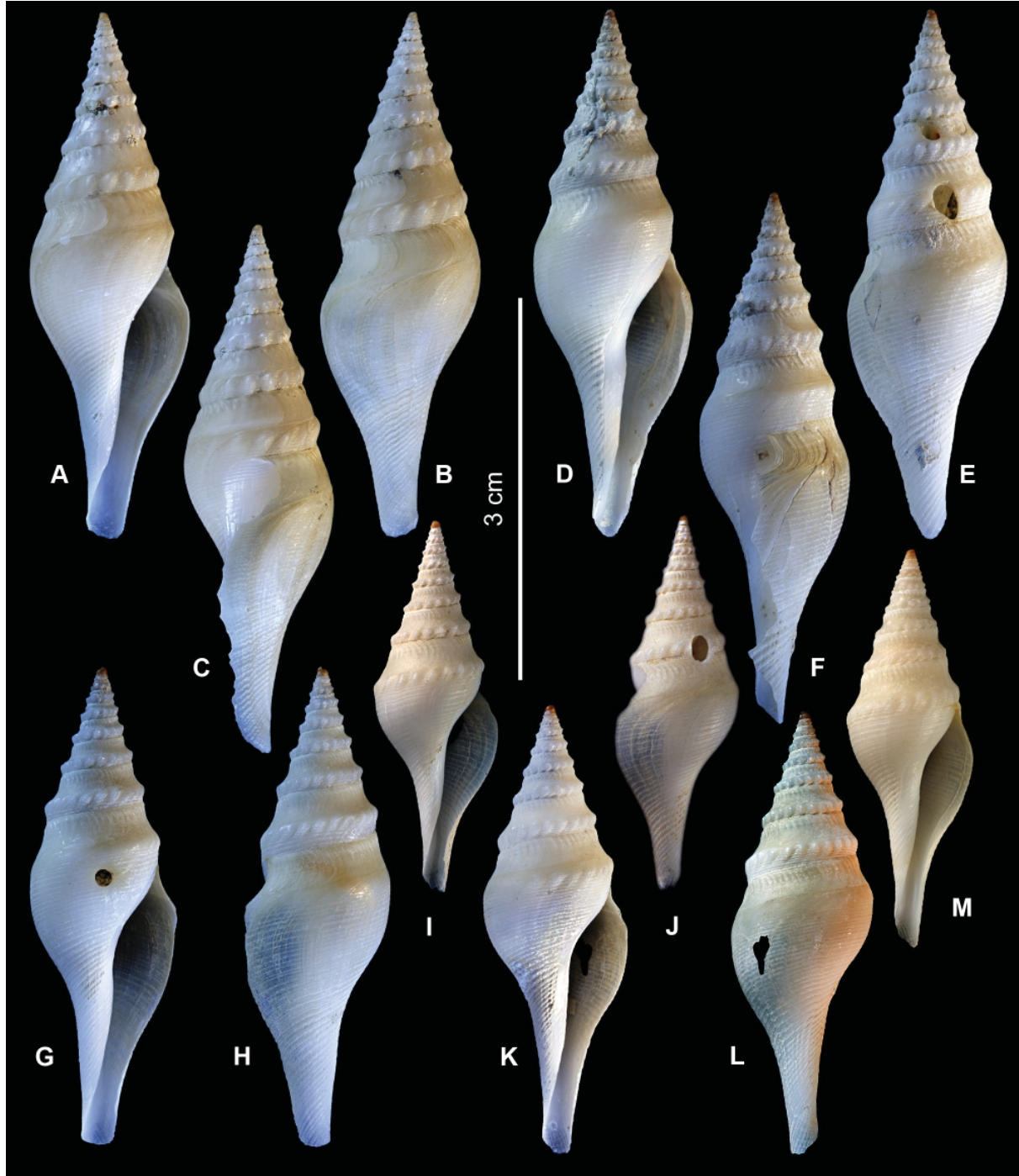


Fig. 10. A–C. *Sibogasyrinx maximei* sp. nov., Solomon Sea, holotype, MNHN-IM-2013-45883, SL 41.6 mm. D–M. *Sibogasyrinx clausura* sp. nov. D–F. Solomon Islands, holotype, MNHN-IM-2013-48256, SL 41.4 mm. G–H. Coral Sea, Coriolis Bank, MNHN-IM-2013-48167, SL 37.9 mm. I–J. Solomon Islands, MNHN-IM-2009-16763, SL 29.6 mm. K–L. Coral Sea, Coriolis Bank, MNHN-IM-2013-48244, SL 35.6 mm. M. Coral Sea, Coriolis Bank, MNHN-IM-2013-48144, SL 31.7 mm. All shells to same scale.

SHELL. Moderately thick, strong except for fragile and partially broken outer aperture lip, fusiform, with high, conical spire and moderately long, broad, straight siphonal canal. Protoconch small, globose, of about 1.5 strongly convex, microshagreened whorls. Protoconch/teleoconch transition marked by strongly arcuate axial rib, corresponding to shape of growth line. Protoconch diameter 1.0 mm, height 0.83 mm. Spire whorls weakly angled at shoulder, last whorl with hardly discernible shoulder. Total teleoconch whorls 8.5. Suture shallowly impressed, subsutural ramp broad, weakly concave on first four teleoconch whorls, flat on later whorls. Subsutural ramp with short, distinct, prosocline axial wrinkles, corresponding to upper parts of thickened growth lines, extending from suture to upper $\frac{1}{3}$ of ramp, increasing in number from 20 on first whorl to 34 on penultimate and 43 on last whorl. Subsutural ramp with only traces of indistinct spiral striation. Shoulder of teleoconch whorls (except last one) with a row of distinct elongated nodules, these nearly orthocline on upper whorls and weakly opisthocline on penultimate whorl, 14–17 per whorl, reaching lower suture and intersected by spiral cords. Starting from 2nd teleoconch whorl, spiral cords appearing on shoulder, these intersecting nodules and becoming progressively stronger, from two on 2nd whorl to nine on penultimate one. Cords very closely spaced, separated by narrow grooves. On last whorl cords cover entire shell surface below indistinct shoulder, about 50 cords in total, of which 25 on canal. Cords weak, slightly wavy, very closely spaced just below suture and with intervals 0.5–1.0 times width of cords on shell base and canal. Shell base gradually narrowing towards moderately broad, almost straight siphonal canal. Aperture narrow, constricted posteriorly, with narrow and very thin parietal callus, outer lip partially broken, evenly convex and weakly concave at transition to canal. Anal sinus moderately deep, subsutural, broadly arcuate, confluent with large forward extension of outer lip. Shell very light yellowish, protoconch light tan. Periostracum smooth, tightly adhering.

RADULA (n = 1; MNHN-IM-2013-45883) (Fig. 8E). Medium-long, comprising 40 rows of teeth, 12 nascent. Radula length 1.8 mm (11.4% of AL without canal), width up to 290 μ m (1.85% of AL without canal). Central tooth with basal plate, having distinct borders and long, narrow, sharp cusp, anterior margin overlapped by preceding row, posterior margin formed by two straight sections meeting at obtuse angle in midline. Marginal teeth flat when formed, becoming trough-shaped with weakly thickened edges during maturation, folded longitudinally when fully formed, with both margins overlapping at tooth tip. Resulting folded tooth moderately broad with sharply pointed tip, border between both margins present as a narrow slit at anterior edge. Tooth folding occurring within 14th row of teeth (counting from rear).

Remarks

The species is known from the holotype alone and is very similar to *Sibogasyrinx clausura* sp. nov. (for comparison see remarks under the following species). In shell outline it is very similar to *S. cf. pyramidalis* 1 and 2, but differs in having fewer nodules on the shoulder; the holotype has 17 nodules on the penultimate whorl, whereas specimens of *S. cf. pyramidalis* 1 and 2 of similar size have up to 26 nodules. There are additional differences in radular morphology.

Distribution

Known only from the type locality.

Sibogasyrinx clausura sp. nov. (= PSH 10)

urn:lsid:zoobank.org:act:27ED0BF0-C78A-41E1-9064-E3EB0492864A

Figs 10D–M, 11A–B

Diagnosis

Shell medium-sized, reaching 41.5 mm in length, fusiform, subsutural ramp concave on upper teleoconch whorls, weakly so on last whorl, nearly smooth (except for the axial riblets), shoulder bearing nodules on

spire whorls, absent on last whorl. Spiral sculpture of weak, closely spaced cords on and below shoulder. Radula with central tooth and longitudinally folded marginal teeth with weakly thickened edges.

Etymology

Latin '*clausura*' (noun in apposition), meaning 'lockdown', with reference to the sanitary restrictions associated with SARS-COV-2 that prevailed over much of the World when this manuscript was finalized.

Material examined

Holotype

NEW CALEDONIA • Coral Sea, Coriolis Bank; 21°20' S, 157°55' E; depth 963–970 m; KANADEEP, stn CP4964; MNHN-IM-2013-48256.

Other material (all sequenced)

AUSTRALIA • 1 lv; New South Wales, off Byron Bay; 28°03' S, 154°05' E; depth 999–1013 m; R/V *Investigator*, cruise IN2017_V03_100; AMS C.519344.

NEW CALEDONIA • 1 lv; Coral Sea, Coriolis Bank; 21°21' S, 158°00' E; depth 978–1000 m; KANADEEP, stn CP4963; MNHN-IM-2013-48244 • 3 lv; Coral Sea, Coriolis Bank; 21°20' S, 157°50' E; depth 961 m; KANADEEP, stn CP4965; MNHN-IM-2013-48144, MNHN-IM-2013-48169, MNHN-IM-2013-48258 • 2 lv; Coral Sea, Coriolis Bank; 21°10' S, 157°46' E; depth 975–980 m; KANADEEP, stn CP4966; MNHN-IM-2013-48167, MNHN-IM-2013-48235.

SOLOMON ISLANDS • 1 lv; Sta Isabel I.; 08°47' S, 159°38' E; depth 762–1060 m; SALOMON 2, stn CP2182; MNHN-IM-2009-16763.

Description

MEASUREMENTS (holotype, largest specimen). SL 41.4 mm, AL (with canal) 23.0 mm, AL (without canal) 13.7 mm, SW 12.4 mm.

SHELL (holotype). Moderately thick, slightly glossy, strong except for fragile and partially broken outer aperture lip, narrowly fusiform, with high spire and moderately long, straight siphonal canal. Protoconch small, globose, of about 1.5 strongly convex, eroded whorls. Protoconch/teleoconch transition marked by strongly arcuate axial rib, corresponding to shape of growth lines, followed by 10 thinner and weaker axial ribs and rather thickened growth lines. Protoconch diameter 1.0 mm, height 0.84 mm. Spire whorls distinctly angled at shoulder, last whorl with scarcely discernible shoulder. Total teleoconch whorls just over 8. Suture shallowly impressed, subsutural ramp broad, concave, on last whorl weakly concave. Subsutural region with a row of distinct, dense, narrow, short, prosocline axial wrinkles, corresponding to upper parts of thickened growth lines, extending from suture to upper $\frac{1}{3}$ of ramp, increasing in number from 22 on first whorl to 42 on penultimate and 50 on last whorl. Shoulder of teleoconch whorls (except last one) with a row of distinct opisthoclinely elongated nodules, extending to abapical suture and intersected by spiral cords, increasing in number from 13 on first whorl to 21 on antepenultimate and penultimate whorls. Subsutural ramp smooth except for axial wrinkles mentioned above. Spiral cords intersecting shoulder nodules beginning on 2nd teleoconch whorls (due to corrosion of shell their number is unclear) and becoming progressively stronger, 7 on antepenultimate and 8 on penultimate whorl. Cords closely spaced with intervals about half the width of cords. On last whorl cords covering entire shell surface below indistinct shoulder, about 40 cords in total, of which 20 on canal. Cords weak, slightly wavy, very closely spaced just below suture and with intervals 0.5–1.0 times cord width on shell base and canal. Shell base gradually narrowing towards narrow, nearly straight siphonal canal. Aperture narrow, constricted posteriorly, with narrow, moderately thick parietal callus, outer lip partially broken, evenly convex and weakly concave at transition to canal. Anal sinus shallow, subsutural, broadly arcuate, confluent with large forward extension of outer lip as deduced from growth lines. Shell off-white, with

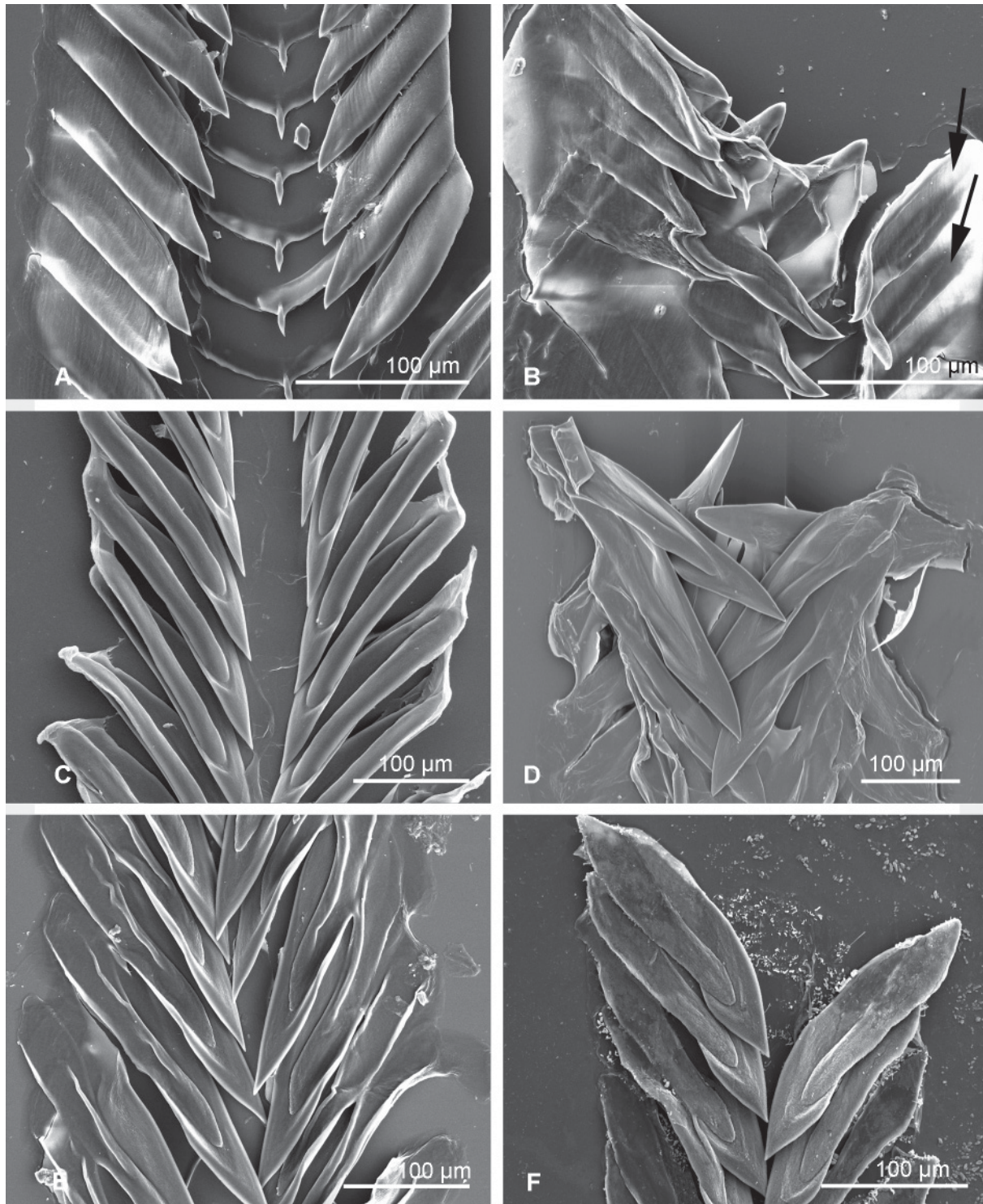


Fig. 11. Radulae of species of *Sibogasyrinx* Powell, 1969 and *Leucosyrinx* Dall, 1889. **A–B.** *Sibogasyrinx clausura* sp. nov., MNHN-IM-2009-16763. **A.** Central part of radula with fully formed teeth. **B.** Anteriormost part of radula at bending plane; marginal teeth at the right (black arrows) are unfolded due to mechanical impact. **C.** *Leucosyrinx verrillii* (Dall, 1881), French Guiana, MNHN-IM-2013-56288 (shell seen on Fig. 13C). **D.** *Leucosyrinx* sp. F, Coral Sea, MNHN-IM-2007-17846 (shell seen on Fig. 13K). **E.** *Leucosyrinx* sp. G, Papua New Guinea, MNHN-IM-2009-17089 (shell seen on Fig. 13D). **F.** *Leucosyrinx* sp. C, Solomon Islands, MNHN-IM-2007-42503 (shell seen on Fig. 13J).

slightly darker subsutural ramp, protoconch light tan. Periostracum smooth, retained between cords and ribs.

ANATOMY (n = 1; MNHN-IM-2009-16763). Male. Penis obliquely truncated at tip with short, large, conical papilla occupying entire anterior part of penis, surrounded by circular fold. Eyes present. Proboscis moderately long, conical, with expanded base. Proboscis retractors not defined, entire posterior part of proboscis base muscular. Salivary glands small, not fused, with very long ducts that run within walls of oesophagus. Buccal mass moderately large, about $\frac{1}{3}$ of proboscis length, basal, protruding backwards beyond proboscis base, radular sac lying outside proboscis. Venom gland very large, thick and strongly convoluted, very constricted before opening into oesophagus in region of nerve ring. Muscular bulb moderately large.

RADULA (n = 1; MNHN-IM-2009-16763, AL 10.6 mm) (Fig. 11A–B). Relatively short, comprising 38 rows of teeth, 16 nascent. Radula length 1.65 mm (15.5% of AL without canal), width up to 250 μ m (2.35% of AL without canal). Central tooth with basal plate, having distinct anterior and lateral borders and long, narrow, sharply-pointed cusp. Anterior margin overlapped by preceding row, posterior margin almost evenly rounded except for narrow protrusion adjoining cusp. Marginal teeth flat when formed, becoming trough-shaped with weakly thickened edges during maturation, folded longitudinally when fully formed, with both margins overlapping at tooth tip. The resulting folded tooth is moderately broad with a sharp pointed tip, border between margins appears as a narrow groove along anterior edge. Tooth folding occurs within 15–16th row of teeth (counting from rear).

Remarks

The other specimens are very similar to the holotype in shell shape and sculpture. In some specimens there is very indistinct spiral striation on the subsutural ramp and a single very weak spiral cord may even be present.

This species is most similar to *Sibogasyrinx maximei* sp. nov., but differs in having more numerous and narrower subsutural axial wrinkles (50 vs 43 on last whorl and 42 vs 34 on penultimate one) and less numerous (40 vs 50) spiral cords on the last whorl, the holotypes of both species being of almost the same size. Nevertheless, *S. maximei* sp. nov. is only represented in our material by a single specimen and thus its intraspecific variability remains unknown. The two species are broadly sympatric in the Solomon Islands, but are clearly differentiated in our molecular analysis.

Distribution

This species occurs in the Solomon Islands, New South Wales and on the Coriolis Bank in the Coral Sea, at 762–1060 m. This bathymetric range corresponds to a single haul in the Solomon Islands, while all other specimens were collected at 960–1000 m, indicating a narrower bathymetric range for the species.

Sibogasyrinx pagodiformis sp. nov. (= PSH 5)

[urn:lsid:zoobank.org:act:DAA613D6-5AB6-4F89-A0AD-0C718A60307E](https://zoobank.org/urn:lsid:zoobank.org:act:DAA613D6-5AB6-4F89-A0AD-0C718A60307E)

Figs 8F, 12A–D

Diagnosis

Shell small, reaching 29 mm in length, pagodiform, with strongly concave subsutural ramp bearing two low spiral cords and distinct subsutural nodules. Axial sculpture of distinct opisthocline ribs extending to shell base, 10–11 per whorl. Spiral sculpture of closely spaced cords on and below shoulder. Radula lacking central tooth, marginal teeth trough-shaped with thickened edges.

Etymology

The name reflects the characteristic shell shape, resembling a pagoda.

Material examined

Holotype

SOLOMON ISLANDS • NW of Malaita I.; 08°28' S, 160°32' E; depth 1250–1402 m; SALOMONBOA 3, stn CP2789; MNHN-IM-2009-16825.

Other material (sequenced)

VANUATU • 1 lv; E of Malekula I.; 16°00' S, 167°38' E; depth 1262–1285 m; SANTO 2006, stn AT139; MNHN-IM-2009-11327.

Description

MEASUREMENTS (holotype). SL 28.8 mm, AL (with canal) 15.2 mm, AL (without canal) 9.9 mm, SW 11.9 mm.

SHELL (holotype). Moderately thick, except for fragile, partially chipped outer aperture lip; pagodiform, with moderately high spire and moderately long, narrow siphonal canal inclined to abaxially left. Protoconch missing (rendering exact an whorl count and protoconch measurements impossible), upper teleoconch whorls eroded. Teleoconch whorls rapidly increasing and strongly angled at shoulder, more than 8 remaining. Suture shallowly impressed, subsutural ramp broad, concave. A row of distinct, sharp, subsutural nodules on upper teleoconch whorls. Nodules less distinct on last three whorls and situated on short, slightly raised, prosocline axial ribs. Number of ribs on uppermost whorls indeterminate due to shell surface erosion, number of nodules per whorl increasing from 16–17 on first intact whorl to 22 on penultimate and 26 on last whorl. Subsutural ramp smooth except for nodules and two low, indistinct subsutural cords. Shoulder with pronounced, thickened, opisthocline axial ribs on all teleoconch whorls. Axial ribs on upper teleoconch whorls situated just above suture, extending to shell base on last whorl, number of ribs constant, 11–12 per whorl. Ribs intersected by closely spaced, rounded spiral cords, number increasing from 5 on uppermost remaining whorl to 10 on penultimate whorl. Last whorl with total of 38 cords, including 18 on canal. Cords narrow, their intervals 0.5–1.5 times cord width. Shell base rapidly narrowing towards narrow, moderately long siphonal canal. Aperture narrow, constricted posteriorly, with thin, moderately broad parietal callus, outer lip partially broken, convex on subsutural ramp, with rounded angle at shoulder, convex below shoulder and weakly concave at transition to canal. Anal sinus judging from growth lines shallow, subsutural, broadly arcuate. Shell flesh-coloured, with darker base, glossy. Periostracum thin, persisting in some cord intervals.

ANATOMY (n = 1; MNHN-IM-2009-11327). Female. Proboscis relatively short, straight, cylindrical. Proboscis retractors large, in two bundles attached at proboscis base. Buccal mass within proboscis, rather long, about half length of proboscis, radular sac opening on right. Venom gland very thick, not long, opening with very short constriction just posterior to nerve ring. Venom bulb moderately large, elongate.

RADULA (n = 2; MNHN-IM-2009-16825, AL 9.9 mm, IM-2009-11327, AL ca 9 mm). Relatively short, comprising 20–24 rows of teeth, 8–9 nascent. Radula length 1.1–1.6 mm (12–16% of AL without canal), tooth length 150 µm (1.7% of AL without canal). Central tooth absent. Marginal teeth trough-shaped when mature (Fig. 8F), with slightly thickened edges and sharp pointed tips. Teeth initially forming as a flat, elongate-oval plate, its edges gradually thickening along radular membrane and then by longitudinal folding of each tooth on 10–11th row, counting from rear.

Remarks

The second live collected specimen has a broken shell base. In sculpture pattern it is very similar to the holotype.

The species is distinct from all congeners in having a relatively broad, pagodiform shell with a shorter canal. Conchologically the species is quite similar to *Comitas paupera* (Watson, 1881), a highly variable species of uncertain generic affinity, but differing in lacking distinct spiral cords on the subsutural ramp.

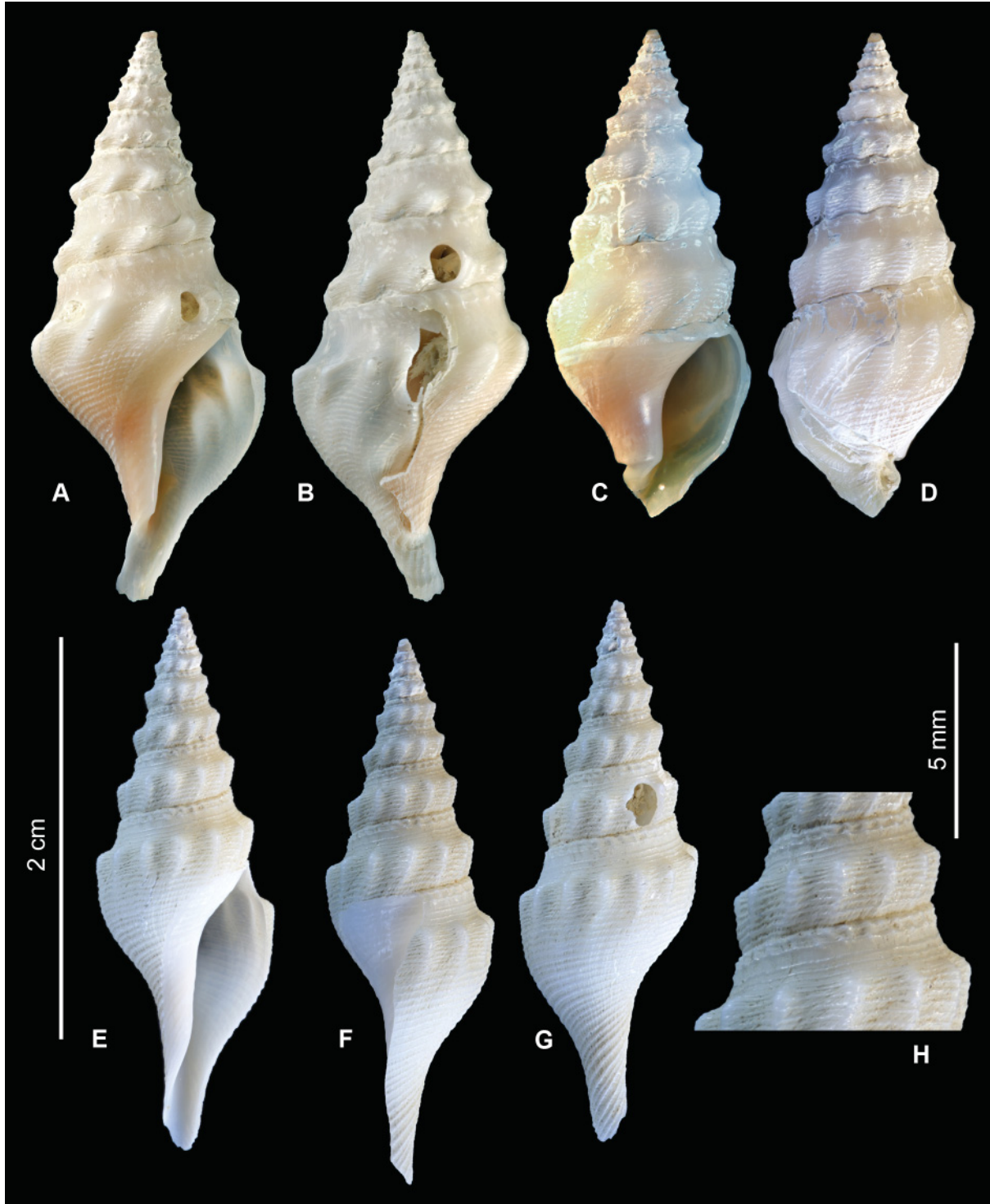


Fig. 12. A–D. *Sibogasyrinx pagodiformis* sp. nov. A–B. Solomon Islands, holotype, MNHN-IM-2009-16825, SL 28.8 mm. C–D. Vanuatu. MNHN-IM-2009-11327, SL 24.3 mm. E–H. *Sibogasyrinx elbakyanae* Kantor, Puillandre & Bouchet sp. nov., holotype, Solomon Islands, MNHN-IM-2009-16834, SL 27.3 mm. H. Enlarged fragment of penultimate and antepenultimate whorls. A–G to same scale.

The lectotype and paralectotypes of the latter were illustrated by Sysoev (1996: figs 42–48). Superficially, the new species also strongly resembles a miniature copy of *Leucosyrinx luzonica* (Powell, 1969) (see Kantor *et al.* 2018: fig. 21), but differs in the shape of the marginal radular teeth and foregut anatomy. Another species of *Leucosyrinx* from the Solomon Islands, *Leucosyrinx* sp. D, is similar to the new species in shell outline (Fig. 13F), differing in radular morphology.

Distribution

This species was found in the Solomon Islands and Vanuatu at 1250–1262 m.

Sibogasyrinx elbakyanae Kantor, Puillandre & Bouchet sp. nov. (= PSH 4)
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Fig. 12E–H

Diagnosis

Shell small, reaching 27.5 mm in length, fusiform, subsutural ramp strongly concave with distinct, broadly-spaced spiral cords and dense subsutural nodules. Axial sculpture of distinct opisthocline ribs extending to shell periphery. Spiral sculpture of distinct cords on and below shoulder.

Etymology

Philippe Bouchet joins us in dedicating this species to honor Alexandra Elbakyan, creator of the famous sci-hub portal.

Material examined

Holotype

SOLOMON ISLANDS • S of Malaita I.; 09°55' S, 161°33' E; depth 1136–1750 m; SALOMONBOA 3, stn CP2817; MNHN-IM-2009-16834.

Description (holotype)

MEASUREMENTS. SL 27.3 mm, AL (with canal) 15.0 mm, AL (without canal) 9.6 mm, SW 8.9 mm.

SHELL. Moderately thick, except for fragile outer aperture lip, partially chipped; fusiform, with high spire and long, narrow, straight siphonal canal. Protoconch eroded and partially decollated, thus rendering whorl count and measurements impossible. Teleoconch whorls strongly angled at shoulder, about 8 whorls in total. Suture deeply impressed, subsutural ramp moderately broad, strongly concave. Subsutural region with a row of dense, distinct, sigmoidal axial ribs that correspond in shape to upper parts of thickened growth lines and form small rounded nodules at intersections with spiral cords. Rib counts on uppermost whorls not possible due to shell surface erosion, about 24 on antepenultimate whorl, 27 on penultimate and 34 on last whorl. Subsutural ramp with thin but distinct spiral cords, 3 on first preserved teleoconch whorl and 5 on last three whorls, one immediately subsutural followed by another with interval about three times cord width, then three more closely spaced ones separated from second cord by an interval of about five times cord width. Upper two cords forming nodules at intersections with axial ribs. Shoulder with pronounced, thickened, opisthocline axial ribs on all teleoconch whorls, about 12 on upper whorls, including penultimate one and 14 on last whorl. Ribs extending to abapical suture on spire whorls, intersected by spiral cords, uppermost 2–3 very thin and closely spaced followed by 5–8 more broadly spaced. Last whorl with about 35 cords on shoulder and below, including 15 on canal. Cords narrow and separated by intervals 1–3 times the width of cords on axial ribs on shoulder, more broadly spaced on shell base and canal. Shell base gradually narrowing towards narrow, moderately long, nearly straight siphonal canal. Aperture narrow, constricted posteriorly, with moderately broad, thin parietal callus, outer lip partially broken, with rounded angle at shoulder, weakly convex below

shoulder and weakly concave at transition to canal. Anal sinus shallow, subsutural, broadly arcuate. Shell base off-white, upper part of last whorl and teleoconch whorls very light yellow. Periostracum thin, persisting in intervals between cords and ribs.

ANATOMY. Adult male, penis long, gradually narrowing towards tip, obliquely truncated at tip with a small but rather long conical papilla, surrounded by circular fold. Proboscis not long, conical, proboscis retractors not defined, entire posterior part of proboscis base muscular. Salivary glands fused, small. Single oval accessory salivary gland present at level of anterior part of proboscis. Venom gland large, thick and strongly convoluted, very constricted before opening into oesophagus within nerve ring. Muscular bulb moderately large.

RADULA. Minute, comprising about 15 rows of teeth. Radula length 650 μm (6.8% of AL without canal), width up to 100 μm (1% of AL without canal). Central tooth present, with long cusp. Marginal teeth trough-shaped. Due to poor preparation it was impossible to study tooth morphology in detail.

Remarks

This species is most similar to *Sibogasyrinx filosa*, but differs in having a more stout shell with a relatively shorter canal, fewer, more distinct axial ribs on the shoulder (35 vs 46 on last whorl), and thinner, more widely spaced spiral cords. In shell outline the new species resembles some species of *Leucosyrinx*, particularly *Leucosyrinx verrillii* (Dall, 1881) (Fig. 13A–C), but differs in its smaller size, less numerous shoulder nodules and radular morphology.

Distribution

Known only from the type locality.

Discussion

Conchologically, the species of *Sibogasyrinx* described herein are rather heterogeneous on one hand, while on the other, some species are very similar to each other (e.g. *S. cf. pyramidalis* 1 and *S. cf. pyramidalis* 2; *S. filosa* and *S. lolae* sp. nov.). Furthermore, species of *Sibogasyrinx* are superficially similar in shell shape and sculpture to species of *Leucosyrinx* (Fig. 13); thus, based on shell alone, it is not possible to reliably attribute the species to either genus. Comparisons of species of *Sibogasyrinx* with similar species of *Leucosyrinx* (still mostly undescribed) are provided in the remark sections. This similarity in shell morphology between unrelated genera suggests that additional species of *Sibogasyrinx* may be found among taxa that are presently, but incorrectly, classified within *Leucosyrinx*. Whether the occurrence of similar shells in taxa that potentially diverged more than 130 mya (Abdelkrim *et al.* 2018) is linked to the retention of ancestral state characters or to convergence remains to be determined.

Anatomically, species of *Sibogasyrinx* are rather variable interspecifically, particularly with regard to radula characters. Three radula types were observed within the species of this genus, which is uncommon for Conoidea, where intrageneric variation in radula form is generally limited. Two of these types are confined to highly supported subclades within *Sibogasyrinx*. The Type 1 of radula is found in *S. cf. pyramidalis* 1 and 2 and *S. subula* sp. nov. (Fig. 4). Here, fully matured marginal teeth are similar to duplex teeth found in different families of Conoidea (e.g., in Turridae and some Pseudomelatomidae, including *Leucosyrinx*; Fig. 11C–F). The developing teeth in the younger, posterior part of the membrane (Fig. 4A) are trough-shaped, with the anterior edge (Fig. 4A, ae) of the tooth poorly sclerotized and attached to the membrane, while the posterior edge (Fig. 4A, pe) becomes progressively thicker along the membrane, lifting from the membrane and drawing closer to the anterior edge, thus making the tooth fold longitudinally. The fully formed and immature marginal teeth in the same radula membrane look markedly different (compare Fig. 4A and 4B). In this radula type, the central teeth are well developed.

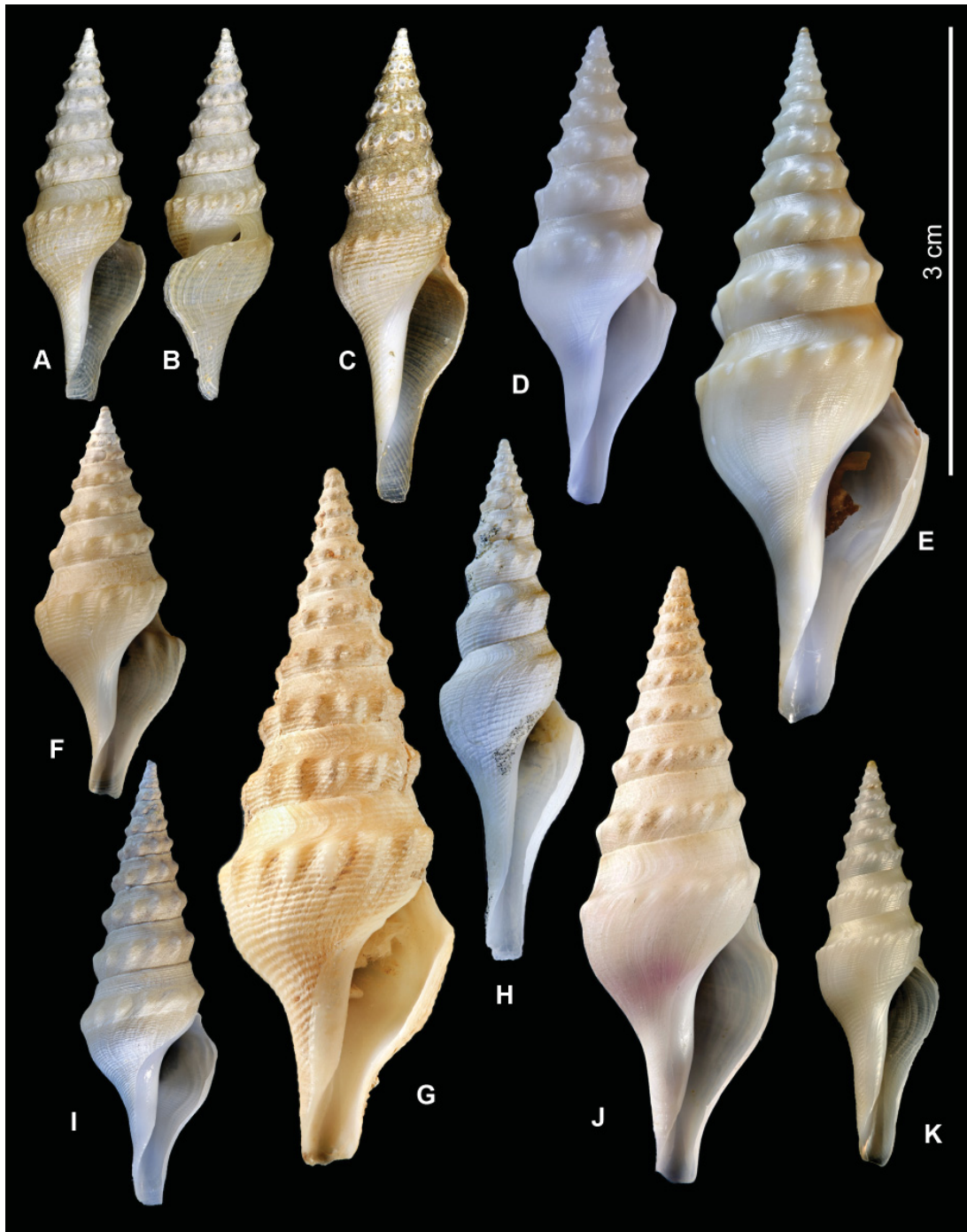


Fig. 13. Shells of species of *Leucosyrinx* Dall, 1889. **A–B.** *Leucosyrinx verrillii* (Dall, 1881), French Guiana, MNHN-IM-2013-56840, SL 25.1 mm. **C.** *L. verrillii*, French Guiana, MNHN-IM-2013-56288, SL 31.9 mm (radula seen on Fig. 11C). **D–E.** *Leucosyrinx* sp. G. **D.** Papua New Guinea, MNHN-IM-2009-17089, SL 32.2 mm (radula seen on Fig. 11E). **E.** Bismarck Sea, MNHN-IM-2013-19689, SL 47.3 mm. **F.** *Leucosyrinx* sp. D, Solomon Islands, MNHN-IM-2009-16769, SL 25 mm. **G.** *Leucosyrinx* sp. E, Madagascar, MNHN-IM-2009-16897, SL 46.1 mm. **H.** *Leucosyrinx* sp. A, Philippines, MNHN-IM-2007-42445, SL 34.1 mm. **I.** *Leucosyrinx* sp. B, Solomon Islands, MNHN IM-2009-16764, SL 29.9 mm. **J.** *Leucosyrinx* sp. C, Solomon Islands, MNHN-IM-2007-42503, SL 41.2 mm (radula seen on Fig. 11F). **K.** *Leucosyrinx* sp. F, Coral Sea, Chesterfield Plateau, MNHN-IM-2007-17846, SL 27.3 mm (radula seen on Fig. 11D). All shells to same scale.

The Type 2 of radula is recorded in several species forming a well-supported clade: *Sibogasyrinx sangeri*, *S. filosa*, *S. lolae* sp. nov., *S. maxime* sp. nov. and *S. clausura* sp. nov. While the central teeth are well developed and similar in shape to the teeth of the first radula type, the marginal teeth are markedly different and so far appear to be unique within the Conoidea (Figs 8A–E, 11A–B). When formed and during maturation the teeth transform from the initial flat plates, to trough-shaped plates with a weakly thickened anterior edge (Fig. 8B, ae) and a not thickened posterior edge (Fig. 8B, pe). Then, mid-way along the membrane, the teeth are abruptly folded longitudinally. The resulting folded tooth (Fig. 8A) is moderately broad (half the width of the original unfolded plate) with a sharply pointed tip. The border between both edges is evident as a narrow slit along the anterior margin of the tooth. Although this folded pattern of the marginal teeth is rather stable and evidently remains unchanged in most of the radulae studied, the teeth may become unfolded due to mechanical impact (on Fig. 11B such an unfolded tooth on the working part of the membrane is marked by a black arrow).

Finally, the Type 3 of radula was found in *Sibogasyrinx pagodiformis* sp. nov. (Fig. 8F). Here the marginal teeth are more similar to those of radula type 1, with a more thickened posterior edge, although they retain a clear trough shape when fully formed. The central teeth are absent, which is unique for Cochlespiridae in general and *Sibogasyrinx* in particular.

Sibogasyrinx pagodiformis sp. nov. has a broad, pagodiform shell, which is rather atypical for the genus. Nevertheless, its position in *Sibogasyrinx* is confirmed both by molecular data and the anatomy of the anterior foregut. The venom gland in this species opens into the oesophagus just posterior to the nerve ring, as in the other species of *Sibogasyrinx* examined (this character is a symplesiomorphy of the Cochlespiridae; Abdelkrim *et al.* 2018), while in other families of Conoidea the venom gland passes through the nerve ring (with a significant part of its length situated anterior to the ring) and inserts just posterior to the radular sac.

The foregut anatomy is similar in the other species of *Sibogasyrinx* studied (Fig. 5), differing only in minor details, such as the arrangement of the proboscis retractors (well defined, grouped in two lateral bundles attached to the most posterior part of the proboscis sheath in *S. pagodiformis* sp. nov., *S. lolae* sp. nov., *S. subula* sp. nov. and *S. cf. pyramidalis*, or absent as in *S. elbakyanae* sp. nov., *S. clausura* sp. nov., *S. filosa*). The buccal mass is usually situated posterior to the proboscis, but may be partially (*S. clausura* sp. nov.) or completely (e.g., *S. lolae* sp. nov.) contained within the proboscis. The salivary glands may be separate or fused. An accessory salivary gland was found in *Sibogasyrinx cf. pyramidalis* 1 and *S. lolae* sp. nov., but this structure is difficult to observe during manual dissection and it may be present in some other species as well.

Eyes may be present (*S. filosa*, *S. clausura* sp. nov.) or absent (*S. cf. pyramidalis*, *S. subula* sp. nov.), and this showed no relation to the bathymetric range of the species.

Presently, species of *Sibogasyrinx* are known only from the central West Pacific – from the South China Sea and the Philippines to Indonesia (type species, *S. pyramidalis*) and south to Vanuatu, New Caledonia and Australia. Despite a number of cruises led by MNHN at appropriate depths in the Indian Ocean, as well as in Fiji, Tonga and French Polynesia, *Sibogasyrinx* was not recorded there, as well as in Japan despite adequate sampling effort in that region. The genus is most diverse off the Solomon Islands (8 species recorded) and Papua New Guinea (4 species), but it is not clear at present whether this is a result of more intense sampling in these areas or a genuine distributional feature. The species are confined to the upper bathyal (300–800 m) with a few species penetrating the upper portion of the lower bathyal (800–2000 m). Only one species (*S. filosa*) was recorded as shallow as 150 m, but it also extends to 1100 m (508 m as confirmed by molecular data). For species that are represented by numerous samples, the bathymetric range is rather large, spanning several hundred meters, although, as mentioned earlier, some species seem to have more limited bathymetric ranges.

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