*Ruthenica*, 2018, vol. 28, No. 2: 47-82.

# New and unusual deep-water Conoidea revised with shell, radula and DNA characters

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urn:lsid:zoobank.org:pub:4F802973-612F-422D-BA0F-5C19391FC4DB

**ABSTRACT.** In the course of preparation of a new molecular phylogeny of Conoidea based on exon-capture some new species and species with notable morphology were revealed. The taxonomy of these species is discussed and the radula of most of them illustrated for the first time. New genera are described: ***Comispira*** gen. nov. (Cochlespiridae), type species *Leucosyrinx mai* Li et Li, 2008; ***Pagodaturris*** gen. nov. (Clavatulidae), type species *Pleurotoma molengraaffi* Tesch, 1915. New species described: ***Comispira compta*** gen. et sp. nov., *Sibogasyrinx* ***sangeri*** sp. nov. (both Cochlespiridae), ***Pagodaturris philippinensis*** gen. et sp. nov. (Clavatulidae), *Horaiclavus* ***micans*** sp. nov., *Iwaoa* ***invenusta*** sp. nov. (both Horaiclavidae), *Lucerapex* ***cracens*** sp. nov., *Lucerapex* ***laevicarinatus*** sp. nov. (Turridae), *Heteroturris* ***kanacospira*** sp. nov. (Borsoniidae). *Epideira* Hedley, 1918 is reallocated from Pseudomelatomidae to Horaiclavidae. The radulae of *Kuroshioturris nipponica* (Shuto, 1961) (Turridae), *Leucosyrinx verrillii* (Dall, 1881), and *Leucosyrinx luzonica* (Powell, 1969) comb. nov. are illustrated for the first time.

## Introduction

The superfamily Conoidea constitutes one of the most diverse and taxonomically challenging groups of marine molluscs. The classification of this crown clade of the caenogastropods has drastically changed in the last 25 years, starting with the work of Taylor *et al.* [1993] based on morphological analysis. A new era came with development of molecular phylogenetic techniques. The phylogenetic analysis based on a multigene approach allowed resolution of many previously polytomic nodes, leading to re-definition of the different clades of Conoidea [Puillandre *et al.*, 2008, 2011]. To implement these results in the taxonomy of the Conoidea, a new family (Horaiclavidae) was proposed, while at the same time some previously recognized families and subfamilies were resurrected and others were absorbed within other taxa.

The next step in the reconstruction of the relationships within the superfamily Conoidea is the upcoming phylogeny based on exon-capture [details are provided in Abdelkrim *et al.*, 2018]. During the preparation of this new phylogeny, the species sequenced underwent thorough investigation, which in many cases revealed notable morphological characters, or demonstrated taxonomic issues that needed to be resolved. Some sequenced species appeared to be new to science, while for others generic or familial attribution has changed. Most of them were unstudied in respect of radular morphology, and a few constituted unique lineages in the tree, potentially corresponding to new families. The taxonomy of these taxa is discussed in the present paper to avoid burdening the purely phylogenetic study of Abdelkrim *et al.* [2018] with a lengthy taxonomic account.

In most cases the justification for including the species in particular genus and family is based on the exon-capture tree, and we will refer to it wherever needed. However, we include COI trees in this article that may not be informative at the family and sometimes even genus levels. These are used to illustrate the molecular data obtained for the concerned species to show the distinctiveness of the new species from close relatives, and to allow evaluation of the intraspecific variability, that in few cases was high enough to suspect the existence of several species within the single one as defined here.

## Material and methods

### *Sampling*

Most specimens were collected during cruises and shore-based expeditions organized between 2004 and 2015 by the Muséum National d'Histoire Naturelle, Paris (MNHN) and Institut de Recherche pour le Développement (IRD) (details are provided in Table 1).

Until 2012, live specimens for molecular analysis were anaesthetized with an isotonic solution of $MgCl_2$ and preserved in 96% ethanol. Specimens collected during later expeditions were processed with a microwave oven [Galindo *et al.*, 2014]: the living molluscs in small volumes of sea water were exposed to microwaves for 7–30 sec, depending on specimen size. Bodies were immediately removed from shells and dropped in 96% ethanol. Specimens are registered in the MNHN collection and specimens and sequences were deposited in BOLD (Barcode of Life Datasystem) and GenBank (Table 1).

### *DNA sequencing*

DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the manufacturer's recommendations. A fragment of the COI gene was amplified using universal primers LCO1490/HCO2198 [Folmer *et al.*, 1994]. PCRs were performed in 25 µl, containing 3 ng of DNA, 1× reaction buffer, 2.5mM $MgCl_2$, 0.26mM dNTP, 0.3mM each primer, 5% DMSO and 1.5 units of Qbiogene Q-Bio Taq. Amplification consisted of an initial denaturation step at 94°C for 4 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 50°C for 30 s, followed by extension at 72°C for 1 min. The final extension was at 72°C for 5 min. PCR products were purified and sequenced by the Eurofins sequencing facility.

Because COI sequences alone generally provide poorly resolved trees for deeper relationships, leading to the non-monophyly of some well-established taxa [see e.g. Puillandre *et al.*, 2008 and 2011], the available sequences were analyzed separately in five datasets, each including only one (or two, in one case) family, and a sample of another family used as an outgroup: Borsoniidae, Cochlespiridae, Horaiclavidae and *Pagodaturris* (Clavatulidae), *Leucosyrinx* (Pseudomelatomidae) and *Lucerapex* (Turridae).

All the sequences were aligned manually (no indel was detected), and each dataset was analysed using a Bayesian approach as implemented in MrBayes v. 3.2 [Huelsenbeck, Ronquist, Hall, 2001], with two runs consisting of four Markov chains of 10,000,000 generations each, with 8 chains, 5 swaps, and a sampling frequency of one tree every 2,000 generations. Each codon position of the COI gene was treated as an unlinked partition, each following a general time reversible (GTR) model, with a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites. Convergence of each analysis was evaluated using Tracer v. 1.6 [Rambaut, Drummond, 2014] to check that all ESS values were greater than 200. The trees were then calculated after omitting the first 20% trees as burnin. Statistical support was evaluated as Bayesian posterior probability (PP). P-distances were calculated using MEGA 6 [Tamura *et al.*, 2013].

### *Shell morphology and radula*

Radulae were prepared following a standard protocol detailed in [Kantor, Puillandre, 2012] and examined by scanning electron microscope TeScan TS5130MM in the Institute of Ecology and Evolution of Russian Academy of Sciences (IEE RAS). Protoconchs were measured in standard position and the number of whorls counted according to Bouchet and Kantor [2004].

### *Abbreviations and conventions:*

AL – aperture length;
AMS – Australian Museum, Sydney;
dd – dead shell;
lv – live collected specimen;
MNHN – Muséum National d'Histoire Naturelle, Paris, France;
SL – shell length;
st. – station;
SW – shell width;
USNM – National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

## Taxonomy

## Cochlespiridae Powell, 1942

### ***Comispira*** gen. nov.

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**Type species:** *Leucosyrinx mai* Li et Li, 2008 (here designated).

**Diagnosis**: Shell medium-sized, fusiform, with rather high spire and long nearly straight siphonal canal. Protoconch probably paucispiral. Whorls angulated at shoulder which bears a row of distinct nodules on all whorls. Additional subsutural row of much smaller nodules. Spiral sculpture of prominent spiral cords below shoulder and on shell base and canal. Concave subsutural zone smooth or with microscopic spiral striations. Axial sculpture limited to nodules and growth lines some of which thickened and slightly raised above surface.

Aperture oval, constricted posteriorly, with a narrow parietal callus, gradually passing into siphonal canal. Anal sinus subsutural broadly arcuate, medium deep, symmetrical, U-shaped, confluent with large forward extension of outer lip. Teleo-

Table 1. List of examined material.

Табл. 1. Список исследованного материала.

| MNHN No. | Fam* | Genus/species | Expedition | Locality, station and depth** | BOLD ID | GenBank numbers (COI) |
|---|---|---|---|---|---|---|
| IM-2007-17857 | Bo | *Bathytoma neocaledonica* | EBISCO | Coral Sea, CP2551, 637-650 m | CONO187-08 | EU015653 |
| IM-2009-8165 | Bo | *Belaturricula ergata* | CEAMARC | | CONO1118-10 | KT448832 |
| IM-2009-29355 | Bo | *Borsonia* cf. *symbiophora* | BIOPAPUA | | CONO2075-18 | MG968435 |
| IM-2007-17932 | Bo | *Borsonia* sp. | SALOMON 2 | CP2197, 897-1057 m | CONO350-08 | EU015737 |
| IM-2007-42293 | Bo | *Genota mitriformis* | | Angola, AF7, Pta. Das Lagostas | CONO531-08 | HQ401576 |
| IM-2009-29105 | Bo | *Heteroturris* ***kanacospira*** | EXBODI | | CONO2077-18 | MG968442 |
| IM-2009-19004 | Bo | *Heteroturris* sp. | AURORA 2007 | | CONO2073-18 | MG968440 |
| IM-2007-35068 | Bo | *Heteroturris sola* | PANGLAO 2005 | | CONO1104-10 | MG968439 |
| IM-2007-42483 | Bo | *Heteroturris sola* | PANGLAO 2005 | | CONO754-08 | MG968443 |
| IM-2009-18971 | Bo | *Heteroturris sola* | AURORA 2007 | | CONO2068-18 | MG968441 |
| IM-2007-17911 | Bo | *Heteroturris* sp. | PANGLAO 2005 | Philippines, CP2333, 584 -596 m | CONO290-08 | EU015718 |
| IM-2007-17887 | Bo | *Microdrillia* cf. *optima* | PANGLAO 2004 | Philippines,, T36, 95-128 m | CONO275-08 | EU015710 |
| IM-2009-29365 | Bo | *Tomopleura* cf. *reevei* | INHACA 2011 | Mozambique, MR19, 2-3 m | CONO2076-18 | MG968506 |
| IM-2009-18963 | Cl | ***Pagodaturris*** *molengraaffi* | SALOMONBOA 3 | | CONO2071-18 | MG968482 |
| IM-2007-42458 | Cl | ***Pagodaturris philippinensis*** | PANGLAO 2005 | | CONO729-08 | MG968436 |
| IM-2013-19215 | Co | ***Comispira compta*** | PAPUA NIUGINI 2012 | | CONO2081-18 | MG968437 |
| IM-2013-44247 | Co | ***Comispira*** *mai* | NANHAI 2014 | | CONO2093-18 | MG968460 |
| IM-2013-52033 | Co | ***Comispira*** *mai* | NANHAI 2014 | | CONO2086-18 | MG968459 |
| IM-2013-59407 | Co | ***Comispira*** *mai* | ZHONGSHA 2015 | | CONO2119-18 | MG968463 |
| IM-2013-61656 | Co | ***Comispira*** *mai* | ZHONGSHA 2015 | | CONO2117-18 | MG968464 |
| IM-2013-61657 | Co | ***Comispira*** *mai* | ZHONGSHA 2015 | | CONO2118-18 | MG968461 |
| IM-2013-61658 | Co | ***Comispira*** *mai* | ZHONGSHA 2015 | | CONO2113-18 | MG968462 |
| IM-2009-13451 | Co | *Sibogasyrinx pyramidalis* | AURORA 2007 | | CONO2061-18 | MG968492 |
| IM-2013-44574 | Co | *Sibogasyrinx pyramidalis* | NANHAI 2014 | | CONO2095-18 | MG968491 |
| IM-2013-44605 | Co | *Sibogasyrinx pyramidalis* | NANHAI 2014 | | CONO2096-18 | MG968493 |
| IM-2013-50215 | Co | *Sibogasyrinx pyramidalis* | DONGSHA 2014 | | CONO2097-18 | MG968494 |
| IM-2009-16779 | Co | *Sibogasyrinx* ***sangeri*** | SALOMON 2 | | CONO2063-18 | MG968503 |
| IM-2007-42523 | Co | *Sibogasyrinx* ***sangeri*** | SALOMON 2 | | CONO799-08 | MG968466 |
| IM-2013-52052 | Co | *Sibogasyrinx* ***sangeri*** | BIOPAPUA | | CONO2088-18 | MG968498 |
| IM-2009-13434 | Co | *Sibogasyrinx* ***sangeri*** | AURORA 2007 | | CONO2064-18 | MG968500 |
| IM-2009-16766 | Co | *Sibogasyrinx* ***sangeri*** | SALOMON 2 | | CONO2062-18 | MG968505 |
| IM-2009-16989 | Co | *Sibogasyrinx* ***sangeri*** | BIOPAPUA | | CONO2079-18 | MG968501 |
| IM-2009-16995 | Co | *Sibogasyrinx* ***sangeri*** | BIOPAPUA | | CONO2057-18 | MG968495 |
| IM-2009-17021 | Co | *Sibogasyrinx* ***sangeri*** | BIOPAPUA | | CONO2058-18 | MG968502 |
| IM-2009-17022 | Co | *Sibogasyrinx* ***sangeri*** | BIOPAPUA | | CONO2059-18 | MG968496 |
| IM-2009-17057 | Co | *Sibogasyrinx* ***sangeri*** | BIOPAPUA | | CONO2060-18 | MG968499 |
| IM-2013-19752 | Co | *Sibogasyrinx* ***sangeri*** | PAPUA NIUGINI 2012 | | CONO2080-18 | MG968497 |
| IM-2013-19961 | Co | *Sibogasyrinx* ***sangeri*** | PAPUA NIUGINI 2012 | | CONO2082-18 | MG968504 |
| IM-2007-42614 | Ho | *Anacithara lita* | SANTO 2006 | Vanuatu, DS99, 100-105 m | CONO931-08 | HQ401571 |
| IM-2007-17868 | Ho | *Carinapex minutissima* | PANGLAO 2004 | Philippines, B19, 17 m | CONO246-08 | EU015690 |
| IM-2013-52072 | Ho | *Epideira sibogae* | EXBODI | | CONO2092-18 | MG968438 |
| IM-2009-13540 | Ho | *Horaiclavus* ***micans*** | CONCALIS | | CONO2078-18 | MG968444 |
| IM-2013-52054 | Ho | *Horaiclavus* ***micans*** | EXBODI | | CONO2089-18 | MG968445 |
| IM-2007-17840 | Ho | *Horaiclavus splendidus* | EBISCO | Coral Sea, DW2631, 372-404 m | CONO183-08 | EU015649 |
| IM-2007-17908 | Ho | *Iwaoa reticulata* | PANGLAO 2005 | Philippines, CP2332, 396-418 m | CONO288-08 | EU015717 |

Table 1. List of examined material.

Табл. 1. Список исследованного материала.

| MNHN No. | Fam* | Genus/species | Expedition | Locality, station and depth** | BOLD ID | GenBank numbers (COI) |
|---|---|---|---|---|---|---|
| IM-2013-4878 | Ho | *Iwaoa* ***invenusta*** | PAPUA NIUGINI 2012 | | CONO2083-18 | MG968447 |
| IM-2013-4880 | Ho | *Iwaoa* ***invenusta*** | PAPUA NIUGINI 2012 | | CONO2084-18 | MG968446 |
| IM-2013-52044 | Ho | *Iwaoa* ***invenusta*** | PAPUA NIUGINI 2012 | | CONO2087-18 | MG968448 |
| IM-2013-44303 | NF | *Leucosyrinx luzonica* | NANHAI 2014 | | CONO2094-18 | MG968457 |
| IM-2013-59549 | NF | *Leucosyrinx luzonica* | ZHONGSHA 2015 | | CONO2115-18 | MG968456 |
| IM-2013-59550 | NF | *Leucosyrinx luzonica* | ZHONGSHA 2015 | | CONO2116-18 | MG968455 |
| IM-2013-59551 | NF | *Leucosyrinx luzonica* | ZHONGSHA 2015 | | CONO2114-18 | MG968458 |
| IM-2013-60376 | NF | *Leucosyrinx pelagia* | KARUBENTHOS 2015 | Guadeloupe, DW4544, 413-423 m | CONO2120-18 | MG968465 |
| IM-2013-56287 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2100-18 | MG968476 |
| IM-2013-56288 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2101-18 | MG968474 |
| IM-2013-56341 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2102-18 | MG968467 |
| IM-2013-56355 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2103-18 | MG968478 |
| IM-2013-56356 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2104-18 | MG968469 |
| IM-2013-56357 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2098-18 | MG968475 |
| IM-2013-56806 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2105-18 | MG968477 |
| IM-2013-56807 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2099-18 | MG968468 |
| IM-2013-56809 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2106-18 | MG968471 |
| IM-2013-56811 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2107-18 | MG968473 |
| IM-2013-56823 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2108-18 | MG968480 |
| IM-2013-56840 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2109-18 | MG968470 |
| IM-2013-56841 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2110-18 | MG968472 |
| IM-2013-56842 | NF | *Leucosyrinx verrillii* | GUYANE 2014 | | CONO2111-18 | MG968479 |
| IM-2009-18984 | Tu | *Kuroshioturris nipponicus* | AURORA 2007 | | CONO2065-18 | MG968451 |
| IM-2009-19090 | Tu | *Kuroshioturris nipponicus* | AURORA 2007 | | CONO2066-18 | MG968449 |
| IM-2009-19091 | Tu | *Kuroshioturris nipponicus* | AURORA 2007 | | CONO2067-18 | MG968452 |
| IM-2009-19092 | Tu | *Kuroshioturris nipponicus* | AURORA 2007 | | CONO2069-18 | MG968453 |
| IM-2009-19093 | Tu | *Kuroshioturris nipponicus* | AURORA 2007 | | CONO2074-18 | MG968450 |
| IM-2009-19094 | Tu | *Kuroshioturris nipponicus* | AURORA 2007 | | CONO2070-18 | MG968454 |
| IM-2013-45481 | Tu | *Lucerapex adenica* | MADEEP | | CONO2112-18 | MG968481 |
| IM-2007-42542 | Tu | *Lucerapex adenica* | SALOMONBOA 3 | | CONO838-08 | MG968489 |
| IM-2007-42448 | Tu | *Lucerapex casearia* | PANGLAO 2005 | Philippines, CP2363, 437-439 m | CONO719-08 | HQ401581 |
| IM-2007-42635 | Tu | *Lucerapex* ***cracens*** | SANTO 2006 | | CONO952-08 | MG968483 |
| IM-2007-42636 | Tu | *Lucerapex* ***cracens*** | SANTO 2006 | | CONO953-08 | MG968487 |
| IM-2009-13549 | Tu | *Lucerapex* ***cracens*** | CONCALIS | | CONO2056-18 | MG968485 |
| IM-2009-18966 | Tu | *Lucerapex* ***cracens*** | SALOMONBOA 3 | | CONO2072-18 | MG968488 |
| IM-2013-19988 | Tu | *Lucerapex* ***cracens*** | PAPUA NIUGINI 2012 | | CONO2085-18 | MG968490 |
| IM-2013-52064 | Tu | *Lucerapex* ***cracens*** | BIOPAPUA | | CONO2091-18 | MG968484 |
| IM-2013-52063 | Tu | *Lucerapex* ***laevicarinatus*** | EXBODI | | CONO2090-18 | MG968486 |

*Legend for the family abbreviations: Bo – Borsoniidae, Cl – Clavatulidae, Co – Cochlespiridae, Ho – Horaiclavidae, NF – new family to be described in Abdelkrim *et al.*, 2018, Tu – Turridae.

**Locality, station and depth are provided only for the specimens used as outgroups and not mentioned in the **Material examined** sections. Station coordinates can be found at MNHN site at https://science.mnhn.fr/institution/mnhn/collection/im/item/ with adding the registration number of the specimen (without prefix IM-) after last back slash.

conch uniformly off-white, covered by adherent light yellow periostracum. Operculum large, occupying 2/3 of aperture, narrow, leaf-shaped, with terminal inclined leftward nucleus.

Radula with large unicuspid central tooth and duplex marginal teeth with unequal limbs – larger major limb and much smaller accessory limb.

**Remarks.** The new genus has strong similarity

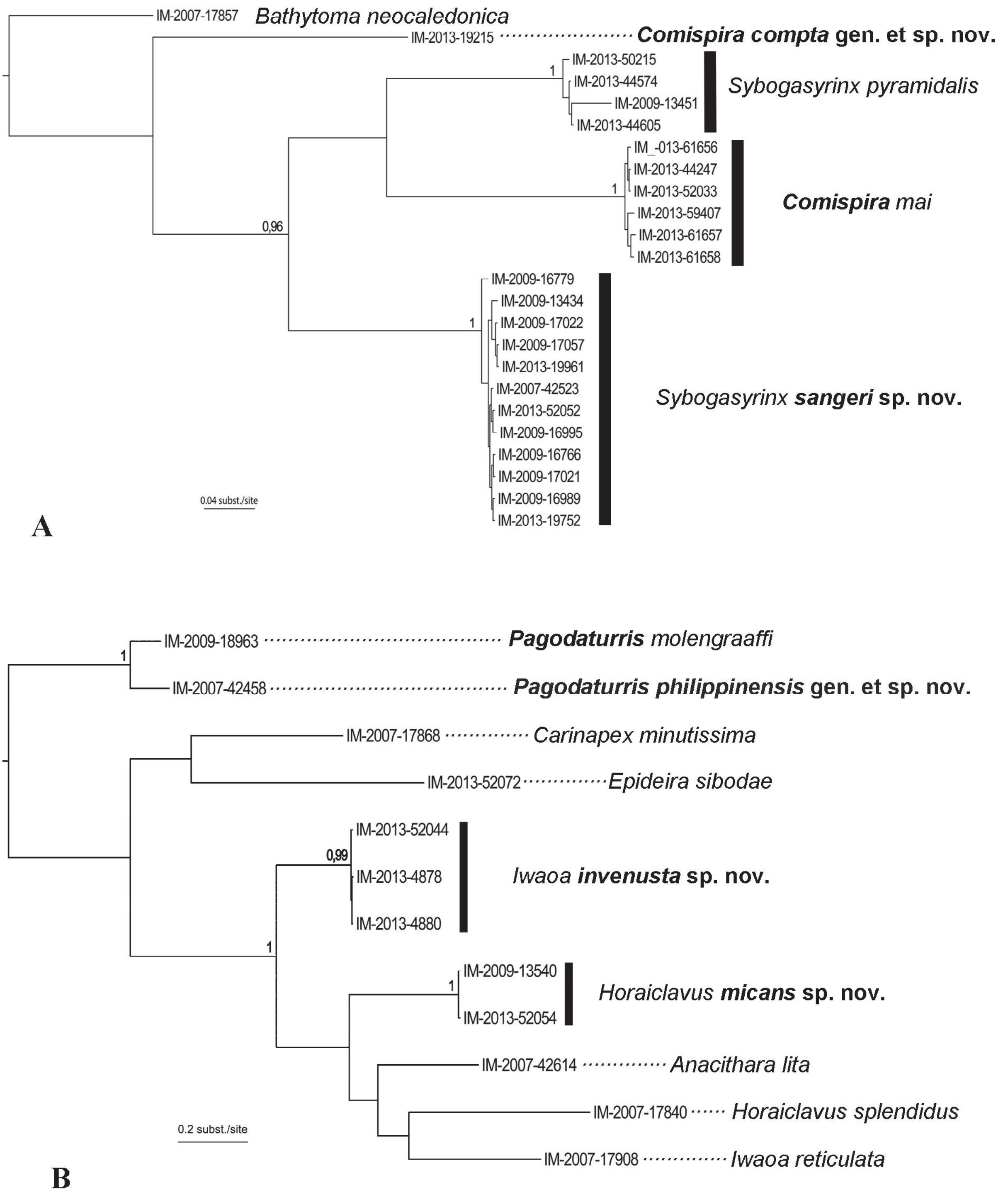

FIG. 1. Phylogenetic tree of Cochlespiridae (**A**) and Horaiclavidae (**B**) obtained with Bayesian analysis of COI gene sequences. Support values shown for the supported nodes with posterior probability values between 0.95 and 1.00 only.

РИС. 1. Филогенетические деревья Cochlespiridae (**A**) и Horaiclavidae (**B**), полученные Бэйесовским анализом на основе последовательностей гена COI. Значения статистической поддержки узлов показаны только для узлов со значениями апостериорной вероятности между 0,95 и 1,00.

to various species, attributed previously to *Comitas* Finlay, 1926, particularly to *Comitas subsuturalis* (von Martens, 1902) from East Aftrica and *Comitas obtusigemmata* (Schepman, 1913) from Indonesia. Other similar species are *Leucosyrinx erna* Thiele, 1925 and *L. juliae* Thiele, 1925. It is highly possible that those and maybe some other species actually belong to this new genus, but without radular or DNA data, we cannot be sure of their generic allocation. From true *Comitas* species (family

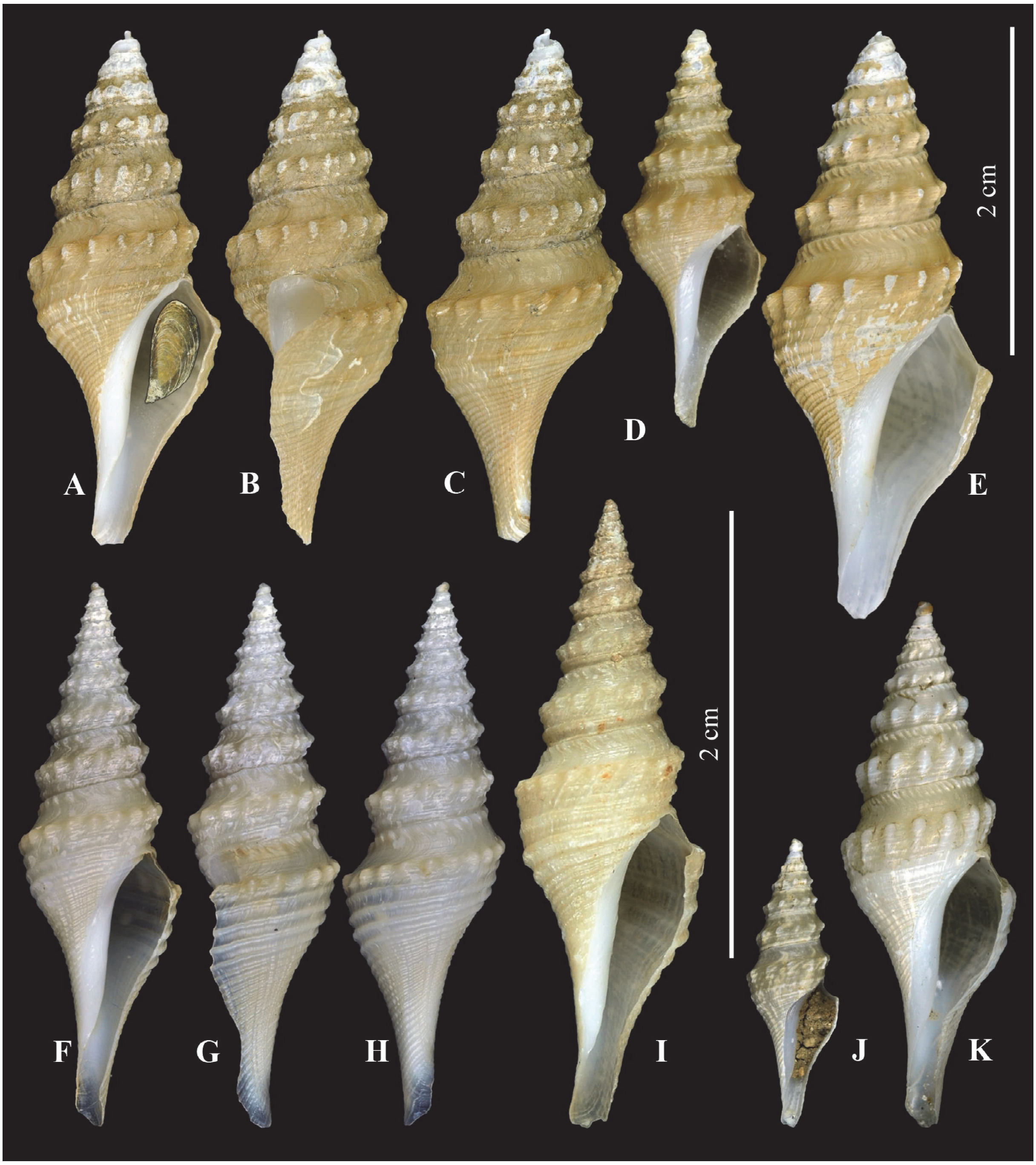

FIG. 2. Shells of *Comispira* spp. **A-E.** ***Comispira mai*** (Li et Li, 2008), South China Sea. **A-C.** MNHN-IM-2013-61657, SL 35.5 mm. **D.** MNHN-IM-2013-52033, SL 24.4 mm (radula see Fig. 3 A-B). **E.** MNHN-IM-2013-61658, SL 36 mm. **F-K.** ***Comispira compta*** gen. et sp. nov. **F-H.** Holotype, MNHN-IM-2013-19215, SL 24.4 mm. **I.** Solomon Islands, MNHN-IM-2009-16801, SL 28 mm. **J.** Philippines, AURORA 2007, st. CP2750, SL 12.9 mm. **K.** Vanuatu**,** MUSORSTOM 8, st. CP1109, SL 23.5 mm (radula see Fig. 3 C-D). A-E – at the same scale, F-K – at the same scale.

РИС. 2. Раковины *Comispira* spp. **A-E.** ***Comispira mai*** (Li et Li, 2008), Южно-Китайское море. **A-C.** MNHN-IM-2013-61657, SL 35,5 мм. **D.** MNHN-IM-2013-52033, SL 24,4 мм (радула на Рис. 3 A-B). **E.** MNHN-IM-2013-61658, SL 36 мм. **F-K.** ***Comispira compta*** gen. et sp. nov. **F-H.** Голотип, MNHN-IM-2013-19215, SL 24,4 мм. **I.** Соломоновы острова, MNHN-IM-2009-16801, SL 28 мм. **J.** Филиппины, AURORA 2007, st. CP2750, SL 12,9 мм. **K.** Вануату, MUSORSTOM 8, st. CP1109, SL 23,5 мм (радула на Рис. 3 C-D). A-E – в одном масштабе, F-K – в одном масштабе.

Pseudomelatomidae Morrison, 1965), the new genus differs in the morphology of marginal teeth, which are in *Comitas* flat, broadly oval, with thickened edges and tooth tips and without a pronounced accessory limb [Bouchet *et al.*, 2011: figs 15 B-D].

With COI data only (Fig. 1), ***Comispira*** gen. nov. is not monophyletic, being mixed with *Sibogasyrinx* (see below). In the upcoming exon-capture-based phylogeny [Abdelkrim *et al.*, 2018], the two species ***C. compta*** gen. et sp. nov.

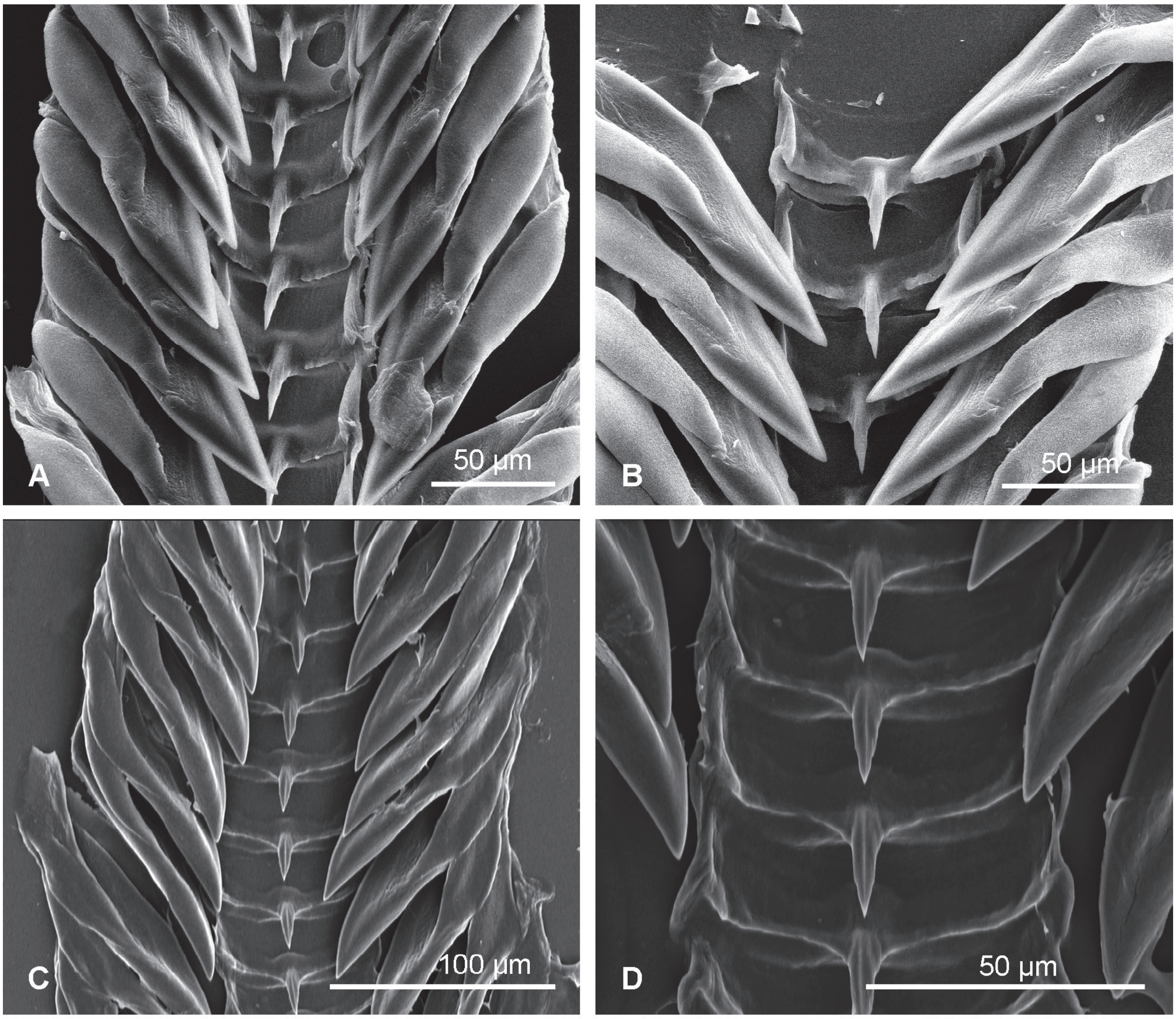

FIG. 3. Radulae of ***Comispira*** spp. **A-B. *Comispira mai* (**Li et Li, 2008), MNHN-IM-2013-52033 (shell on Fig. 2D). **A.** Dorsal view of the central portion of the radula. **B.** Enlarged central teeth. **C-D. *Comispira compta*** gen. et sp. nov., Vanuatu, MUSORSTOM 8, st. CP1109 (shell on Fig. 2K); **C –** dorsal view of the central portion of the radula, **D** – enlarged central teeth.

РИС. 3. Радулы ***Comispira*** spp. **A-B. *Comispira mai*** (Li et Li, 2008), MNHN-IM-2013-52033 (раковина на Рис. 2D). **A.** Вид центральной части радулы с дорсальной стороны. **B.** Увеличенные центральные зубы. **C-D. *Comispira compta*** gen. et sp. nov., Вануату, MUSORSTOM 8, st. CP1109 (раковина на Рис. 2K); **C –** вид центральной части радулы с дорсальной стороны, **D** – Увеличенные центральные зубы.

and ***C. mai*** are sister species, included in Cochlespiridae.

**Species composition:** Presently the genus contains two species – ***C. mai*** (Li et Li, 2008) and ***C. compta*** sp. nov.

**Etymology.** The name comes from combination of two generic names of Conoidea – *Comitas* Finlay, 1926 and *Cochlespira* Conrad, 1865, which species of the new genus resemble.

## ***Comispira mai*** (Li et Li, 2008)
(Figs 2, 3 A-B, 4)

*Leucosyrinx mai* Li, Li, 2008: 37, figs 5-6; Hasegawa *in* Okutani, 2017: 1034, pl. 328, fig. 1.

**Type locality**: Nansha Islands, 9°49.82'N, 117°47.98'E, 1241 m, AT, 09.08.1988.

**Material examined: South China Sea**, 10°18'N, 114°13'E, 1292-1321 m, NANHAI 2014, st. CP4106, 06.01.2014, 1 lv (MNHN-IM-2013-44247); off Taiping Island, 10°22'N, 114°16'E, 1381-1397 m, NANHAI 2014, st. CP4107, 06.01.2014, 1 lv (MNHN-IM-2013-52033); S.W. off Dong Sha, 19°50'N, 116°27'E, 1128-1278 m, ZHONGSHA 2015, st. CP4134, 22.07.2015, 3 lv (MNHN-IM-2013-61656, MNHN-IM-2013-61657, MNHN-IM-2013-61658); S.W. off Dong Sha, 19°48'N, 116°29'E, 1205-1389 m, ZHONGSHA 2015, st. CP4137, 29.09.2015, 1 lv (MNHN-IM-2013-59407).

**Remarks**. The species was described on the basis of a highly worn dead-collected holotype with the SL 27.0 mm. In our material the largest speci-

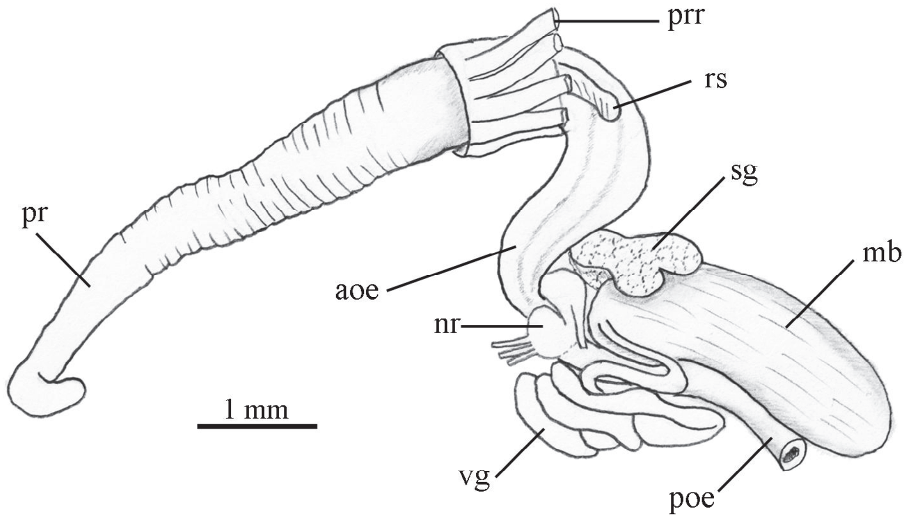

FIG. 4. Foregut anatomy of ***Comispira** mai* (Li et Li, 2008). Abbreviations: aoe – anterior oesophagus; mb – muscular bulb of the venom gland; poe – posterior oesophagus; pr – proboscis; prr – proboscis retractors; nr – circumoesophageal nerve ring; rs – radular sac; sg – salivary gland; vg – venom gland.

РИС. 4. Анатомия переднего отдела пищеварительной системы ***Comispira** mai* (Li et Li, 2008). Сокращения: aoe – передний пищевод; mb – пропульсаторный орган ядовитой железы; poe – задний пищевод; pr – хобот; prr – ретракторы хобота; nr – окологлоточное нервное кольцо; rs – радулярное влагалище; sg – слюнная железа; vg – ядовитая железа.

men reaches SL 35.5 mm. Our specimens were collected very close to the type locality and at similar depths, so despite poor preservation of the holotype the identification poses little problem.

The protoconch is missing in all available specimens, but the remaining part in the youngest specimen suggests that it is probably paucispiral.

The radula (Fig. 3 A-B) was examined in two specimens [MNHN-IM-2013-52033 (complete, used in the description below), MNHN-IM-2013-61656 (fragmented)] and was practically identical; long, around 1.9 mm (30% of AL without canal), consists of *ca* 60 rows with long (23 rows) nascent part. Radula width up to 270 μm (4.3% of AL). Central tooth with subrectangular, anteriorly shallowly arcuate basal plate, having distinct borders and large sharply pointed cusp. Marginal teeth duplex, with large flattened and pointed major limb and accessory limb, constituting about 0.5 of major limb length. Anterior tooth margins thickened and appear rounded in section.

Two specimens were dissected. One (MNHN-IM-2013-52033, Fig. 4) was preserved with the proboscis extended and protruding through rhynchostome. In extended proboscis the buccal mass with radula sac are situated within the proboscis at its base, while in the specimen with a contracted proboscis the buccal mass is situated behind the proboscis. The oesophagus forms a long loop before passing through nerve ring, shorter in the specimen with extended proboscis. Oesophagus broad, strongly constricting before passing through nerve ring. Salivary glands compact, acinous. Venom gland highly convoluted, medium-sized, with large elongate-oval muscular bulb. The opening of the venom gland into oesophagus is covered by the nerve ring.

The species was originally placed in the genus *Leucosyrinx* and compared to *L. julia* Thiele, 1925, a species described from an immature specimen from East Africa and later also found in the Gulf of Aden [Powell, 1969: 338]. *Comispira mai* has a strong similarity to *L. julia* in shell shape and sculpture, but the species description was based on a much smaller specimen [SL 10.5 mm, Thiele, 1925: pl. 36(24), fig. 24], differing in the absence of the strong basal angulation of the shell base. The larger specimen [SL 53 mm from *John Murray* Expedition illustrated by Powell, 1969: pl. 257, fig. 5] lacks this basal angulation and is not very similar to the type of *L. julia*. Knowing the high homoplasy rate of conchological characters in Conoidea, as well as distant geographical range we prefer at the moment to consider *C. mai* and *L. julia* as separate species in distinct genera, but the latter may also belong to ***Comispira***.

## ***Comispira compta*** gen. et sp. nov.
## (Figs 2 F-K, 3 C-D)

urn:lsid:zoobank.org:act:486E4F94-8671-4858-8E8E-64AE08CD20E4

**Holotype**: MNHN-IM-2013-19215 (sequenced).

**Type locality:** Bismarck Sea, Papua New Guinea, Dogreto Bay, 3°18’S, 143°02’E, 440 m, PAPUA NIUGINI, st. CP4066, 22.12.2012.

**Other material. Solomon Islands**, 06°39'S, 156°14'E, 490-520 m, SOLOMON 2, st. CP2226, 28.10.2004, 1 lv (MNHN-IM-2009-16801);

**Philippines**, 15°53'N, 121°54'E, 518-538 m, AURORA 2007, st. CP2750, 02.06.2007 (4 dd).

**Vanuatu,** 14°52'S, 167°18'E, 1550-1620 m, MUSORSTOM 8, st. CP1109, 8.10.1994 (1 lv).

**Description** (holotype). Shell narrow, fusiform, with high spire and long narrow slightly inclined leftward siphonal canal. Protoconch eroded and part of it missing, probably paucispiral. Teleoconch whorls distinctly angulated at shoulder, about 8 in total. Suture deep, subsutural ramp weakly concave, with subsutural row of distinct nodules, 23 on last whorl, 19 on penultimate. On upper whorls subsutural nodules rounded, on penultimate and last whorls nodules elongated along shell axis, opisthocline. On whorl shoulder a spiral row of very distinct large oval prosocline nodules, 20 on last whorl, 16 on penultimate. In interspaces between nodules a few irregularly spaced, very thin, spiral riblets. Subsutural ramp nearly smooth, with faint microscopic spiral threads. Distinct spiral cords below shoulder one on upper teleoconch whorls, 2 on penultimate. On last whorl four upper cords subequal, rounded in profile, with interspaces of about twice cord width, on shell base and canal cords are thinner and more closely spaced, 21 in total. Interspaces between larger spiral cords smooth.

Shell base gradually narrowing towards narrow and long nearly straight siphonal canal, slightly inclined leftwards. Aperture narrow, oval, constricted posteriorly with narrow thin parietal callus, outer lip partially broken, weakly convex in upper part angulated at shoulder and weakly convex below shoulder, and weakly concave at transition to canal.

Anal sinus subsutural, broadly arcuate, medium deep, symmetrical, U-shaped, confluent with large forward extension of outer lip (according to growth lines). Teleoconch uniformly off-white, covered by adherent pale yellow periostracum.

Measurements (holotype): SL 24.4 mm, AL (with canal) 12.5 mm, SW 7.0 mm. Largest specimen attains SL 28 mm.

**Remarks.** The holotype is the only sequenced specimen. The new species differs from *Comispira mai* in a more elongate shell and in less developed spiral threads in interspaces between shoulder nodules. The genetic distance between the holotype of *C. compta* and the six sequenced specimens of *C. mai* is greater than 20%.

In three specimens from the Philippines, the protoconchs are better preserved, bulbous and high, with smooth convex whorls. Since upper teleoconch whorls are strongly eroded, it is not possible to count the exact number of protoconch whorls (the transition is not discernible), but is estimated between 1.5 and 2 whorls. Being similar to the holotype in shell outline and sculpture pattern they express variability in the prominence of spiral cords below suture, which are in general less pronounced and less regularly spaced compared to the holotype.

One specimen, that is conchologically similar to the holotype, was collected in Vanuatu at significantly greater depths (1550-1620 m) (Fig. 2 K). It differs in having more dense subsutural nodules as well as in longer nodules on whorl shoulder. Therefore, we attribute it to ***Comispira compta*** with some reservations. Its radula was examined (Fig. 3 C-D). Radula long, around 1.7 mm (25% of AL without canal), consisting of *ca* 65 rows with long (27 rows) nascent part. Radula width up to 200 µm (2.9% of AL). Central tooth with subrectangular, shallowly arcuate anteriorly basal plate, having distinct borders and large sharply pointed cusp. Marginal teeth duplex, with large flattened and pointed major limb and accessory limb constituting about 2/3 of major limb length. It is very similar in morphology to the type species, ***C.*** *mai*.

**Etymology** Compta (lat.) ornamented, reflecting distinct sculpture of the shell.

**Distribution.** Papua New Guinea, Solomon Islands and the Philippines, 440-538 m. Possibly Vanuatu in 1550-1620 m.

## *Sibogasyrinx* Powell, 1969

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

**Type species**: *Surcula pyramidalis* Schepman, 1913 (OD).

**Remarks.** The genus was established initially as a subgenus to incorporate three species with "peripheral angle right down at the lower suture" [Powell, 1969: 343]. Later [Bouchet *et al.*, 2011] it was found that the species of the genus are characterized by a radula typical for Cochlespiridae – with well-defined central teeth, contrary to *Leucosyrinx* spp. in which the central teeth or central formations were absent. The position of the genus in Cochlespiridae was also confirmed by molecular analysis [Puillandre *et al.,* 2011]. At the same time the single diagnostic character – low position of the peripheral angulation – was found to be inconsistent, since in most still unnamed species, as well as in *Sibogasyrinx* ***sangeri*** sp. nov. described herein, the angulation can be situated in the middle of whorls. Besides, it is a rather variable character and is subjected to strong intraspecific variability. Thus the shell outline is a poor diagnostic character of the genus. It should be noted that similar fusiform shells were attributed at least to three genera – *Sibogasyrinx, Leucosyrinx* [separate family described in Abdelkrim *et al.*, 2018] and more rarely to *Comitas* Finlay, 1926 (Pseudomelatomidae Morrison, 1966). All three genera are well separated by radular morphology. As for *Comispi-*

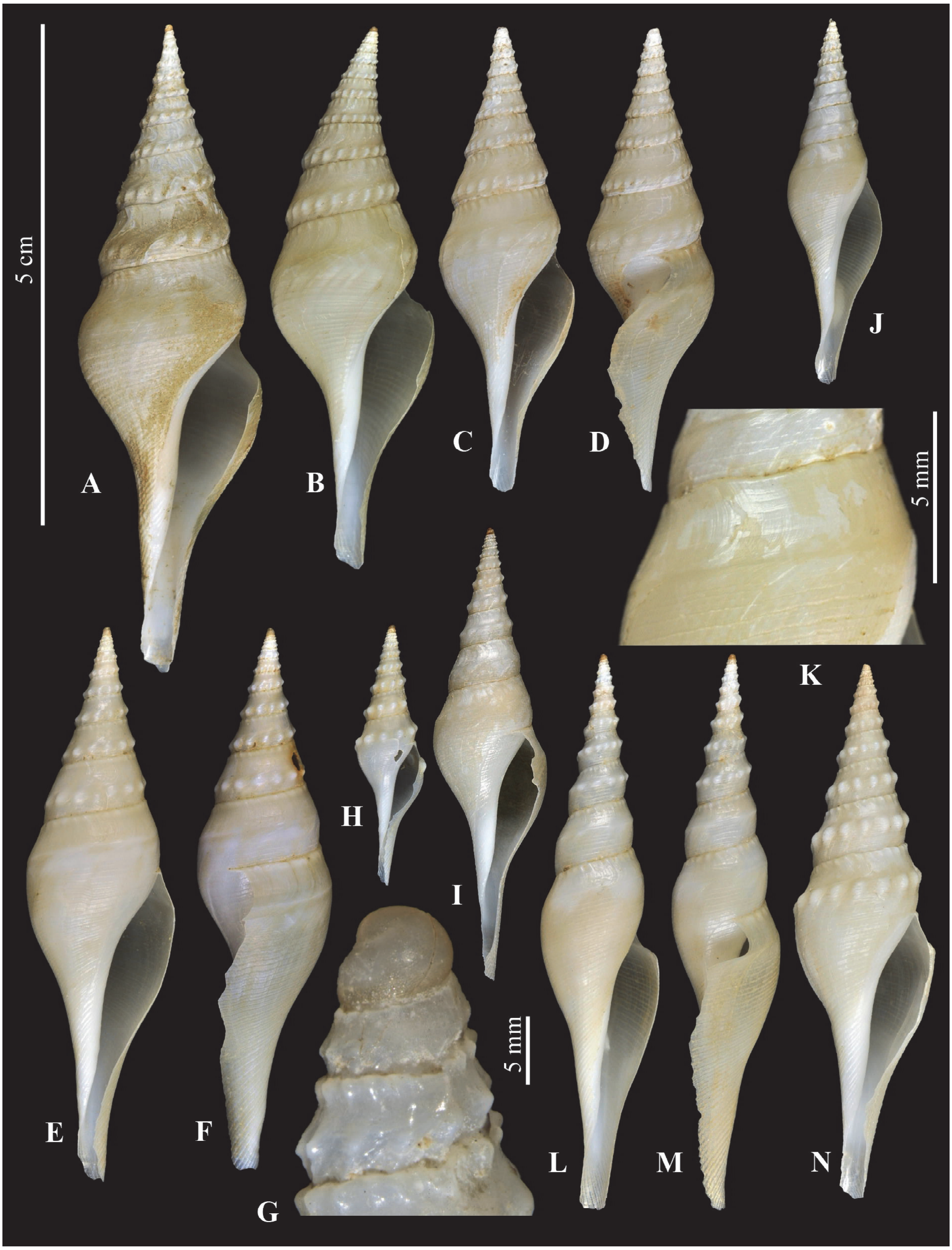

FIG. 5. Shells of *Sibogasyrinx*. **A-D.** *Sibogasyrinx pyramidalis* (Schepman, 1913). **A.** MNHN-IM- 2013-44605, SL 65 mm. **B.** MNHN-IM-2013-50215, SL 54.4 mm. **C-D**. MNHN-IM-2009-13451, SL 46.5 mm. **E-M.** *Sibogasyrinx* ***sangeri*** sp. nov. **E-G.** Holotype, SL 54.1 mm. **H.** MNHN-IM-2009-16766, SL 26.3 mm. **I.** MNHN-IM-2009-16995, SL 47.7 mm (radula see on Fig. 6 C-D). **J-K.** MNHN-IM-2009-13434, SL 36.9 mm. **L-M.** MNHN-IM-2009-16779, SL 55.8 mm. **N.** MNHN-IM-2009-17021, SL 53.7 mm. All shells at the same scale.

РИС. 5. Раковины *Sibogasyrinx*. **A-D.** *Sibogasyrinx pyramidalis* (Schepman, 1913). **A.** MNHN-IM- 2013-44605, SL 65 мм. **B.** MNHN-IM-2013-50215, SL 54,4 мм. **C-D**. MNHN-IM-2009-13451, SL 46,5 мм. **E-M.** *Sibogasyrinx* ***sangeri*** sp. nov. **E-G.** Голотип, SL 54,1 мм. **H.** MNHN-IM-2009-16766, SL 26,3 мм. **I.** MNHN-IM-2009-16995, SL 47,7 мм (радула на Рис. 6 C-D). **J-K.** MNHN-IM-2009-13434, SL 36,9 мм. **L-M.** MNHN-IM-2009-16779, SL 55,8 мм. **N.** MNHN-IM-2009-17021, SL 53,7 мм. Все раковины в одном масштабе.

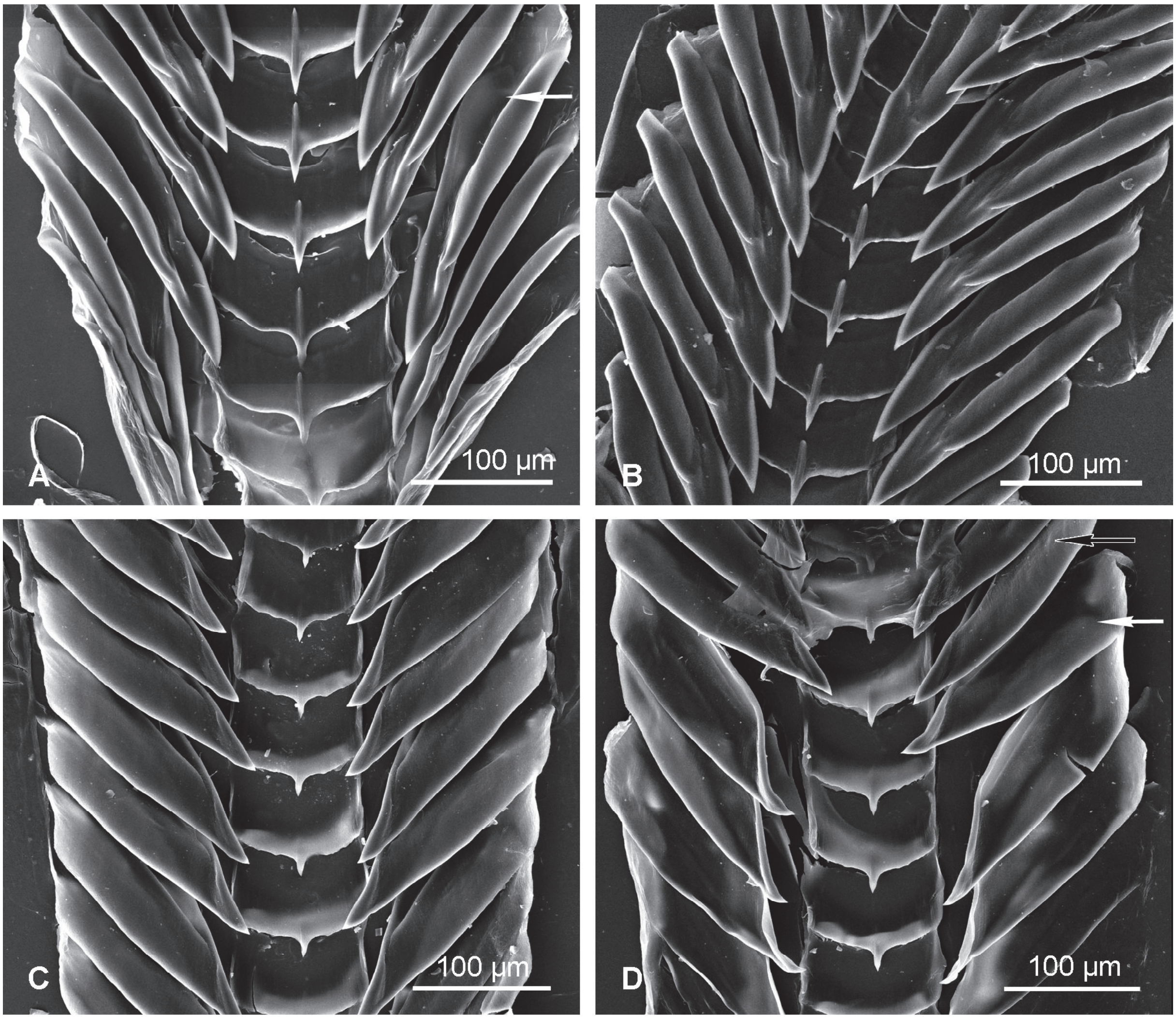

FIG. 6. Radulae of *Sibogasyrinx*. **A-B.** *Sibogasyrinx pyramidalis* (Schepman, 1913), MNHN-IM-2009-13451 (shell see on Fig. 5 C-D); **A** – part of radula with not fully formed marginal teeth, **B** – part of radula with fully formed marginal teeth. **C-D.** *Sibogasyrinx* ***sangeri*** sp. nov., MNHN-IM-2009-16995 (shell see on Fig. 5 I); **C** – part of radula with fully formed marginal teeth, **D** – part of radula with transition of not folded (white arrow) to completely folded lengthwise (black arrow) marginal teeth.

РИС. 6. Радулы *Sibogasyrinx*. **A-B.** *Sibogasyrinx pyramidalis* (Schepman, 1913), MNHN-IM-2009-13451 (раковина на Рис. 5 C-D); **A** – часть радулы с неполностью сформированными маргинальными зубами, **B** – часть радулы с полностью сформированными маргинальными зубами. **C-D.** *Sibogasyrinx* ***sangeri*** sp. nov., MNHN-IM-2009-16995 (раковина на Рис. 5 I); **C** – часть радулы с полностью сформированными маргинальными зубами, **D** – часть радулы в месте перехода от несложенных (белая стрелка) к полностью сложенным вдоль маргинальными зубами (черная стрелка).

*ra*, *Sibogasyrinx* is not monophyletic with the COI gene (Fig. 1), but *S. pyramidalis* and *S.* ***sangeri*** sp. nov. are sister species in the exon-capture-based phylogeny [Abdelkrim *et al.*, 2018].

## *Sibogasyrinx pyramidalis* (Schepman, 1913)
## (Figs 5 A-D; 6 A-B)

*Surcula pyramidalis* Schepman, 1913: 59(423), pl. 27, figs. 10a, b.

**Type locality:** Timor Sea, 10°48.6’S, 123°23.1’E, 918 m.

**Sequenced material**: **Philippines**. 15°20'N, 121°37’E, 593-600, AURORA 2007, st. CP2729, 31.05.2004, 1 lv (MNHN-IM-2009-13451).

**South China Sea**, 20°01’N, 115°02’E, 700-723 m, NANHAI 2014, st. CP4118, 12.01.2014, 2 lv (MNHN-IM-2013-44574, MNHN-IM-2013-44605). 20°29’N, 116°08’E, 590-633 m, DONGSHA 2014, st. CP4129, 1 lv (MNHN-IM-2013-50215).

**Remarks.** The species is variable in shell shape and in the degree of concavity of subsutural ramp – from nearly flat to distinctly concave. The holotype is medium-sized specimen (SL 45 mm) and is very similar to our specimen of comparable size (Fig. 5 C-D, SL 46.5 mm). It should be specified that we do not have any specimens from the Timor Sea (type locality) and our identification is based solely on conchological characters.

Radulae examined in two specimens (MNHN-IM-2009-13451, MNHN-IM-2013-50215) were very similar consisting of 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 subrectangular broad but short, anteriorly shallowly arcuate basal plate, having distinct borders and with a narrow but rather long sharply pointed cusp. Marginal teeth flat, with thickened edges, folded lengtwise. On a developing part of the radula the tooth folding is clearly visible (on Fig. 6A, not fully folded tooth is marked by white arrow, while next fully folded tooth is marked by black arrow). During teeth maturation the edges are progressively thickened, so that fully formed tooth looks like a normal duplex one (Fig. 6B).

Proboscis long, partially coiled within rhynchocoel, very thick in posterior part and much narrower tubular in anterior 3/4. Oesophagus behind the proboscis forms a rather long loop before the nerve ring. Venom gland opens into oesophagus immediately posterior to nerve ring. Buccal mass is situated outside proboscis in its contracted state, broad, passing in oesophagus of same diameter without visible external border. Salivary glands medium sized, acinous, abutting the nerve ring. Small rounded accessory salivary gland.

**Distribution.** Based on sequenced specimens, the species is distributed in the South China Sea and off the Philippines at 590-723 m.

## *Sibogasyrinx* **sangeri** sp. nov.

(Figs 5 E-N, 6 C-D)

urn:lsid:zoobank.org:act:F2106FD6-850E-4D17-8446-16358FF2603A

**Holotype:** MNHN-IM-2009-17022 (sequenced).

**Type locality:** Papua New Guinea, 07°52’S, 148°03’E, 575-655 m, BIOPAPUA, st. CP3729, 10.08.2010.

**Other sequenced material examined: Papua New Guinea**, 04°04’S, 151°56’E, 585-601 m, BIOPAPUA, st. CP3671, 2 lv (MNHN-IM-2009-16989, MNHN-IM-2013-52052); 04°24’S, 151°50’E, 788-805 m, BIOPAPUA, st. CP3674, 24.09.2010, 1 lv (MNHN-IM-2009-16995); off Woodlark Islands, 09°08’S, 152°19’E, 448-470 m, BIOPAPUA, st. CP3742, 10.10.2010, 1 lv (MNHN-IM-2009-17057); 05°39’S, 153°59'E, 654-660 m, BIOPAPUA, st. CP3750, 12.10.2010, 1 lv (MNHN-IM-2009-17021); N of Long I., 05°10’S, 147°03’E, 724 m, PAPUA NIUGINI, st. CP3982, 06.12.2012, 1 lv (MNHN-IM-2013-19752); Dampier Strait, E Umboi Island, 05°35’S , 148°13’E, 630-870 m, PAPUA NIUGINI, st. CP4014, 12.12.2012, 1 lv (MNHN-IM-2013-19961).

**Solomon Islands**, Sta Isabel, 08°47’S, 159°40’E, 645-840 m, SALOMON 2, st. CP2181, 22.10.2004, 1 lv (MNHN-IM-2009-16766); Rendova Id., 08°36’S, 157°27’E, 509-520 m, SALOMON 2, st. CP2288, 11.07.2004, 2 lv (MNHN-IM-2007-42523, MNHN-IM-2009-16779).

**Philippines**, 15°45’N, 121°45’E, 562 m, AURORA 2007, st. CP2663, 21.05.2007, 1 lv (MNHN-IM-2009-13434);

**Description** (holotype). Shell thin, fragile, fusiform, with rather high spire and long, narrow, straight siphonal canal. Protoconch small, globose (Fig. 5G), of 1.75 strongly convex, microshagreened whorls. Protoconch/teleoconch transition not clear due to erosion of upper teleoconch whorls. Protoconch diameter 1.1 mm, height 1.2 mm. Upper teleoconch whorls angulated in lowermost part just above suture, last whorl nearly evenly rounded and weakly convex. About 10 teleoconch whorls. Suture shallow, subsutural ramp with row of distinct closely spaced nodules, 10 on first whorl, 14 on second whorl. Nodules become more broadly spaced and on later whorls less discernible, absent on posterior half of last whorl. Subsutural zone very weakly concave, nearly straight on penultimate and last whorls, smooth except few irregularly spaced sometimes oblique indistinct spiral threads. Row of pronounced larger nodules on lower part of the whorls, just above suture in upper whorls and slightly higher on penultimate whorl. On last whorl nodules absent. Last whorl with low carina on periphery giving it very weakly angulated outline.

Below periphery 2-3 distinct spiral cords on penultimate whorl and about 30 cords below carina on last whorl and 22 on canal.

Shell base gradually narrowing towards long nearly straight siphonal canal. Aperture irregularly narrow oval, constricted posteriorly with broad very thin parietal callus, outer lip partially broken, convex and weakly angulated in upper part and weakly convex below shoulder, and weakly concave at transition to canal. Anal sinus medium deep, subsutural, broadly arcuate, according to growth lines confluent with large forward extension of outer lip. Growth lines thin but distinct. Shell uniformly off-white, protoconch light tan.

Measurements (holotype): SL 54.1 mm, AL (with canal) 31.3 mm, SW 14.1 mm. Largest available specimen attains SL 55.8 mm (MNHN-IM-2009-16779 – Fig. 5 L-M).

Proboscis medium long in contracted stage, buccal mass situated outside the proboscis. Oesophagus very broad, forming short loop before passing through nerve ring. Venom gland opens into oesophagus ventrally immediately posterior to the nerve ring.

Radula (Fig. 6 C-D) was examined in one specimen (MNHN-IM-2009-16995), relatively short, consisting of *ca* 40 rows of teeth, with long (15-16 rows) nascent part. 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 very shallowly arcuate anteriorly basal plate, having distinct borders and medium-sized weak cusp. Marginal teeth flat, folded lengtwise. On a forming part of the radula the teeth folding is clearly visible, which occurs within one subsequent row (on Fig. 6D white arrow indicates last still unfolded tooth, while black arrow with white outline indicate the first folded tooth). The folding occurred at the 17th row in studied radula. Resulting folded tooth is medium broad, with narrow thickened inner margin and sharp pointed tip.

**Remarks.** In one specimen (MNHN-IM-2009-16766) the protoconch was intact. It consists of 1.75 whorls, latest 0.25 whorl with 3 distinct strongly oblique prosocline axial ribs; the transition to teleoconch is marked by appearance of row of subsutural wrinkles, which quicky transform into subsutural nodules.

The species is rather variable in sculpture and shell shape, particularly in the degree of shell slenderness (SW/SL ratio varies from 0.22 to 0.27), with the holotype being the broadest specimen. There is clear ontogenetic variability – the nodules on the shoulder become obsolete on last whorl in large specimens, while in smaller specimens and on upper teleoconch whorls the nodules are well developed and the whorl profile is clearly angulated. The upper subsutural row of nodules usually becomes obsolete with age, but in some adult specimens it is present even on last whorl. While in the holotype the subsutural zone is nearly smooth, in some specimens there are several rather pronounced flattened spiral cords (Fig. 5J – MNHN-IM-2009-13434). Without molecular data it would be difficult to attribute all available specimens to a single species.

So far only two species are attributed to *Sibogasyrinx* – *Surcula pyramidalis* Schepman, 1913 and *Leucosyrinx* (*Sibogasyrinx*) *archibenthalis* Powell, 1969. From both of them the new species differs in a more narrow elongated fusiform shell and also the evenly convex last whorl (except one specimen that still has angulated last whorl – MNHN-IM-2009-17021, Fig. 5N).

Genetic distances between the four and twelve sequenced specimens of *S. pyramidalis* and *S.* ***sangeri*** sp.nov., respectively, are between 14.4 and 15.2%, whereas the genetic distances between samples of the same species are below 4 and 1% for *S. pyramidalis* and *S.* ***sangeri***, respectively.

**Etymology.** The species is named after Frederick Sanger, commemorating his 100 anniversary, twice Noble Price winner, who proposed the procedure of DNA sequencing, “Sanger sequencing”, which is now a universal tool in molecular studies, including molluscs.

**Distribution**. The species is found in the Philippines, Solomon Islands and Papua New Guinea, 448-805 m.

## Clavatulidae Gray, 1853
## *Pagodaturris* gen. nov.

urn:lsid:zoobank.org:act:AE176526-4DC5-4E88-857D-3A3E6D3FD34C

**Type species:** *Pleurotoma molengraaffi* Tesch, 1915 (here designated). Timor. Pliocene.

**Diagnosis.** Shell small to medium-sized, fusiform to biconic, with high spire and long nearly straight siphonal canal. Protoconch paucispiral. Whorls strongly angulated at shoulder which bears median peripheral keel with row of large distinct nodules on all whorls. The tips of nodules attenuated and usually directed adapically. Concave subsutural zone smooth or with indistinct spiral riblets. Shell base and canal with weak narrow spiral riblets. Axial sculpture limited to nodules and growth lines.

Aperture narrow, oval or irregularly shaped, constricted posteriorly, with narrow parietal callus, gradually passing into siphonal canal. Anal sinus judging from growth lines, broad, medium-deep, deepest point on center of median keel. Teleoconch flesh-coloured, axially striped with irregularly altering darker and lighter zones.

Radula with only marginal teeth. Marginal teeth of modified duplex type, major limb pointed, with sharp anterior edge and thickened posterior edge that receives the accessory limb. Accessory limb bipartite, divided by deep longitudinal furrow along most of its length in two lobes (Fig 8 A-D).

**Remarks.** The new genus has strong similarity to species of the genus *Lucerapex* Wenz, 1943 (Turridae) and the type species of the new genus, *P. molengraaffi* was attributed to *Lucerapex* by Powell [1964] and later Sysoev [1996]. The difference is that in species of *Pagodaturris* the tips of the nodules on median peripheral keel are attenuated and usually directed adapically, while in *Lucerapex* they are more rounded. Nevertheless this difference is very subtle. Both genera differ in morphology of the marginal radular teeth, which in *Lucerapex* are duplex, typical of Turridae, while in *Pagodaturris* the teeth are tripartite, with accessory limb clearly subdivided in two lobes longitudinally, somewhat similar to the tripartite marginal teeth found in *Makiyamaia* Kuroda in MacNeil, 1961 (Fig. 8 E-F). Both genera *Pagodaturris* and *Makiyamaia* are early offshoots of Clavatulidae in the upcoming exon-capture-based phylogeny [Abdelkrim *et al*., 2018].

**Etymology.** The name reflects the similarity of the outline of the spire of the species due to attenuated and elevated tips of nodules similar to roof corners in pagoda buildings.

**Genus composition:** in addition to the type species, ***Pagodaturris*** *molengraaffi*, we attribute to the genus on the basis of conchological and radular similarities as well as molecular data ***Pagodaturris philippinensis*** gen. et sp. nov. Only two samples of *Pagodaturris*, one for each species *P. molengraaffi* and *P. philippinensis*, have been sequenced for the COI gene so far, and they are sister lineages in the COI tree (Fig. 1B). One more new species still unsequenced is represented in our material by a single specimen, in shell and radular characters very similar to the species mentioned above (Fig. 7J, radula on Fig. 8 D). In the absence of molecular data we abstain from description. Another species, that we attribute conditionally to *Pagodaturris*, is *Lucerapex casearia regilla* Iredale, 1936 (holotype on Fig. 7 H-I) from off Sydney in 110 fms. The holotype is conchologically similar to the other species of *Pagodaturris.*

## ***Pagodaturris*** *molengraaffi* (Tesch, 1915)
## (Figs 7 A-D, 8 A-B)

*Pleurotoma molengraaffi* Tesch, 1915: 28, pl. 77(5), figs. 54-56.

*Lucerapex molengraaffi* (Tesch, 1915) – Powell, 1964: 287(22-839), pl. 220, figs. 3, 4, pl. 221, figs. 1, 2; Sysoev, 1996: 19, figs. 77, 78.

**Material examined: Solomon Islands,** E of San Cristobal, 10°45'S, 162°20'E, 410-430 m, SOLOMONBOA 3, st. CP2832, 1 lv (MNHN-IM-2009-18963).

**Remarks.** The species originally described from Pliocene of Timor was recorded also from Borneo, Celebes, the Philippines and the Maldives, in 464-1022 m [Powell, 1964; Sysoev, 1996]. Our single sequenced specimen has SL 25.5 mm, while Powell [1964] reported SL up to 33 mm.

Protoconch paucispiral, consists of about two smooth convex whorls. Transition to teleoconch is marked by appearance of median peripheral keel with nodules. Protoconch diameter 0.88 mm, height 0.75 mm.

Radula (Fig. 8 A-B) of marginal teeth only. Marginal teeth of modified duplex type, major limb pointed, medium broad, with thickened edges and depressed central portion, outer end (tooth base) poorly sclerotized. Accessory limb much narrower, although long and extends on outer edge beyond the limit of major limb. It is divided by deep longitudinal furrow along most of its length into two lobes, the inner lobe longer.

## ***Pagodaturris philippinensis*** gen. et sp. nov.
## (Figs 7 E-G, 8 C)

urn:lsid:zoobank.org:act:0F94A03D-BB90-4DF0-9DD3-2E684B9A91CB

**Holotype**: MNHN-IM-2007-42458 (sequenced).

**Type locality: Philippines,** Bohol/Sulu seas, 08°39'N, 123°16'E, 255-301 m, PANGLAO 2005, st. CP2372.

**Description** (holotype). Shell thin, fusiform, with high spire and long narrow straight siphonal canal. Protoconch paucispiral, globose, of nearly two smooth strongly convex smooth whorls, slightly eroded in holotype (Fig. 7 G). Protoconch/teleoconch transition is eroded and not discernible. Protoconch diameter around 1.1 mm, height around 1 mm. Teleoconch whorls strongly angulated at periphery, slightly over 6 in total. Suture shallow, subsutural region wide, distinctly concave, having indistinct spiral riblets. Median peripheral keel strong, on upper teleoconch whorls slightly above suture, then progressively albeit slightly shifting upwards. Keel forming distinct broadly spaced nodules (10 on first whorl, 14 on second), penultimate whorl with 16 nodules, last with 15. Upper corners of intact nodules slightly attenuated and raised adapically. Median keel with 2-3 irregularly spaced riblets seen in interspaces between nodules. Below median keel few irregularly spaced and very weak riblets.

Shell base sharply narrowing towards siphonal canal. Aperture oval, constricted posteriorly with broad but very thin parietal callus, outer lip fragile, very weakly concave in upper part, with distinct notch corresponding to median keel and weakly convex below shoulder, gradually passing into canal. Anal sinus judging from growth lines broad, medium-deep, deepest point in center of median keel. Growth lines numerous, thin. Shell yellowish, with contrasting lighter and darker axial lines corresponding to growth lines. Interspaces between nodules light brownish.

Measurements (holotype): SL 17.4 mm, AL (with canal) 9.2 mm, SW 6.4 mm.

Radula (Fig. 8C) of marginal teeth only, very similar to ***P.*** *molengraaffi*. Marginal teeth of modified duplex type, major limb pointed, lanceolate, medium broad, with thickened edges and depressed central portion, outer end (tooth base) poorly sclerotized. Accessory limb much narrower, although long and extends on outer edge beyond the limit of major limb. It is divided by deep longitudinal furrow along most of its length in two lobes, inner longer.

**Remarks.** The new species differs from ***P.*** *molengraaffi* in having slightly smaller shell with more abruptly narrowing shell base and weaker spiral threads on shell base. Nevertheless only one specimen of the new species is known and its variability therefore is unstudied. The genetic distance between the two sequenced samples, one of *P. philippinensis* and one of ***P.*** *molengraaffi*, is 11.4%.

**Etymology:** the species epithet refers to the type locality.

**Distribution**. Type locality only.

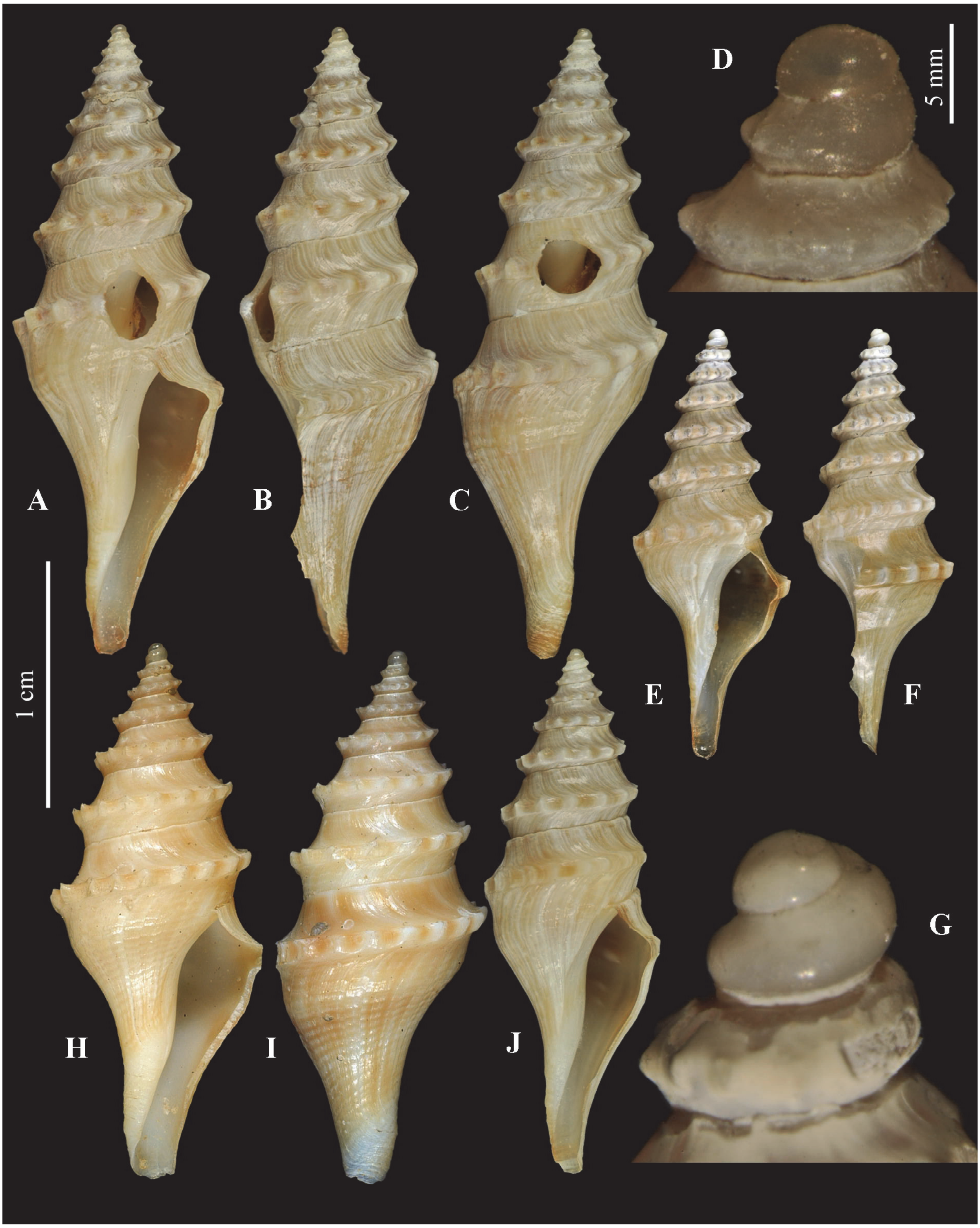

FIG 7. Shells of ***Pagodaturris*** gen. nov. **A-D.** ***Pagodaturris*** *molengraaffi* Tesch, 1915, MNHN-IM-2009-18963, SL 25.5 mm; **D** – protoconch. **E-G.** ***Pagodaturris philippinensis*** gen. et sp. nov., holotype, MNHN-IM-2007-42458, SL 17.4 mm; **G** – protoconch. **H-I.** ***Pagodaturris*** *regilla* (Iredale, 1936), holotype of *Lucerapex casearia regilla*, AMS C.60710, SL 20.5 mm. **J.** ***Pagodaturris*** sp., MNHN-IM-2007-42504, Solomon Islands, 08°24'S, 159°27'E, 362-432 m, SOLOMON 2, st. CP2193, SL 21.2 mm (radula on Fig. 8D). All shells at the same scale. H-I – photos courtesy of AMS.

РИС. 7. Раковины ***Pagodaturris*** gen. nov. **A-D.** ***Pagodaturris*** *molengraaffi* Tesch, 1915, MNHN-IM-2009-18963, SL 25,5 мм; **D** – протоконх. **E-G.** ***Pagodaturris philippinensis*** gen. et sp. nov., голотип, MNHN-IM-2007-42458, SL 17,4 мм; **G** – протоконх. **H-I.** ***Pagodaturris*** *regilla* (Iredale, 1936), голотип *Lucerapex casearia regilla*, AMS C.60710, SL 20,5 мм. **J.** ***Pagodaturris*** sp., MNHN-IM-2007-42504, Соломоновы острова, 08°24'S, 159°27'E, 362-432 m, SOLOMON 2, st. CP2193, SL 21,2 мм (радула на Рис. 8D). Все раковины в одном масштабе. H-I – фотографии AMS.

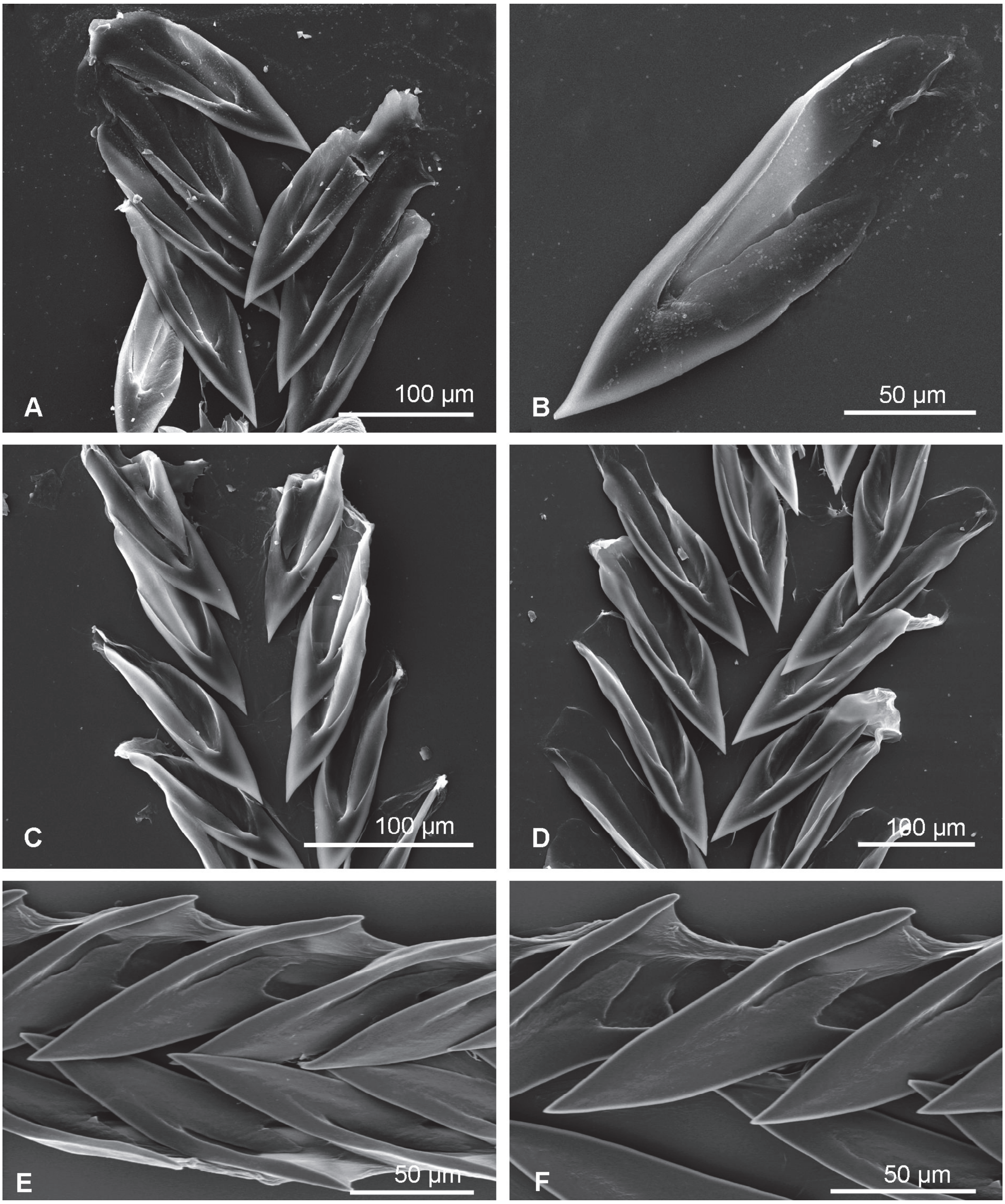

FIG. 8. Radulae of ***Pagodaturris*** gen. nov. **(**A-D) and *Makiyamaia mamillata* Kuroda, 1961 (**E-F**). **A-B.** ***Pagodaturris*** *molengraaffi* Tesch, 1915, MNHN-IM-2009-18963 (shell see on Fig. 7 A-C); **A** – anterior part of radular ribbon, **B** – enlarged separate marginal tooth. **C.** ***Pagodaturris philippinensis*** gen. et sp. nov., holotype, MNHN-IM-2007-42458 (shell see on Fig. 7 E-G). **D.** ***Pagodaturris*** sp., MNHN-IM-2007-42504 (shell see on Fig. 7J). **E-F.** *Makiyamaia mamillata* Kuroda, 1961, MNHN-IM-2007-17745, NE coast of Taiwan, 24°31'N, 122°06'E, 397-399 m.

РИС. 8. Радулы ***Pagodaturris*** gen. nov. **(**A-D) и *Makiyamaia mamillata* Kuroda, 1961 (**E-F**). **A-B.** ***Pagodaturris*** *molengraaffi* Tesch, 1915, MNHN-IM-2009-18963 (раковина на Рис. 7 A-C); **A** – передняя часть радулярной мембраны, **B** – увеличенный отдельный маргинальный зуб. **C.** ***Pagodaturris philippinensis*** gen. et sp. nov., голотип, MNHN-IM-2007-42458 (раковина на Рис. 7 E-G). **D.** ***Pagodaturris*** sp., MNHN-IM-2007-42504 (раковина на Рис. 7J). **E-F.** *Makiyamaia mamillata* Kuroda, 1961, MNHN-IM-2007-17745, NE побережье Тайваня, 24°31'N, 122°06'E, 397-399 м.

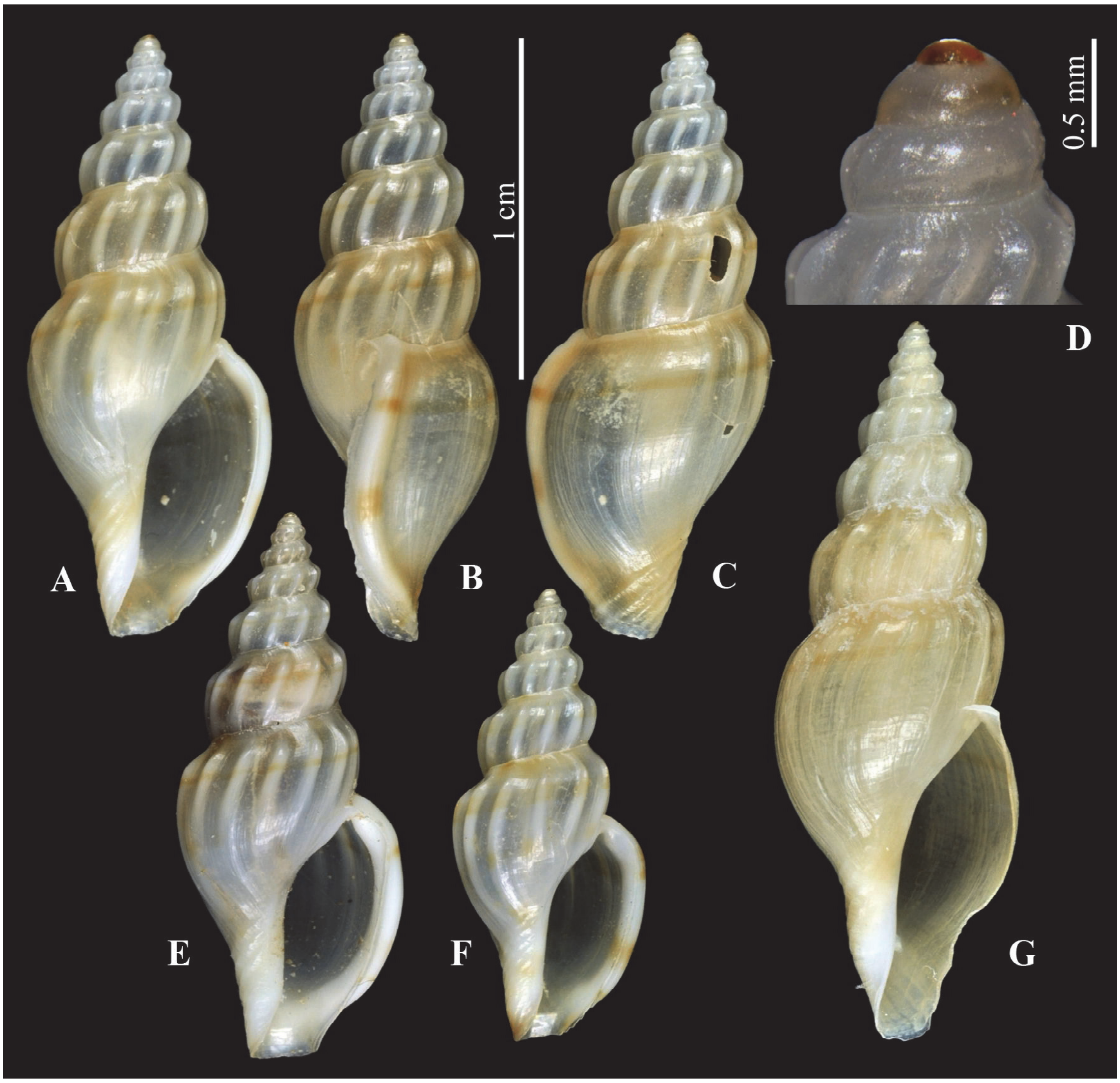

FIG. 9. Shells of *Horaiclavus* ***micans*** sp. nov. **A-D.** Holotype, MNHN-IM-2013-52054, SL 18.0 mm; **D** – protoconch. **E.** Southern New Caledonia, SMIB8, st. DW146-147, SL 16.1 mm. **F.** Northern New Caledonia, 18°47'S, 163°17'E, 610-613 m, BATHUS4, st. CP921, SL 13.3 mm. **G.** MNHN-IM-2009-13540, SL 21.4 mm. All shells at the same scale.

**РИС.** 9. Раковины *Horaiclavus* ***micans*** sp. nov. **A-D.** Голотип, MNHN-IM-2013-52054, SL 18,0 мм; **D** – протоконх. **E.** Южная Новая Каледония, SMIB8, st. DW146-147, SL 16,1 мм. **F.** Northern New Caledonia, 18°47'S, 163°17'E, 610-613 m, BATHUS4, st. CP921, SL 13,3 мм. **G.** MNHN-IM-2009-13540, SL 21,4 мм. Все раковины в одном масштабе.

## Horaiclavidae Bouchet, Kantor, Sysoev et Puillandre, 2011

## *Horaiclavus* Oyama, 1954

Type species: *Mangelia splendida* A. Adams, 1867 (OD). Japan, Recent.

### *Horaiclavus* **micans** sp. nov.
### (Fig. 9)

urn:lsid:zoobank.org:act:515671AA-ADFE-44F4-97BE-1EF672EFD225

**Holotype:** MNHN-IM-2013-52054 (sequenced).

**Type locality**: New Caledonia, 22°53'S, 169°25'E, 580-780 m, EXBODI, st. CP3871, 16.09.2011.

**Sequenced material: Northern New Caledonia,** 18°50'S, 163°14'E, 616-628 m, CONCALIS, st. CP3012, 8.05.2008, 1 lv (MNHN-IM-2009-13540).

**Other material examined: Northern New Caledonia**, 18°46'S, 163°16'E, 600 m, MUSORSTOM 4, st. DW 159, 15.09.198, 1 dd; 18°51'S, 163°21'E, 560 m, MUSORSTOM 4, st. DW197, 1 dd; 18°47'S, 163°17'E, 610-613 m, BATHUS4, st. CP921, 6.08.1994, 1 lv; 18°01'S, 163°02'E, 367-430 m, CONCALIS, st. DW2983, 5.05.2008, 1 dd; 19°04'S, 163°11'E, 220-390 m, CONCALIS, st. CP2961, 1.05.2008, 1 dd; 18°50'S, 163°14'E, 616-628 m, CONCALIS, st. CP3012, 8.05.2008, 3 dd.

**Southern New Caledonia**, 24°55'S, 168°22'E, 508-532 m, SMIB8, st. DW146-147, 27.01.1983, 1 dd; 24°45'S, 168°06'E, 600-896 m, NORFOLK 2, st. DW2091, 29.10.2003, 1 dd.

**Description** (holotype): Shell claviform, with moderately high spire. Protoconch of about 2 smooth whorls (Fig. 9D), protoconch/teleoconch transition indistinct, can be deduced by appearance of axial folds. Teleoconch of 6.5 convex whorls weakly angulated at shoulder. Suture shallow, adpressed, slightly wavy. Subsutural ramp very narrow, poorly pronounced. Axial sculpture of strong, rounded on top, slightly arcuate and weakly opisthocline ribs, running from suture to suture but fading on subsutural ramp and shell base, 13 on first teleoconch whorl, 11 on second, 10 on third, 12 on penultimate whorl and only 10 on last whorl, where they become obsolete on latest 1/3 whorl. Interspaces between ribs 1.5-2 times width the ribs. Spiral sculpture of thin, poorly visible spiral threads covering entire shell surface and five ridged spiral cords on lowest part of shell base and canal. Base evenly convex, concave at passing to canal. Aperture oval, with very short broad siphonal canal. Anal sinus very shallow, subsutural, just slight insinuation of lip edge. Inner lip with nearly straight columellar part and weakly convex parietal. Parietal callus very thin and narrow, but forming a distinct pad in upper part of aperture. Outer lip with strong varix behind thin lip edge (Fig. 9B). Shell glossy, yellowish, semitransparent, with two indistinct light brown spiral lines, one subsutural, one on shoulder, as well as brown spot approximately at middle of varix seen from dorsal side. First protoconch whorl brownish.

Measurements (holotype): SL 18.0 mm, AL (with canal) 9.5 mm, SW 7.2 mm.

Largest available specimen SL 21.4 mm (MNHN-IM-2009-13540).

**Remarks.** The species is rather costant in shell shape and sculpture. In some specimens the spiral threads are more discernible. The axial ribs can extend further to shell base in some specimens and can be present on latest part of last whorl, so that the total number of ribs may reach 14. Nevertheless there is always a smooth gap behind the varix. The tip of canal can have brownish spot

So far two species are described from New Caledonia, although many more morphospecies have been isolated in the material from that region. From *H. phaeocercus* Sysoev, 2008, the new species differs in non-coloured or very weakly coloured tip of the canal, as well as more elongated and larger shell (maximal size of *H. phaeocercus* is 12.5 mm). From *H. anaimus* Sysoev, 2008, the new species differs in having a much larger shell (21.2 vs 12 mm in *H. anaimus*), less angulated shoulder and brownish first whorl of protoconch versus colourless.

The species is lacking proboscis, venom gland and radula, but has rhynchostomal outgrowth. Its foregut anatomy is similar and of the same type as in *H. phaeocercus* [Fedosov, Kantor, 2008].

The two available COI sequences of *H.* ***micans*** sp. nov. are very similar (genetic distance = 0.5%). In the COI tree (Fig. 1), the phylogenetic relationships with the other species of Horaiclavidae are not supported, but would suggest the non-monophyly of the genera *Horaiclavus* and *Iwaoa*.

**Etymology**: micans (Lat.) – gleaming, glittering, referring to glossy attractive shell of the species.

**Distribution.** Presently the new species is known only from New Caledonia.

## *Iwaoa* Kuroda, 1953

Type species: *Iwaoa reticulata* Kuroda, 1953 (by monotypy) (Japan, Recent)

## *Iwaoa* ***invenusta*** sp. nov.
(Fig. 10)

urn:lsid:zoobank.org:act:FED840BE-DB20-42C0-85DC-F1EAA845317C

**Holotype**: MNHN-IM-2013-4878 (sequenced).

**Type locality**: Papua New Guinea, 05°00'S, 145°50'E, 505-521 m, PAPUA NIUGINI, st. CP3961, 29.11.2012.

**Other sequenced material: Papua New Guinea**, 05°00'S, 145°50'1"E, 505-521 m, PAPUA NIUGINI, st. CP3961, 29.11.2012, 1 lv (MNHN-IM-2013-4880); 04°52'S, 145°53'E, 780 m, PAPUA NIUGINI, st. CP4033, 16.12.2012, 1 lv (MNHN-IM-2013-52044).

**Description (holotype):** Shell turriform, with high spire. Protoconch bulbous (Fig. 10D), of little over 1.5 smooth convex whorls. Protoconch/teleoconch transition marked by single rather strong prosocline axial rib, after which definitive sculpture appears. Protoconch diameter 0.7 mm, exposed height 0.45 mm. Teleoconch of 5.75 convex whorls strongly angulated at shoulder. Suture shallow, wavy in accordance to axial ribs. Subsutural ramp narrow, weakly concave. Axial sculpture represented by strong, sharp on top, slightly arcuate and weakly opisthocline ribs, running from suture to suture but fading at transition of shell base to canal, 8 on first teleoconch whorl, 10 on second, 9 on penultimate whorl and last whorls. Interspaces between ribs nearly twice ribs' width. Spiral sculpture of indistinct spiral cords, poorly visible in interspaces between ribs, but forming nodules at intersections with axial folds, most distinct on shoulder. On last whorl each rib with 5 such nodules, diminishing from shoulder abapically. Base evenly convex, concave at passing to canal. Aperture oval, with short broad leftward inclined siphonal canal. Anal sinus very shallow, subsutural, hardly discernible. Inner lip with nearly straight columellar part and very

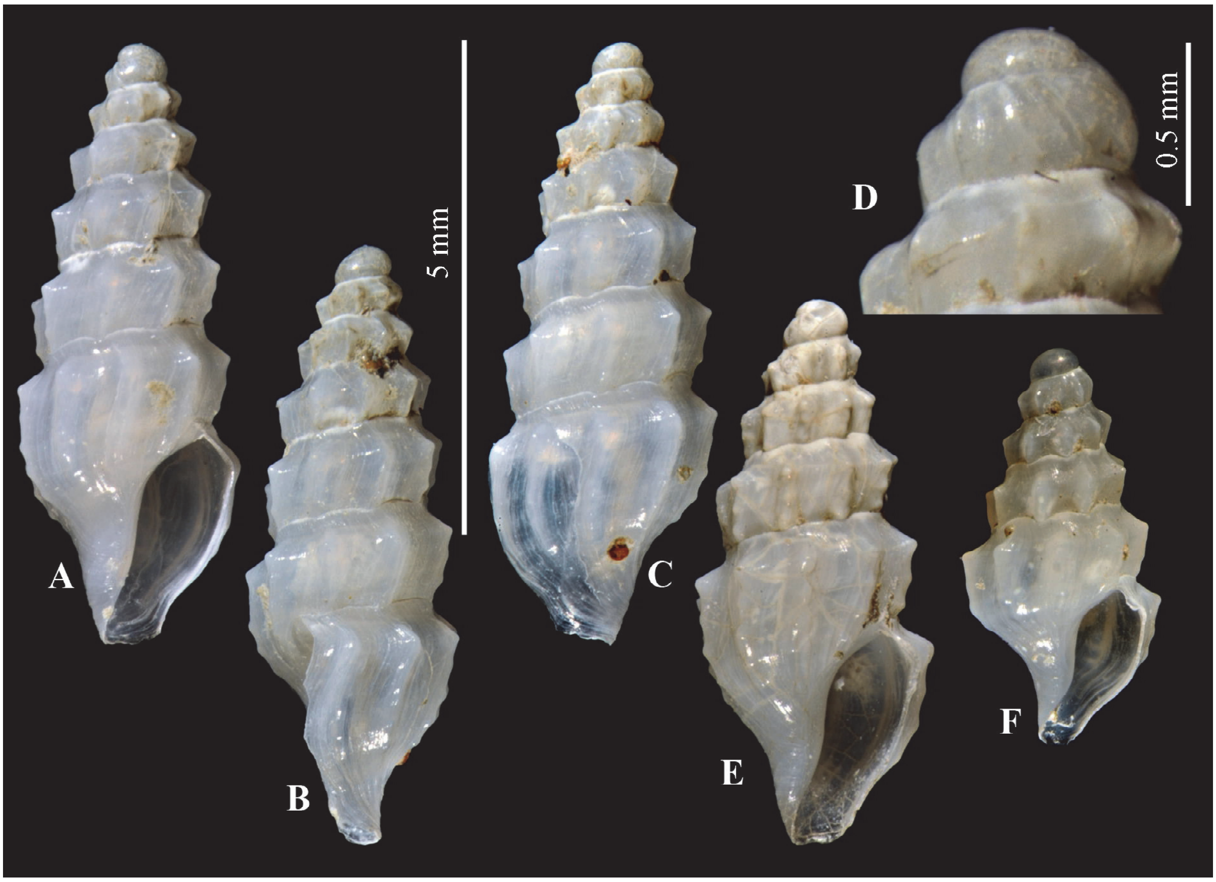

FIG. 10. Shells of *Iwaoa* ***invenusta*** sp. nov. **A-D.** Holotype, MNHN-IM-2013-4878, SL 6.2 mm; **D** – protoconch. **E.** MNHN-IM-2013-52044, SL 5.5 mm. **F.** MNHN-IM-2013-4880, SL 4.0 mm. All shells at the same scale.

РИС. 10. Раковины *Iwaoa* ***invenusta*** sp. nov. **A-D.** Голотип, MNHN-IM-2013-4878, SL 6,2 mm; **D** – протоконх. **E.** MNHN-IM-2013-52044, SL 5,5 мм. **F.** MNHN-IM-2013-4880, SL 4,0 мм. Все раковины в одном масштабе.

weakly convex parietal. Parietal callus very thin and narrow. Outer lip angulated at shoulder and weakly convex below. Shell glossy, semitransparent, off white.

Measurements (holotype largest specimen): SL 6.2 mm, AL (with canal) 3.3 mm, SW 2.2 mm.

Radula and operculum not available for studies.

**Remarks.** The species is rather constant in adult shell characters, but with clearly observed ontogenetic variability. In a small specimen with SL 4.0 mm (Fig. 10F) the shell looks much stouter, with sharply narrowing shell base in comparison with larger ones.

Presently the genus *Iwaoa* remained monotypical and the type species is rather different from the new one. It is much larger, reaching 4 cm, it has better pronounced spiral cords, while the axial ribs are more numerous and smoothened. Nevertheless there are several still unnamed (and mostly unsequenced) deep-water species of Horaiclavidae, that have intermediate morphology between *I. reticulata* and *I.* ***invenusta*** sp. nov. [eg. Bouchet *et al*., 2011: fig. 17Q, *Iwaoa* sp.]. At the moment, among the described genera attributed to Horaiclavidae, *Iwaoa* seems to be the most suitable for the new species. Therefore we prefer to place the new species with reservations in *Iwaoa* rather than describing one more new genus. The three sequenced samples of ***I. invenusta*** sp. nov have almost identical COI sequences, and in the COI tree (Fig. 1), *I.* ***invenusta*** sp. nov. is not sister to *I. reticulata*, but as explained before the relationships between most species of Horaiclavidae are unsupported, and more data are needed to clarify the genera boundaries within Horaiclavidae.

**Etymology:** *invenusta* (Lat.) – unattractive, referring to inconspicuous shell.

**Distribution:** The species presently is endemic to Papua New Guinea, 505-780 m.

## *Epideira* Hedley, 1918

*Epidirona* Iredale, 1931: 225, 233. (Type species – *Epidirona hedleyi* Iredale, 1931; OD).

**Type species:** *Clavatula striata* Gray, 1826; OD.

**Remarks.** It is difficult to identify who first

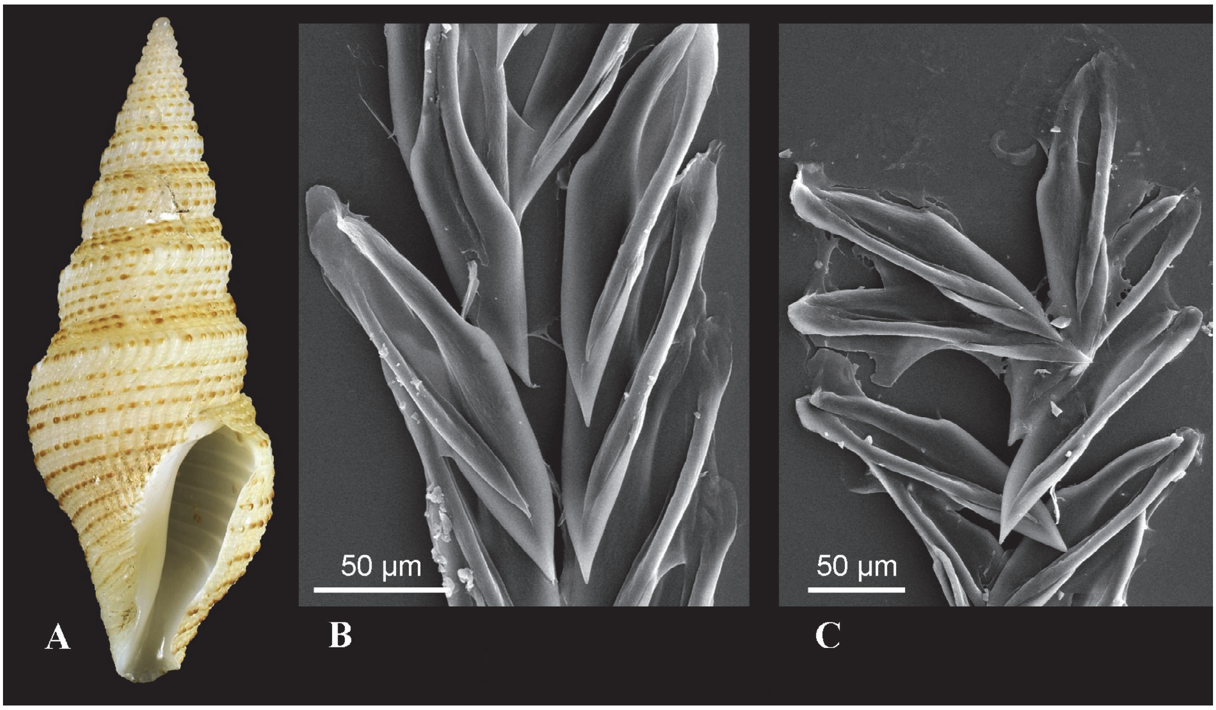

FIG. 11. Shell (**A**) and radula (**B-C**) of *Epideira sibogae* (Schepman, 1913), MNHN-IM-2013-52072, New Caledonia, SL 22.8 mm.

РИС. 11. Раковина (**A**) и радула (**B-C**) *Epideira sibogae* (Schepman, 1913), MNHN-IM-2013-52072, Новая Каледония, SL 22,8 мм.

synonymized the two genera. Most authors used the name of Iredale, some [eg. Sysoev in Taylor *et al.,* 1993] considered *Epideira* and *Epidirona* as synonyms. The major problem was in the identification of the type species of *Epideira* – *Clavatula striata* Gray, 1826, which was regarded by Iredale [1931] as "indeterminate". The question was discussed in details by Li *et al.* [2010]. The authors concluded that "in the type collection of the BMNH is a specimen from the Gray collection labelled *Pleurotoma owenii* Reeve, 1843, which Watson [1886: 312] and Hedley [1922: 230] regarded as a synonym of Gray's (1826) *Clavatula striata*. There is even a possibility that it was based on the same specimen. Although *C. striata* has not subsequently been recognized, it appears to be congeneric with *Epidirona hedleyi* Iredale, 1931, the type species of *Epidirona*."

The genus was attributed to different sub(families) of Conoidea: Turrinae [Powell, 1964, 1966] or Crassispirinae [Sysoev in Taylor *et al.,* 1993; Li *et al*., 2010]. The radula of *Epidirona hedleyi* was illustrated with a line drawing by Powell [1966: fig. B32] and appeared to be similar to the radulae of many Pseudomelatomidae and Horaiclavidae. On the basis of the radula the genus was attributed to Pseudomelatomidae by Bouchet *et al.* [2011], generally following the previous opinions.

Nevertheless, the inclusion of one COI sequence of *Epideira sibogae* in the phylogenetic tree (Fig. 1) demonstrated that it should be included in Horaiclavidae. Here we describe for the first time the radula of the mentioned species.

### *Epideira sibogae* (Schepman, 1913)
(Fig. 11)

*Drillia sibogae* Schepman, 1913:415, pl. 27, fig. 2.
*Epidirona sibogae* – Higo *et al*. 1999: 306; Sysoev in Poppe, 2008: 776, pl. 683, figs. 6, 7.
*Epideira sibogae* – Li, Kilburn, Li, 2010: 712, figs 3A,B.

**Type locality:** Indonesia, Madura Bay in 69-91 m, near north point of Nuhu Jaan, Kei Islands in 90 m.

**Sequenced material:** New Caledonia, 22°00'S, 167°01'E, 300-302 m, EXBODI, st. CP3828, 08.09.2011, 1 lv (MNHN-IM-2013-52072).

**Remarks:** The species was previously known from Indonesia, Japan, Philippines and the China Seas. Here it is recorded in Southern New Caledonia.

Protoconch paucispiral, consists of about two smooth convex whorls.

Radula (Fig. 11 B-C) examined for the first time, consists of marginal teeth only. It is rather short, of 18 rows of which 6 are nascent. Marginal teeth duplex, major limb pointed, medium broad in inner half (facing the median line of the radula and then

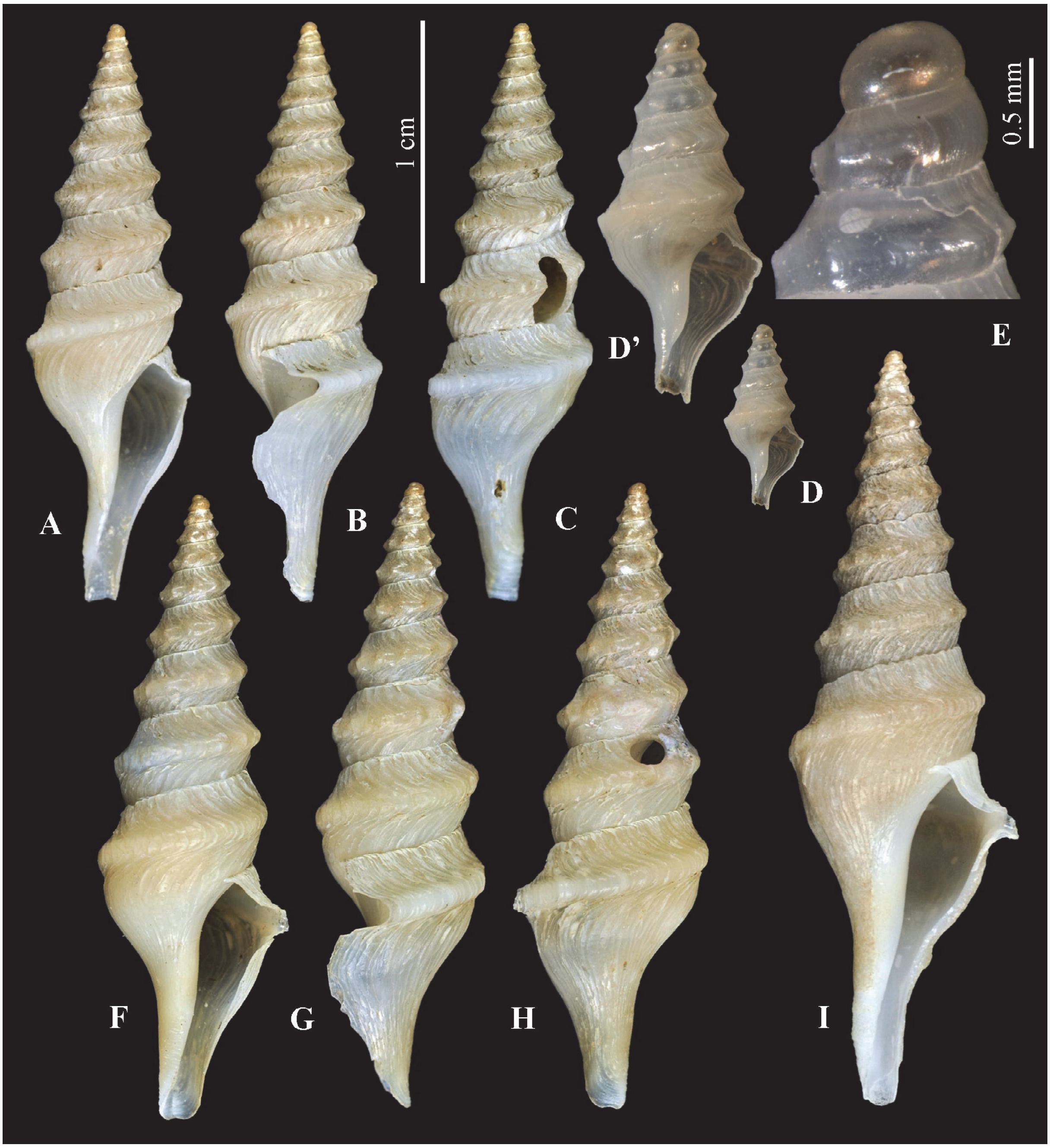

FIG. 12. Shells of *Lucerapex* ***cracens*** sp. nov. **A-C.** Holotype, MNHN-IM-2009-18966, SL 22.2 mm. **D-E.** MNHN-IM-2013-52064, Papua New Guinea, SL 7.0 mm (**D** – at the same scale as other shells, **D'** – enlarged, **E** – protoconch). **F-G.** MNHN-IM-2013-19988, Solomon Sea, SL 24.0 mm. **I.** MNHN-IM-2009-13549, Northern New Caledonia, SL 29 mm (radula see on Fig. 13A). All shells at the same scale (except **D'**).

РИС. 12. Раковины *Lucerapex* ***cracens*** sp. nov. **A-C.** Голотип, MNHN-IM-2009-18966, SL 22,2 мм. **D-E.** MNHN-IM-2013-52064, Папуа Новая Гвинея, SL 7,0 mm (**D** – в том же масштабе, что и остальные раковины, **D'** – увеличено, **E** – протоконх). **F-G.** MNHN-IM-2013-19988, Соломоново море, SL 24,0 мм. **I.** MNHN-IM-2009-13549, Северная Новая Каледония, SL 29 мм (радула на Рис. 13A). Все раковины в одном масштабе (кроме **D'**).

narrowing, forming a “waist”. Accessory limb narrow, although long and extends to outer limit of major limb.

The morphology of the marginal teeth is very similar to many studied Horaiclavidae [see Bouchet *et al.,* 2011: fig. 19].

## Turridae H. Adams et A. Adams, 1853

## *Lucerapex* Wenz, 1943

Type species: *Pleurotoma casearia* Hedley et Petterd, 1906 (OD).

**Remarks.** The genus name is usually attributed to Iredale [1936], eg. by Powell [1964], but no diagnosis was provided and therefore the name is not available from Iredale.

## *Lucerapex* ***cracens*** sp. nov.
## (Figs 12, 13A)

urn:lsid:zoobank.org:act:30679133-A2FB-474D-B66C-CB60ED7BE449

**Holotype:** MNHN-IM-2009-18966.

**Type locality:** Solomon Islands, 09°36'S, 160°46'E, 448-523 m, SOLOMONBOA 3, st. CP2849, 4.10.2007.

**Other sequenced material examined: Vanuatu**, 16°22'S, 167°50'E, 637-644 m, SANTO 2006, st. AT130, 21.10.2006, 2 lv (MNHN-IM-2007-42635, MNHN-IM-2007-42636). **Northern New Caledonia**, 20°17'S, 163°50'E, 600-1100 m, CONCALIS, st. CP3027, 10.05.2008, 1 lv (MNHN-IM-2009-13549). **Solomon Sea**, 05°36'S, 148°13'E, 500-640 m, PAPUA NIUGINI, st. CP4012, 12.12.2012, 1 lv (MNHN-IM-2013-19988). **Papua New Guinea**, 09°07'S, 152°14'E, 473-491 m, BIOPAPUA, st. DW3738, 10.10.2007, 1 lv (MNHN-IM-2013-52064).

**Description** (holotype). Shell thin, narrow fusiform, with high spire and long narrow siphonal canal very slightly sinuous and inclined to left. Protoconch globose, of nearly two strongly convex smooth whorls, slightly eroded in holotype. [Intact protoconch present in juvenile specimen, MNHN-IM-2013-52064 (Fig. 12 D-E). Protoconch/teleoconch transition is marked by appearance of the median peripheral keel. Protoconch diameter 0.97 mm, height 0.92 mm.] Teleoconch whorls angulated at periphery, 9 in total. Suture shallow, subsutural region wide, distinctly concave. Spiral sculpture limited to median peripheral keel; keel strong, rounded in profile, on upper three teleoconch whorls situated in lowest part of whorl, just above suture, then progressively shifting towards median part of whorls, on penultimate whorl median. Keel forming distinct nodules, broadly spaced on upper teleoconch whorls (9 on first and second whorls), then becoming more numerous, closer spaced and weaker, around 22 on the 5th whorl, around 40 on penultimate whorl, on last whorl nodules particularly poorly pronounced on last half of whorl. Axial sculpture of very distinct irregularly spaced lamelliform growth lines, pronounced on all spire whorls.

Shell base gradually narrowing towards siphonal canal. Aperture irregularly oval, constricted posteriorly with narrow parietal callus, outer lip concave in upper part and weakly convex below shoulder, gradually passing into canal. Anal sinus deep, symmetrical, U-shaped, deepest point in center of median keel, confluent with large forward extension of outer lip. Shell light yellowish. Operculum narrow leaf shaped, with terminal nucleus, slightly inclined to left.

Measurements (holotype): SL 22.2 mm, AL (with canal) 10.0 mm, SW 6.3 mm. Largest available specimen attains SL 29.2 mm (MNHN-IM-2009-13549, Fig. 12I).

Radula (Fig. 13 A) was examined in one specimen (MNHN-IM-2009-13549), relatively short, consists of *ca* 30 rows of teeth, 11 nascent. Radula length 1.1 mm (13% of AL without canal), width up to 200 µm (2.5% of AL without canal). Radula of marginal duplex teeth only. Major limb pointed, narrow, with sharp cutting edges. Accessory limb very narrow, constituting about 2/3 of tooth length.

**Remarks**. Other available specimens are very similar to the holotype in shell shape and sculpture pattern.

The species in the shell shape is most similar to *Lucarapex adenica* Powell, 1964 (type locality Gulf of Aden), differing in slightly smaller size, absence of the spiral sculpture on last whorl, absence of the row of subsutural nodules and in much less pronounced nodules on the medial keel.

Six specimens of *L.* ***cracens*** sp. nov. were sequenced and compared with COI sequences from other *Lucerapex* species: *L. adenica* (two specimens), *L. casearia* (one specimen) and *L.* ***laevicarinatus*** sp. nov (one specimen). The genetic distances between species are all greater than 10.5%, whereas the genetic distances between samples of the same species never exceed 1% (for *L. adenica*) and 2.4% (for *L. cracens*). Both species with more than one sample are found monophyletic (PP = 1) and the four species are clustered in a single clade in the COI tree (Fig. 14A).

**Etymology:** *cracens* (lat.) – slender, graceful.

**Distribution:** The species is distributed in Santo, New Caledonia, Solomon Islands and Papua New Guinea, 448-1100 m.

## *Lucerapex* ***laevicarinatus*** sp. nov.
## (Figs 13 B-C, 15)

urn:lsid:zoobank.org:act:9319EAC1-2AD3-4F9A-A1AD-975494299398

**Holotype:** MNHN-IM-2013-52063.

**Type locality:** New Caledonia, 18°37'S, 164°26'E, 459-603 m, EXBODI, st. CP3934, 27.09.2011.

**Other material examined: Philippines,** 14°42'N, 123°37'E, 363 m, AURORA 2007, st. DW2693, 26.05.2007, MNHN uncataloged. **Solomon Islands,** N Malaita, 08°19'S, 160°37'E, 314-586 m, SALOMONBOA 3, st. DW2790, 15.09.2007, MNHN uncataloged.

**Description** (holotype). Shell thin, narrow fusiform, with moderately high spire and long narrow siphonal canal very slightly sinuous and inclined to left. Protoconch (Fig. 15D) globose, of 1.5 convex smooth whorls. Protoconch/teleoconch transition is marked by appearance of the median peripheral

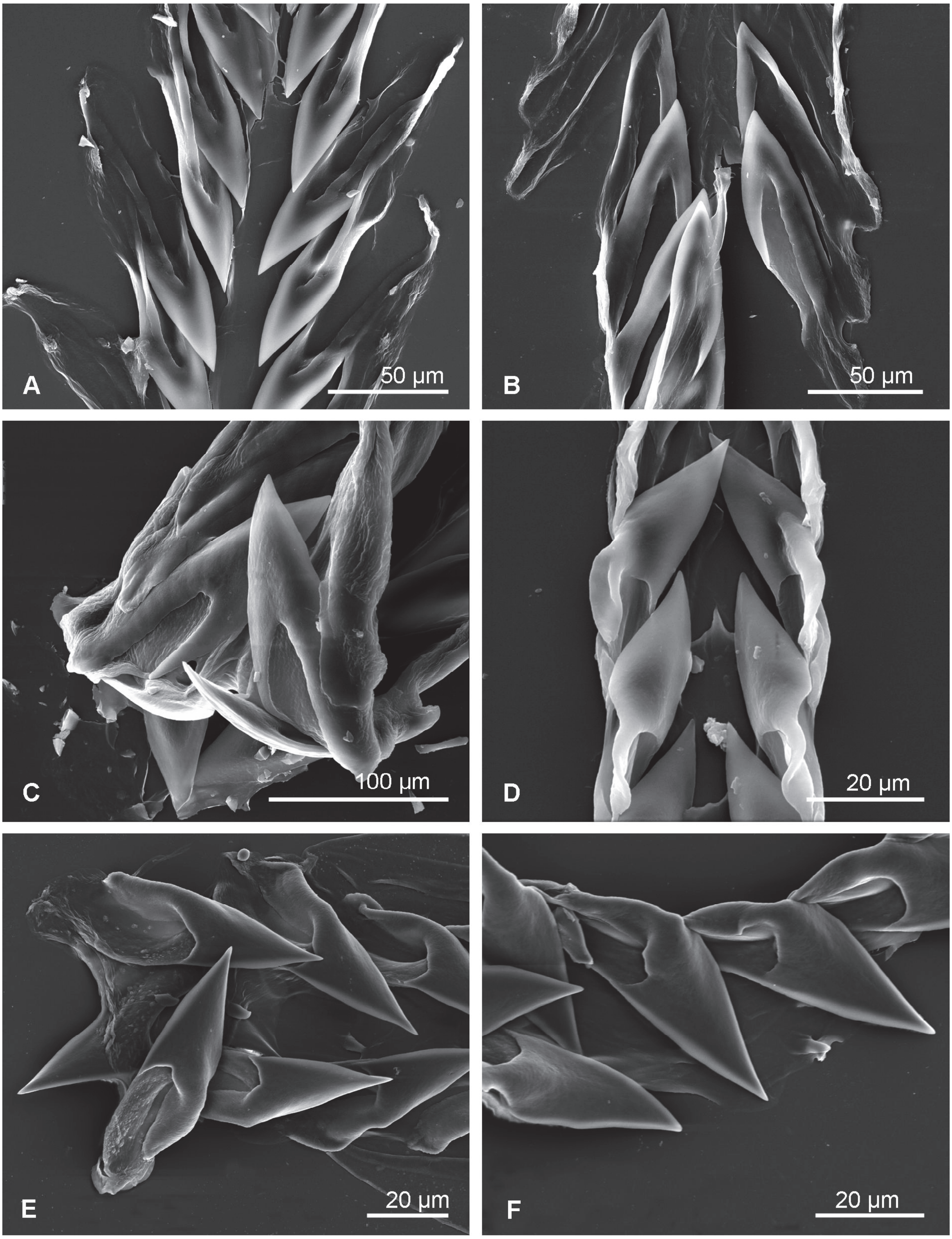

FIG. 13. Radulae of Turridae. **A.** *Lucerapex* ***cracens*** sp. nov., MNHN-IM-2009-13549 (shell see on Fig. 12I). **B-C.** *Lucerapex* ***laevicarinatus*** **sp. nov.,** holotype, MNHN-IM-2013-52063; **B** – radular membrane in the zone of complete teeth maturation; **C** – radular bending plane. **D.** *Kuroshioturris nipponica*, MNHN-IM-2009-19092 (shell on Fig. 16 D-E). **E-F.** *Kuroshioturris nipponica*, MNHN-IM-2009-18984 (shell on Fig. 16 A).

РИС. 13. Радулы Turridae. **A.** *Lucerapex* ***cracens*** sp. nov., MNHN-IM-2009-13549 (раковина на Рис. 12I). **B-C.** *Lucerapex* ***laevicarinatus*** **sp. nov.,** голотип, MNHN-IM-2013-52063; **B** – радулярная мембрана в зоне полного формирования зубов; **C** – зона перегиба радулы. **D.** *Kuroshioturris nipponica*, MNHN-IM-2009-19092 (раковина на Рис. 16 D-E). **E-F.** *Kuroshioturris nipponica*, MNHN-IM-2009-18984 (раковина на Рис.16 A).

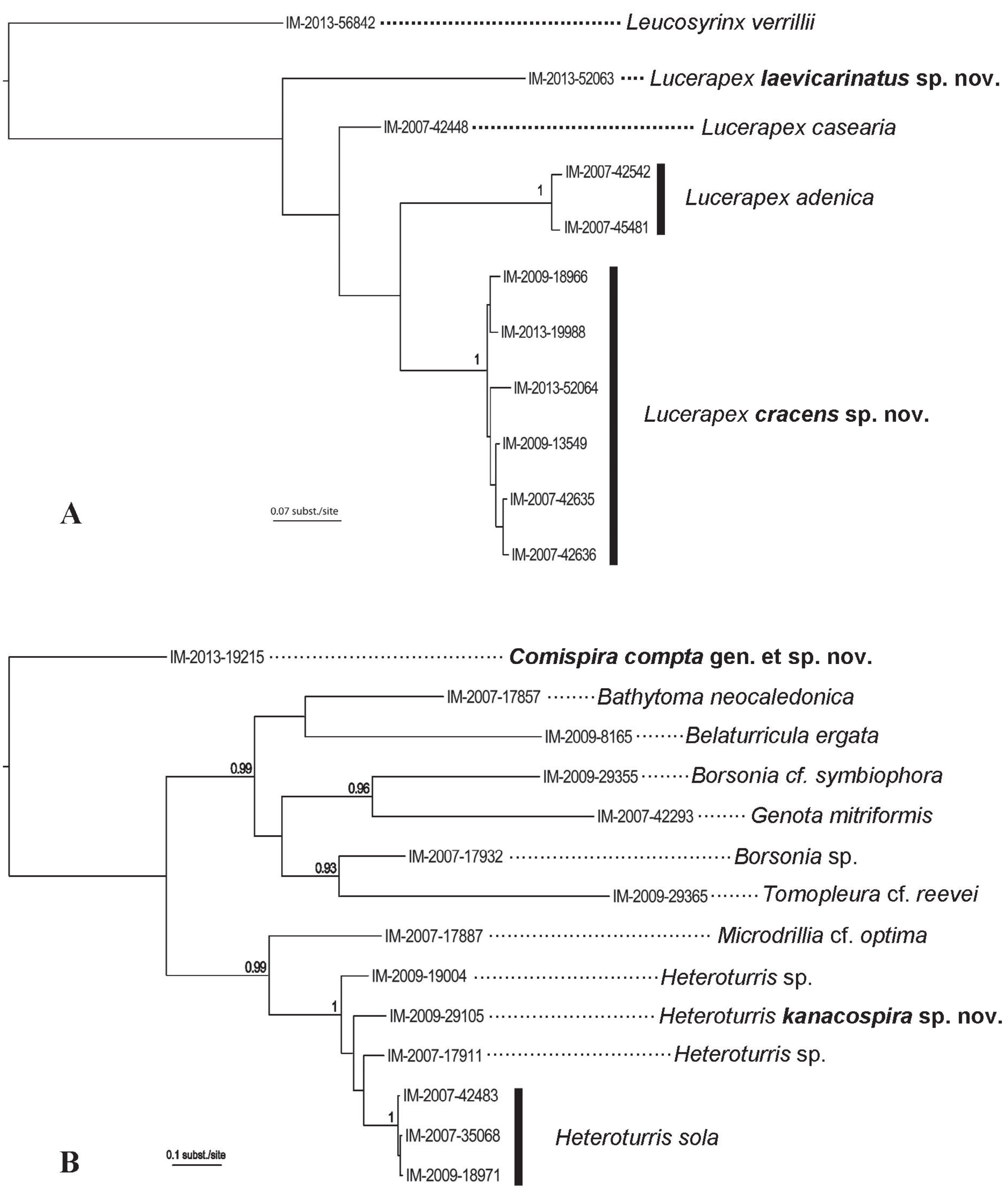

FIG. 14. Phylogenetic tree of *Lucerapex* (**A**) and Borsoniidae (**B**) obtained with Bayesian analysis of COI gene sequences. Only supported nodes with posterior probability values between 0.93 and 1.00 are marked on the tree.

РИС. 14. Филогенетические деревья *Lucerapex* (**A**) и Borsoniidae (**B**), полученные Бэйесовским анализом на основе последовательностей гена COI. На дереве обозначены только поддержанные узлы со значениями апостериорной вероятности между 0,93 и 1,00.

keel. Protoconch diameter 0.78 mm, height 0.68 mm. Teleoconch whorls strongly angulated at periphery, 6.25 in total. Suture shallow, subsutural region wide, distinctly concave. Median peripheral keel is the only spiral element, strong, rounded in profile, on first teleoconch whorl situated in lowest part of the whorl, just above suture, then progressively shifting towards median part of whorls, on penultimate whorl – median. On upper whorls, including penultimate, keel forming weak broadly

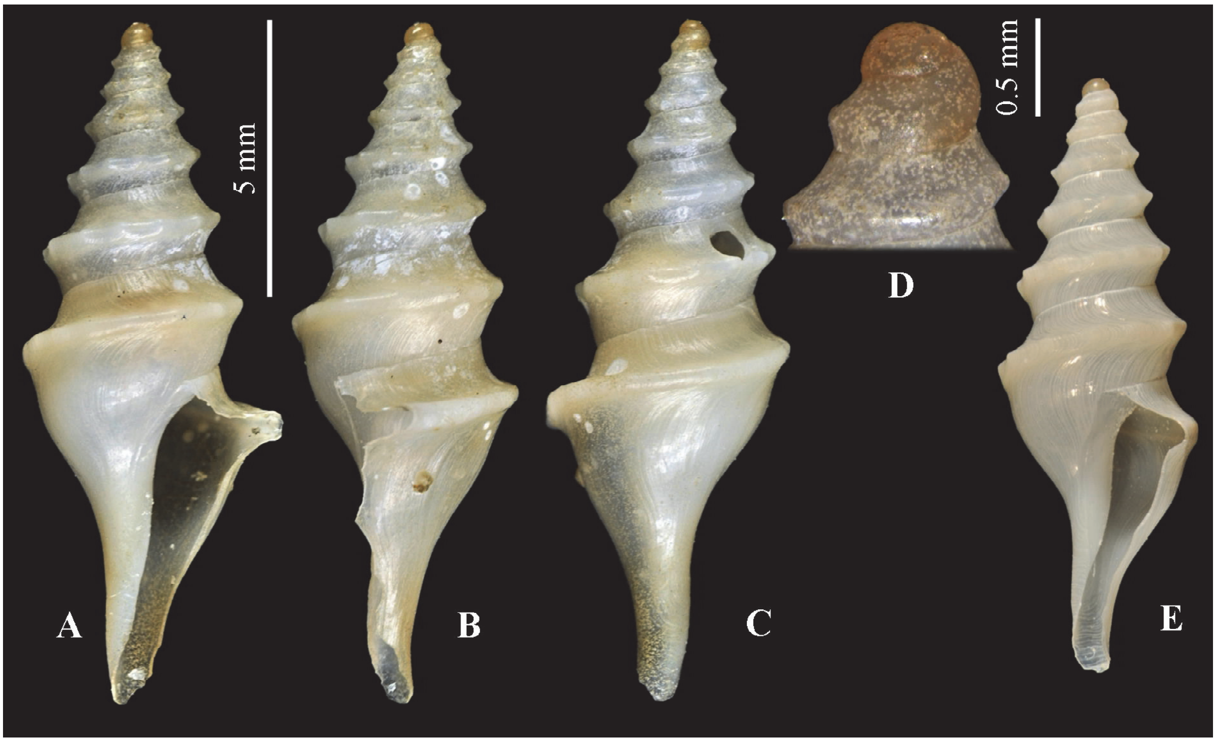

FIG. 15. Shells of *Lucerapex* ***laevicarinatus*** sp. nov. **A-D.** Holotype, MNHN-IM-2013-52063, SL 12.6 mm; **D** – protoconch and upper teleoconch whorls. **E.** Solomon Islands, N Malaita, 08°19'S, 160°37'E, 314-586 m , SALOMONBOA 3, st. DW2790, MNHN uncataloged, SL 10.7 mm.

РИС. 15. Раковины *Lucerapex* ***laevicarinatus*** sp. nov. **A-D.** Голотип, MNHN-IM-2013-52063, SL 12,6 мм; **D** – протоконх и верхние обороты телеоконха. **E.** Соломоновы острова, N от Малаита, 08°19'S, 160°37'E, 314-586 м , SALOMONBOA 3, ст. DW2790, MNHN, SL 10,7 мм.

spaced nodules, on upper teleoconch whorls (7 on first whorl, 9 on second), up to 13 on penultimate whorl. On last whorl nodules absent and keel smooth.

Shell base gradually narrowing towards narrow and long nearly straight siphonal canal. Aperture irregularly narrow oval, constricted posteriorly with narrow parietal callus, outer lip strongly concave in upper part and weakly convex below shoulder, gradually passing into canal. Anal sinus deep, symmetrical, U-shaped, deepest point on center of median keel. Growth lines numerous, very thin. Teleoconch uniformly off-white, protoconch light tan. Operculum narrow leaf-shaped, with terminal nucleus, abraded in holotype.

Measurements (holotype): SL 12.6 mm, AL (with canal) 6.4 mm, SW 4.4 mm.

Radula of holotype (Fig. 13 B-C) short, consists of *ca* 35 rows of teeth, 9 nascent. Radula length 0.9 mm (27% of AL without canal), width up to 160 μm (4.8% of AL without canal). Radula of marginal duplex teeth only. Major limb pointed, broad in inner half facing median line of radula membrane, than narrowing forming a "waist". Accessory limb rather broad, constituting about 4/5 of tooth length.

**Remarks.** Only the holotype was sequenced. Similar smaller dead shells were found in the Philippines (Fig. 15E) and Solomon Islands although without molecular data we attribute them to the new species with some reservations.

The species differs from its congeners in having weak nodules on medial keel, absent on last whorl.

**Etymology.** The name refers to the smooth median keel.

**Distribution.** New Caledonia, Philippines and Solomon Islands, 314-603 m.

## *Kuroshioturris* Shuto, 1961

Type species: *Gemmula* (*Kuroshioturris*) *hyugaensis* Shuto, 1961 (OD). Lowest Pliocene, Japan, Miyazaki Pref.

## *Kuroshioturris nipponica* (Shuto, 1961)
## (Figs 13 E-F, 16)

*Gemmula* (*Phychosyrinx*) *nipponicus* Shuto, 1961: 81, pl. 3, fig. 7, 8, 13, 19, pl. 7, fig. 14.

*Phychosyrinx* (*Kuroshioturris) nipponica* (Shuto) — Powell, 1964: 293 (22-865), pl. 226, figs. 3-4.

*Kuroshioturris nipponica* — Hasegawa in Okutani, 2000: 627, pl. 312, fig. 39.

**Type locality:** Hagenoshita, Uwaye mura, Koyu gun, Miyazaki Prefecture, Japan. L. Takanabe Member, Miyazaki Group, Lower Pliocene.

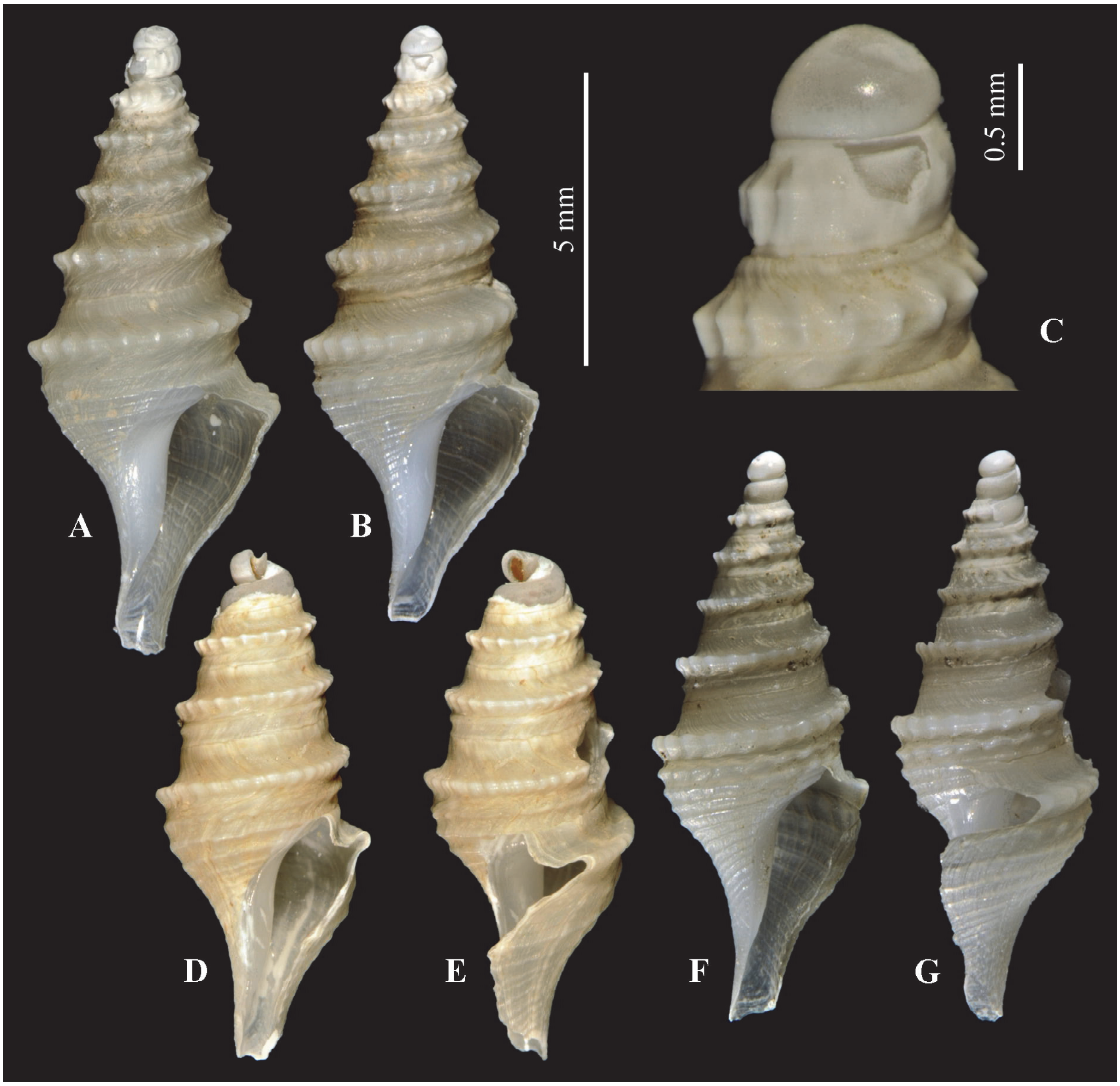

FIG. 16. Shells of *Kuroshioturris nipponica* (Shuto, 1961). **A.** MNHN-IM-2009-18984, SL 10.9 mm (radula see on Fig. 13 E-F). **B-C.** MNHN-IM-2009-19090, SL 10.3 mm; **C** – protoconch. **D-E.** MNHN-IM-2009-19092, SL 8.8 mm (radula see on Fig. 13D). **F-G.** MNHN-IM-2009-19093, SL 9.9 mm. All shells at the same scale.

РИС. 16. Раковины *Kuroshioturris nipponica* (Shuto, 1961). **A.** MNHN-IM-2009-18984, SL 10,9 мм (радула на Рис. 13 E-F). **B-C.** MNHN-IM-2009-19090, SL 10,3 мм; **C** – протоконх. **D-E.** MNHN-IM-2009-19092, SL 8,8 мм (радула на Рис. 13D). **F-G.** MNHN-IM-2009-19093, SL 9,9 мм. Все раковины в одном масштабе.

**Sequenced material: Philippines**, 15°00'N, 123°06'E, 1155-1302 m, AURORA 2007, st. CP2685, 24.05.2007, 3 lv (MNHN-IM-2009-19092, MNHN-IM-2009-19093, MNHN-IM-2009-19094); 14°53'N, 123°16'E, 915-924 m, AURORA 2007, st. CP2680, 23.05.2007, 2 lv (MNHN-IM-2009-18984, MNHN-IM-2009-19090); 15°02'N, 123°05'E, 1413-1449 m, AURORA 2007, st. CP2684, 24.05.2007, 1 lv (MNHN-IM-2009-19091).

**Remarks.** Although described from Lower Pliocene, the species was recorded in Recent fauna by Hasegawa in Okutani [2000]. Our specimens are very similar to that illustrated by Hasegawa, although collected at much greater depths (100-200 m in Japan and at 915-1445 m in the Philippines). This is also a great extension of the distribution area southwards.

A remarkable characteristic of the genus is the paucispiral globose protoconch (Fig. 16C), which places the genus quite aside in the family. The six sequenced specimens are all very similar in the COI gene (maximum genetic distance = 0.5%). If the COI gene only is not enough to place them in the Turridae (results not shown), their family assignation is confirmed in the upcoming exon-capture-based phylogeny [Abdelkrim *et al.*, 2018].

Radula was not previously described for any species of the genus. It was examined in two specimens (MNHN-IM-2009-19092 and MNHN-IM-2009-18984) (Fig. 13 D-F). Marginal teeth duplex, typical for Turridae, major limb medium broad, constricted in outer part. Accessory limb much narrower, and shorter than major limb, constituting about 1/3 of total tooth length and not reaching outer limit of major limb.

**Distribution**. Japan to the Philippines, 100-1445 m.

## Borsoniidae Bellardi, 1875

### *Heteroturris* Powell, 1967

Type species*: Heteroturris sola* Powell, 1967; OD. Philippines, Recent.

**Remarks:** The genus *Heteroturris* brings together species with a long siphonal canal and dominating spiral sculpture; these features giving typical *Heteroturris* similarilty to Turridae appearance. Furthermore, the multispiral protoconch of *Heteroturris* bearing strong arcuate ribs completes this similarity. The relatively shallow rounded anal sinus situated clearly above the peripheral cord, however, immediately rejects this possible relationship. It is noteworthy that the three sequenced specimens of *H. sola*, although sampled from about same locality, close to the type locality of this species, are quite different. The specimen MNHN-IM-2007-42483 (Fig. 17A) closely matches the holotype of this species, whereas the probably immature MNHN-IM-2007-35068 (Fig. 17B) with its strong subsutural fold, shows striking similarity to the holotype of *Heteroturris serta* Sysoev, 1997, thus questioning validity of the latter species. Additional material from the type locality of *H. serta* should be sequenced to resolve this issue.

Our phylogenetic analysis (Fig. 14B) shows the monophyly of *Heteroturris* (PP = 1) within the Borsoniidae and indicates close affinity of *H. sola* with a less elongated species, which, however, bears typical sculpture of *Heteroturris*. This species is here described as *Heteroturris* ***kanacospira*** sp. nov. This species was included in the phylogeny based on exon-capture [Abdelkrim *et al*., 2018]. Both molecular and morphological analyses revealed the presence of two more undescribed species of *Heteroturris*. We abstain from descriptions pending the taxonomic revision of this genus.

### *Heteroturris* ***kanacospira*** sp. nov.

(Fig. 17 F-I)

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**Holotype:** MNHN-IM-2009-29105 (sequenced).

**Type locality**: New Caledonia, 21°48'S, 166°46'E, 550 m, EXBODI, st. CP3816, 06.09.2011, 1 lv (MNHN-IM-2009-29105).

**Description** (holotype). Shell elongate-biconical, with high orthocline spire and rather long tapering siphonal canal. Protoconch (Fig. 17H) brown, multispiral, of about 4 strongly convex whorls. PI smooth, PII sculptured with strong closely set ribs, interspaces between ribs with microsculpture of very fine striae. Protoconch height 1.1 mm, diameter 0.8 mm. Transition protoconch-teleoconch distinct. Teleoconch of about 8.5 shouldered whorls; suture distinct. Suture bordered by low, flattened subsutural cord, slightly widening towards lower suture, followed by wide, steep, clearly concave subsutural ramp. Subsutural ramp sculptured with fine closely set arcuate riblets marking position of anal sinus, on last whorl intersected by fine rounded cords. Shoulder situated about mid-height of spire whorls, bearing a row of wide low crenulations, cut straight above shoulder, and gently rounded abapically. Whorl base sculptured with 1-2 additional spiral cords and somewhat obsolete collabral growth lines. Base of last adult whorl extended into rather long tapering siphonal canal with weak concavity at the transition. Periphery and base of last adult whorl sculptured with 15 regularly arranged, flattened cords, about as wide as interspaces between them, followed by 16 closely set fine cords on siphonal canal.

Aperture elongate, moderately wide, with wide and rather deep rounded subsutural sinus. Outer aperture lip thin, flattened in front view, and distinctly convex in side view. Inner lip smooth, with well-developed callus. Shell pale, inside of aperture off white.

Measurements (holotype largest specimen): SL 21.9 mm, AL (with canal) 10.2 mm, SW 7.2 mm.

Operculum narrow oval, yellow transparent with terminal nucleus. Several hydroids are attached to the underside lowest part of operculum, where it is detached from columellar muscle.

Holotype is a female.

Radula (Fig. 17I) of hypodermic loosely rolled and slightly curved teeth with bulbous base and very large basal opening. Apical opening narrow oval, relatively large, no barbs, indistinct short blade on opposite to apical opening side of tooth. Teeth length around 250 µm (2.4% of AL with canal).

**Remarks**. The shell proportions of *Heteroturris* ***kanacospira*** sp. nov. and its overall weaker spiral elements easily set it apart from the three named species of this genus. Moreover, the well-developed micro-sculpture on the subsutural ramp of *H.* ***kanacospira*** sp. nov. is very close to that of species of *Bathytoma* Harris et Burrows, 1891. Therefore both the shell proportions and sculpture of *H.* ***kanacospira*** sp. nov. appear intermediate between the typical *Heteroturris* and *Bathytoma*. The radula of *H.* ***kanacospira*** sp. nov. is notably different from *Bathytoma neocaledonica* Puillandre *et al.,* 2010

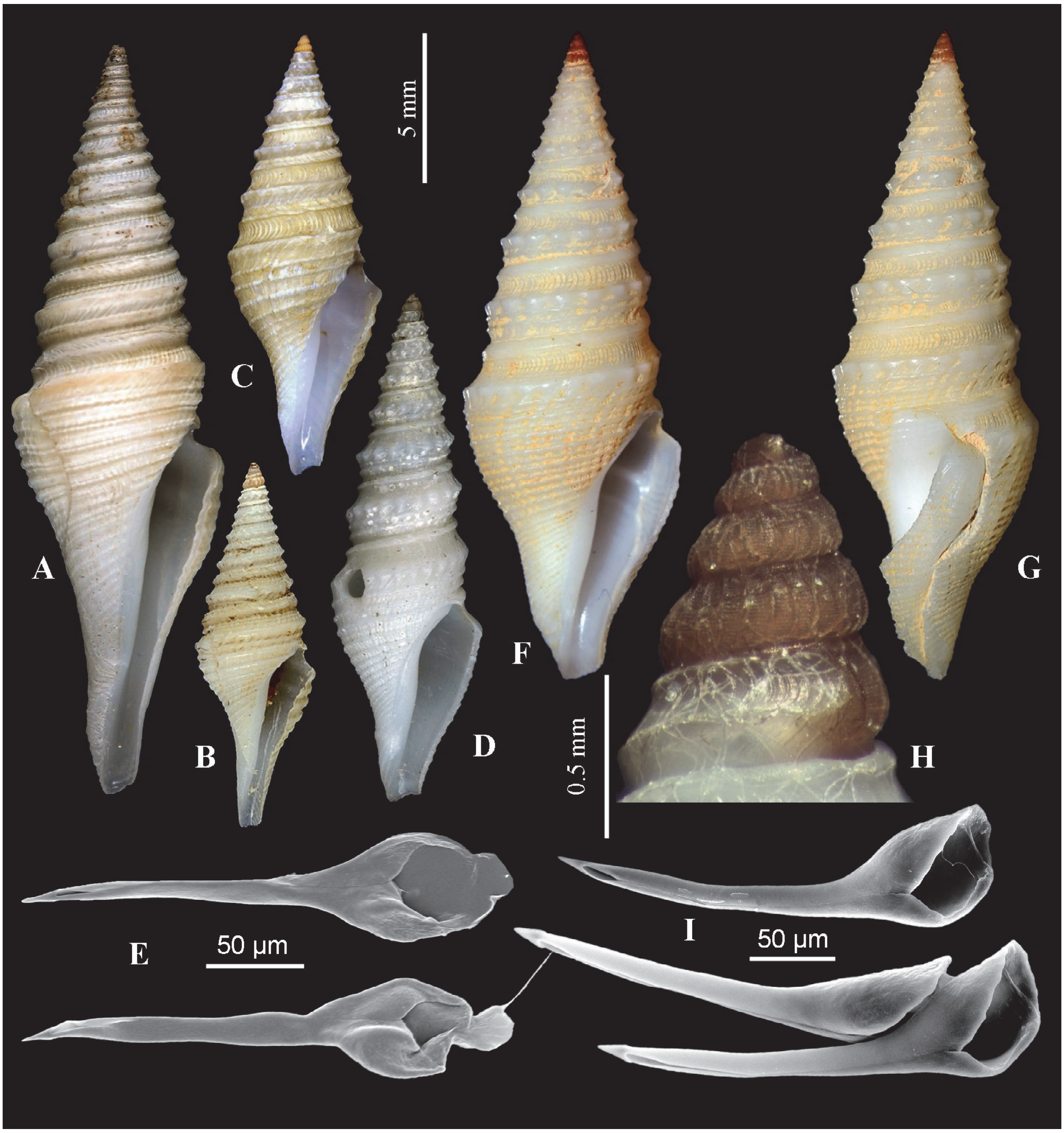

FIG. 17. Shells of *Heteroturris* spp. **A-B**. *Heteroturris sola* Powell, 1967, **A.** MNHN-IM-2007-42483, Philippines, off Bohol, 09°41'N; 123°47'E, 334-389 m, SL 25.3 mm; **B.** MNHN-IM-2007-35068, Philippines, off Mindanao, 08°43'N, 123°19'E, 259-280 m, SL 12.2 mm. **C.** *Heteroturris* sp., MNHN-IM-2009-19004, Philippines, off Luzon, 15°57'N, 121°49'E, 453-460 m, SL 14.9 mm. **D-E**. *Heteroturris* sp., MNHN-IM-2007-17911, Philippines, off Bohol, 09°38'N, 123°43'E, 584-596 m, SL 17.1 mm; **E** – radular teeth. **F-I**. *Heteroturris* ***kanacospira*** sp. nov., MNHN-IM-2009-29105, holotype, SL 21.9 mm; **H** – protoconch; **I** – radular teeth.

РИС. 17. Раковины *Heteroturris* spp. **A-B**. *Heteroturris sola* Powell, 1967, **A.** MNHN-IM-2007-42483, Филиппины, у Бохола, 09°41'N; 123°47'E, 334-389 м, SL 25,3 mm; **B.** MNHN-IM-2007-35068, Филиппины, у Минданао, 08°43'N, 123°19'E, 259-280 м, SL 12,2 мм. **C.** *Heteroturris* sp., MNHN-IM-2009-19004, Филиппины, у Лузона, 15°57'N, 121°49'E, 453-460 м, SL 14,9 мм. **D-E**. *Heteroturris* sp., MNHN-IM-2007-17911, Филиппины, у Бохола, 09°38'N, 123°43'E, 584-596 м, SL 17,1 мм; **E** – зубы радулы. **F-I**. *Heteroturris* ***kanacospira*** sp. nov., MNHN-IM-2009-29105, голотип, SL 21,9 мм; **H** – протоконх; **I** – зубы радулы.

[Bouchet *et al.*, 2011: fig. 3C] in having relatively much shorter teeth with a much broader base. It is very similar to other examined *Heteroturris* sp. (Fig. 17 D-E).

The genetic distances for the COI gene between *H.* ***kanacospira*** sp. nov. and the three other sequenced species (*H. sola* and *H.* spp.) are all greater than 5.8%, whereas the genetic distances between the samples of *H. sola* are all below 0.8%.

**Etymology**: *Kanak* are the indigenous Melanesian inhabitants of New Caledonia, thus the name refers to the origin of the studied specimens off New Caledonia.

## Pseudomelatomidae Morrison, 1965

### *Leucosyrinx* Dall, 1889

**Type species:** *Pleurotoma* (*Pleurotomella*) *verrillii* Dall, 1881 (OD). Caribbean, Recent.

### *Leucosyrinx verrillii* (Dall, 1881)

### (Figs 18, 19, 20 A-C)

*Pleurotoma* (*Pleurotomella*) *Verrillii* Dall, 1881: 57.
*Leucosyrinx Verrillii*: Dall, 1889: 75, pl. 10, fig. 5.
*Leucosyrinx verrillii*: Bouchet, Warén, 1980: 23, figs. 8, 68-69, 197, 202; Figuero, Absalão, 2010: 476-478, figs 2A, B, C.
*Pleurotoma* (*Leucosyrinx*) *tenoceras* Dall, 1889: 76, pl. 36, fig. 5 (**syn. nov.**).
*Leucosyrinx tenoceras* – Figuero, Absalão, 2010: 478, figs 2D, E.

**Type locality:** off Bahia Honda, Cuba, 1550 m (*Blake,* st. 41).

**Sequenced material. French Guiana**, Expedition GUYANE 2014, 07°09'N, 53°01'W, 351-354 m, st. CP4367, 01.08.2014, 2 lv (MNHN-IM-2013-56287; MNHN-IM-2013-56288); 07°12'N, 52°60'W, 444-449 m, st. CP4369, 02.08.2014, 1 lv (MNHN-IM-2013-56341); 07°16'N, 53°01'W, 501-504 m, st. CP4370, 02.08.2014, 3 lv (MNHN-IM-2013-56355, MNHN-IM-2013-56356, MNHN-IM-2013-56357); 06°58'N, 52°37'W, 530-544 m, st. CP4404, 09.08.2014, 3 lv (MNHN-IM-2013-56806, MNHN-IM-2013-56807, MNHN-IM-2013-56809; MNHN-IM-2013-56811); 06°57'N, 52°34'W, 599-602 m, st. CP4406, 09.08.2014, 1 lv (MNHN-IM-2013-56823); 06°53'N, 52°33'W, 495-502 m, st. CP4407, 09.08.2014, 3 lv (MNHN-IM-2013-56840, MNHN-IM-2013-56841, MNHN-IM-2013-56842).

**Remarks.** The sequenced specimens were collected at much shallower depths than previously recorded for the species (351-602 m *versus* 1000-3000 m fide Bouchet, Warén [1980]). The species was considered as highly variable and several names were synonymized by Bouchet, Warén [1980], particularly *Pleurotoma* (*Pleurotomella*) *sigsbeei* Dall, 1881, *Pleurotoma talismani* Locard, 1897, *P. devestitum* Locard, 1897, *Surcula gradata* Thiele, 1925, *Leucosyrinx janetae* Bartsch, 1934. Nevertheless *Leucosyrinx tenoceras* was considered as a separate species on the basis of presence of axial riblets below the suture not reaching the shoulder in *L. tenoceras*, as well as a more slender shell.

The vast number of sequenced specimens allowed re-evalution of intraspecific variability. Even within the same Guiana populations specimens can be found intermediate between the type of *Leucosyrinx verrillii* (compare Fig. 18 A and E) and the type of *L. tenoceras* (compare Fig. 18 H and I). Both specimens with wrinkles or weak subsutural axial folds (Fig. 18H), typical for *L. tenoceras* and with smooth subsutural zone (Fig. 18 B-D) typical for *verrillii* were present in our material. The specimens most similar to *L. tenoceras* are marked on Fig. 19 as *L. verrillii* ("*tenoceras*"). Thus we synonymize *L. tenoceras* with *L. verrillii.*

The radula is studied for the first time for the type species of *Leucosyrinx* (Fig. 20 A-B) (MNHN-IM-2013-56287 and MNHN-IM-2013-56288). It is very similar in both specimens, long, consists of *ca* 55 rows of teeth, 10 nascent and additional 10 rows not fully formed. Radula length 4.3 mm (45% of AL without canal), width up to 400 µm (4.2% of AL without canal). Marginal teeth duplex, narrow lanceolate teeth only. Major limb pointed, narrow, with sharp cutting edges, broadest at mid-length and narrowing towards both ends, form rather distinct socket on dorsal surface where accessory limb embeds. Accessory limb narrow, constituting about 4/5 of tooth length, of the same width along the length. Central formation of indistinct symmetrical folds of the membrane, probably representing remains of the lateral teeth, central cusp absent.

The 14 specimens of *L. verrillii* sequenced for the COI gene were compared with 4 specimens of *L. luzonica* (see below) and one specimen of *L. pelagia* (Dall, 1881). Within species genetic distances never exceed 1.1%, whereas between species genetic distances are all greater than 11%. The two species represented by several samples are monophyletic (PP = 1) (Fig. 19).

### *Leucosyrinx luzonica* (Powell, 1969), **comb. nov.**

### (Figs 20D, 21)

*Comitas luzonica* Powell, 1969: 269(23-281), pl. 225, fig. 7.

**Type locality:** Philippines, off Hermana, Mayor Island, Luzon Island, 15°58'15"N, 119°40'20"E, 1719 m (*Albatross*, st. 5439).

**Sequenced material. South China Sea,** 10°26'N, 114°14'E, 1707-1799 m, NANHAI2014, st. CP4108, 06.01.2014, 1 lv (MNHN-IM-2013-44303); 21°35'N, 118°15'E, 1634-1683 m, ZHONGSHA 2015, st. CP4163, 31.07.2015, 3 lv (MNHN-IM-2013-59549, MNHN-IM-2013-59550, MNHN-IM-2013-59551).

**Remarks.** The species was known from the holotype (immature specimen) only (Fig. 21A). It was recollected in the South China Sea at a similar depth. It reaches significantly larger size, up to 60 mm in our material. The species is variable in terms of shell sculpture. Similar shells were found in New Caledonia, but molecular material is necessary to confirm the presence of the species in this area.

Radula was examined in two specimens (MNHN-IM-2013-44303, MNHN-IM-2013-59549) (Fig. 20D). It is similar in both specimens and to *L.*

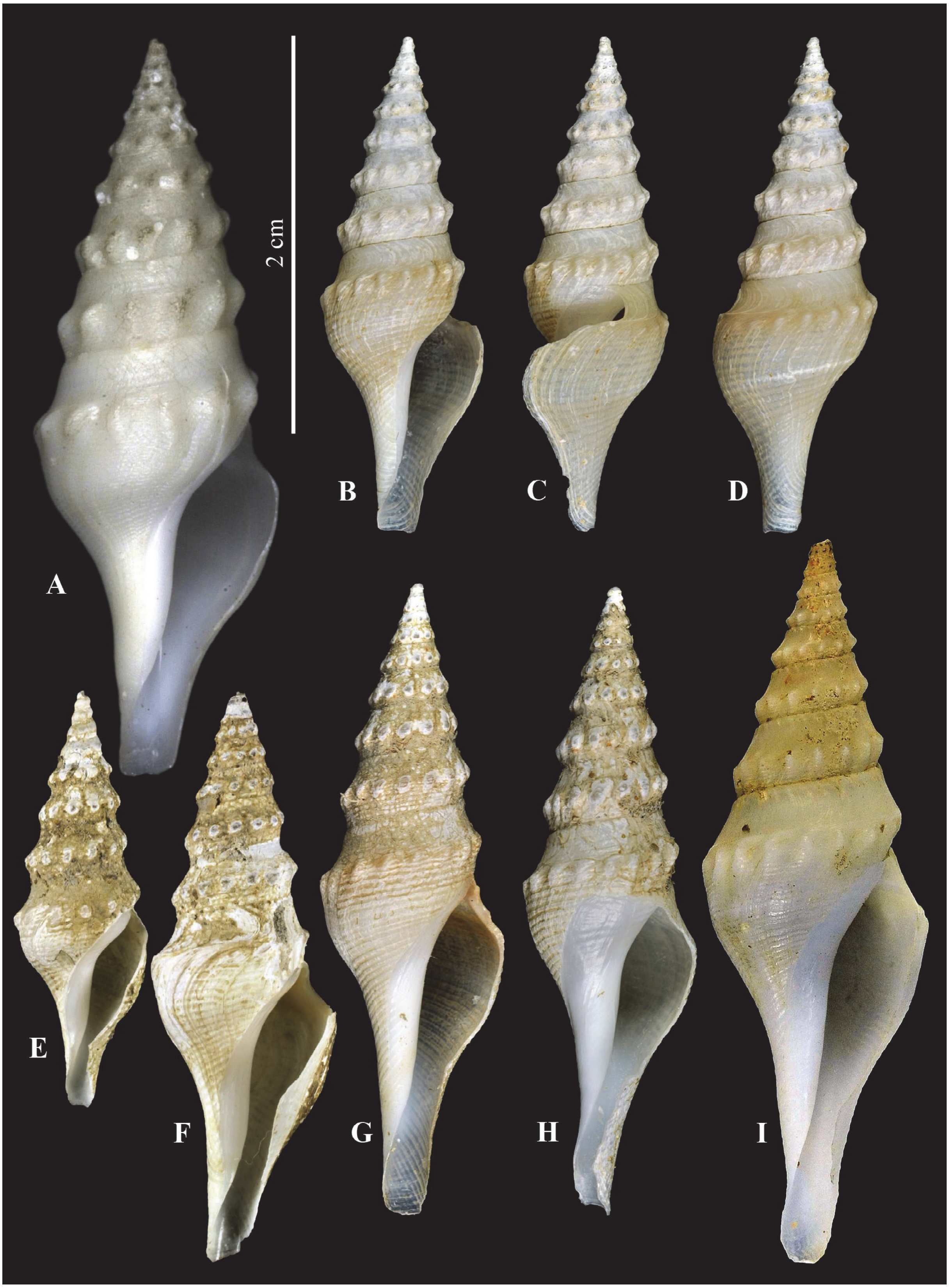

FIG. 18. Shells of *Leucosyrinx verrillii* (Dall, 1881). **A.** USNM 86856, off Cape Fear, North Carolina, 32°39'N, 76°50'30''W, 875 m. The specimen, identified by W.H.Dall and cited in the material of *Leucosyrinx verrillii* in [Dall, 1889], SL 37.5 mm. **B-D.** MNHN-IM-2013-56840, SL 25.1 mm. **E.** MNHN-IM-2013-56355, SL 21.0 mm. **F.** MNHN-IM-2013-56341, SL 29.9 mm. **G.** MNHN-IM-2013-56288, SL 31.9 mm. **H.** MNHN-IM-2013-56287, SL 31.8 mm. **I.** Syntype of *Leucosyrinx tenoceras* Dall, 1889, USNM 87396, Guadeloupe, 16°2'15"N, 61°49'15"W, 1066 m, SL 36.4 mm. All shells at the same scale.

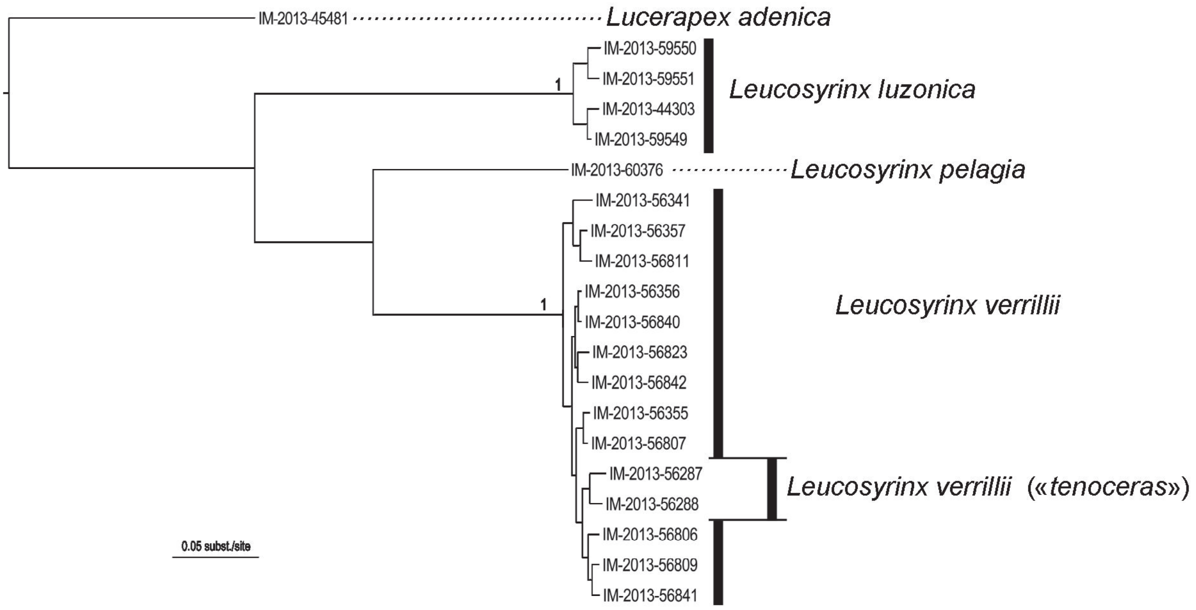

FIG. 19. Phylogenetic tree of *Leucosyrinx* obtained with Bayesian analysis of COI gene sequences. Only supported nodes with posterior probability values between 0.95 and 1.00 are marked on the tree.

РИС. 19. Филогенетическое дерево *Leucosyrinx*, полученное Бэйесовским анализом на основе последовательностей гена COI. На дереве обозначены только поддержанные узлы со значениями апостериорной вероятности между 0,95 и 1,00.

*verrillii*. Radula is long, about 5.6 mm (27% of AL without canal), width up to 730 µm (3.5% of AL without canal). It consists of about 35 rows of teeth, 7-8 nascent. The differences are that in *L. luzonica* the accessory limb of the duplex marginal teeth is distinctly curved *versus* nearly straight in *L. verrillii* and it is narrowing towards both ends, while in *L. verrilii* it has same width along the length.

Thus our data confirm that *Leucosyrinx* is distributed both in Atlantic and Pacific oceans.

## Discussion

While DNA studies are gradually becoming routine in taxonomic practice, the number of described species with inclusion of molecular data remains minuscule. The first holotype associated with DNA sequence was registered in MNHN in 2008. Puillandre *et al.* [2017] estimated that since then only about 3% of newly described species of Mollusca, for which the types are deposited in MNHN, are linked to a DNA sequence. Our decade-long experience of combining molecular and morphological data in Conoidea demonstrated numerous examples of existence of cryptic and pseudocryptic species, as well as wrong generic and familial attributions based on conchological characters alone [e.g. Kantor *et al.,* 2008; Puillandre *et al.*, 2010; Fedosov, Puillandre, 2012; Kantor *et al.,* 2012, 2017; Puillandre *et al.*, 2017].

Conoidea in general are characterized by a high frequency of homoplasy of shell characters, with very similar or nearly undistinguishable shell morphologies arising in distantly related species and genera. One of such groups includes the genera treated herein — *Comitas, Leucosyrinx* and *Sibogasyrinx*. The two former loosely defined genera [eg. *sensu* Powell, 1969] include numerous species which can hardly be attributed to one or another based on shell morphology. Not surprisingly, the generic and even familiar allocation of many of them has been changed. The species originally attributed to *Leucosyrinx* appeared to belong to at least three different families of Conoidea as proved by radular and molecular data – Borsoniidae: *Leucosyrinx badenpowelli* Dell, 1990 and *Leucosyrinx mawsoni* Powell, 1958 were transferred to a new

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РИС. 18 (предыдущая страница). Раковины *Leucosyrinx verrillii* (Dall, 1881). **A.** USNM 86856, у Cape Fear, Северная Каролина, 32°39'N, 76°50'30"W, 875 м. Экземпляр, определенный В.Х.Доллом и процитированный в списке материала *Leucosyrinx verrillii* в [Dall, 1889], SL 37,5 мм. **B-D.** MNHN-IM-2013-56840, SL 25,1 мм. **E.** MNHN-IM-2013-56355, SL 21,0 мм. **F.** MNHN-IM-2013-56341, SL 29,9 мм. **G.** MNHN-IM-2013-56288, SL 31,9 мм. **H.** MNHN-IM-2013-56287, SL 31,8 мм. **I.** Синтип *Leucosyrinx tenoceras* Dall, 1889, USNM 87396, Гваделупа, 16°2'15"N, 61°49'15"W, 1066 м, SL 36,4 мм. Все раковины в одном масштабе.

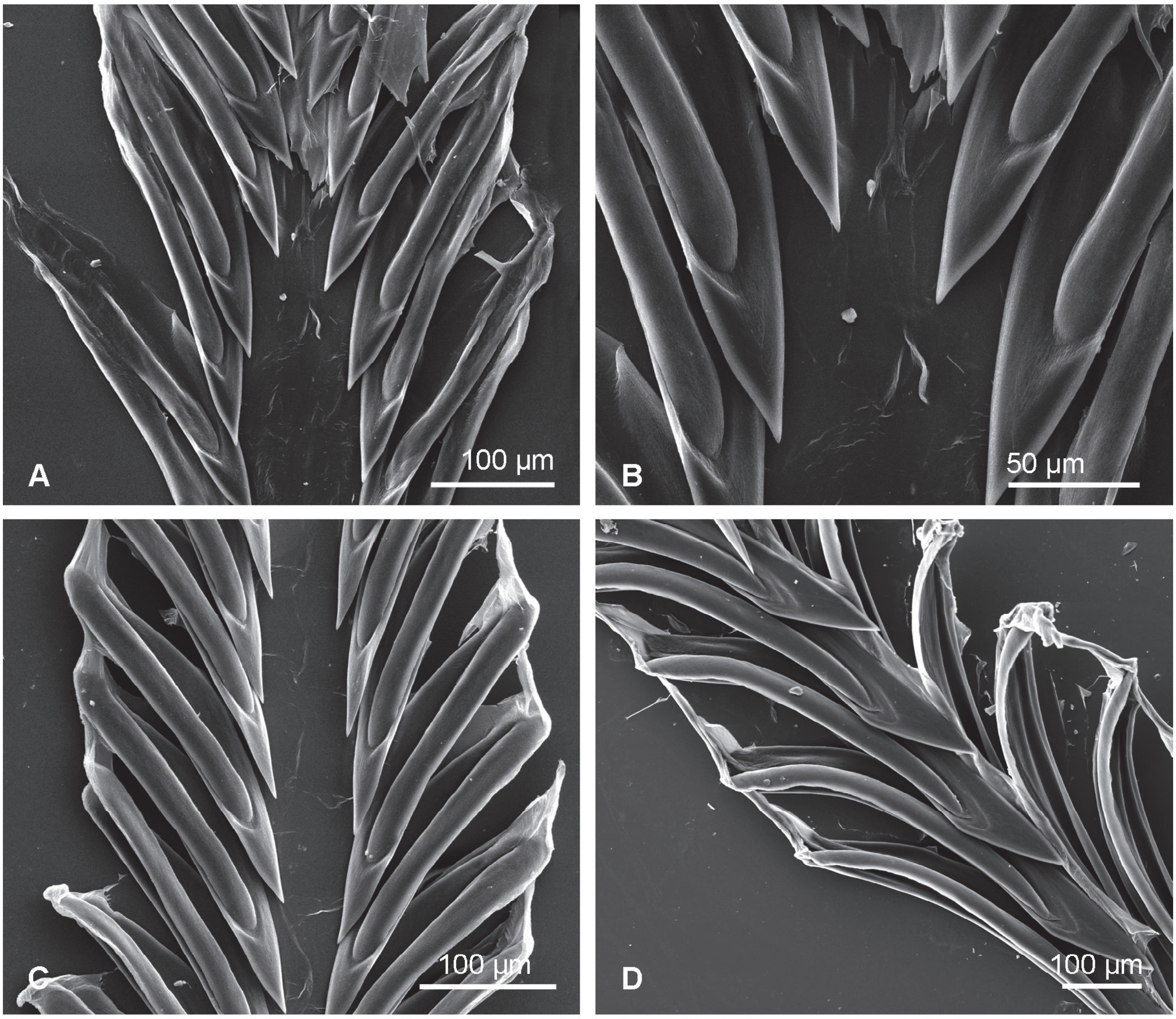

FIG. 20. Radulae of *Leucosyrinx* spp. *Leucosyrinx verrillii* (Dall, 1881) (**A-C**); **A-B.** MNHN-IM-2013-56287 (shell on Fig. 18H). **C.** MNHN-IM-2013-56288 (shell on Fig. 18G). **D.** *Leucosyrinx luzonica* (Powell, 1969), MNHN-IM-2013-59549 (shell see on Fig. 21 E-F).

РИС. 20. Радулы *Leucosyrinx* spp. *Leucosyrinx verrillii* (Dall, 1881) (**A-C**); **A-B.** MNHN-IM-2013-56287 (раковина на Рис. 18H). **C.** MNHN-IM-2013-56288 (раковина на Рис. 18G). **D.** *Leucosyrinx luzonica* (Powell, 1969), MNHN-IM-2013-59549 (раковина на Рис. 21 E-F).

genus *Antarctospira* Kantor, Harasewych et Puillandre, 2016 [Kantor *et al.*, 2016], and *Leucosyrinx paratenoceras* Powell 1951 – to *Typhlodaphne* Powell, 1951; Cochlespiridae: ***Comispira** mai* (herein); and *Leucosyrinx* itself belonging to a separate family. One species, *Leucosyrinx galapagana* Dall, 1919 was transferred to *Exilia* (Phychatractidae, as *Exilia cortezi* (Dall, 1908)) [Kantor *et al.,* 2001].

*Leucosyrinx* itself was first assigned to Cochlespiridae [Powell, 1966; Taylor *et al*., 1993], but with molecular data it was shown to constitute a sister group to Pseudomelatomidae, albeit with low support. Therefore it was conditionally included into the latter family [Bouchet *et al*., 2011]. It is worth mentioning that finally the type species of the genus dwelling in Atlantic has been sequenced, and molecular data indicate that Atlantic and Pacific species attributed to *Leucosyrinx* (in this paper *Leucosyrinx luzonica*) are congeneric.

*Sibogasyrinx* was established as a subgenus of *Leucosyrinx* on the basis of rather minute, and, as appeared, insignificant conchological differences (see above). Moreover, the new species described herein *S.* ***sangeri*** sp. nov. is conchologically more similar to species usually attributed to *Leucosyrinx* than to *S. pyramidalis*, the type species of *Sibogasyrinx*.

The taxonomic history of *Comitas* is less confusing at present and none of the species originally attributed to the genus were transferred to others, except *Comitas luzonica* (herein), that was attributed to *Leucosyrinx* using both morphological and molecular data. Its shell is more similar to other

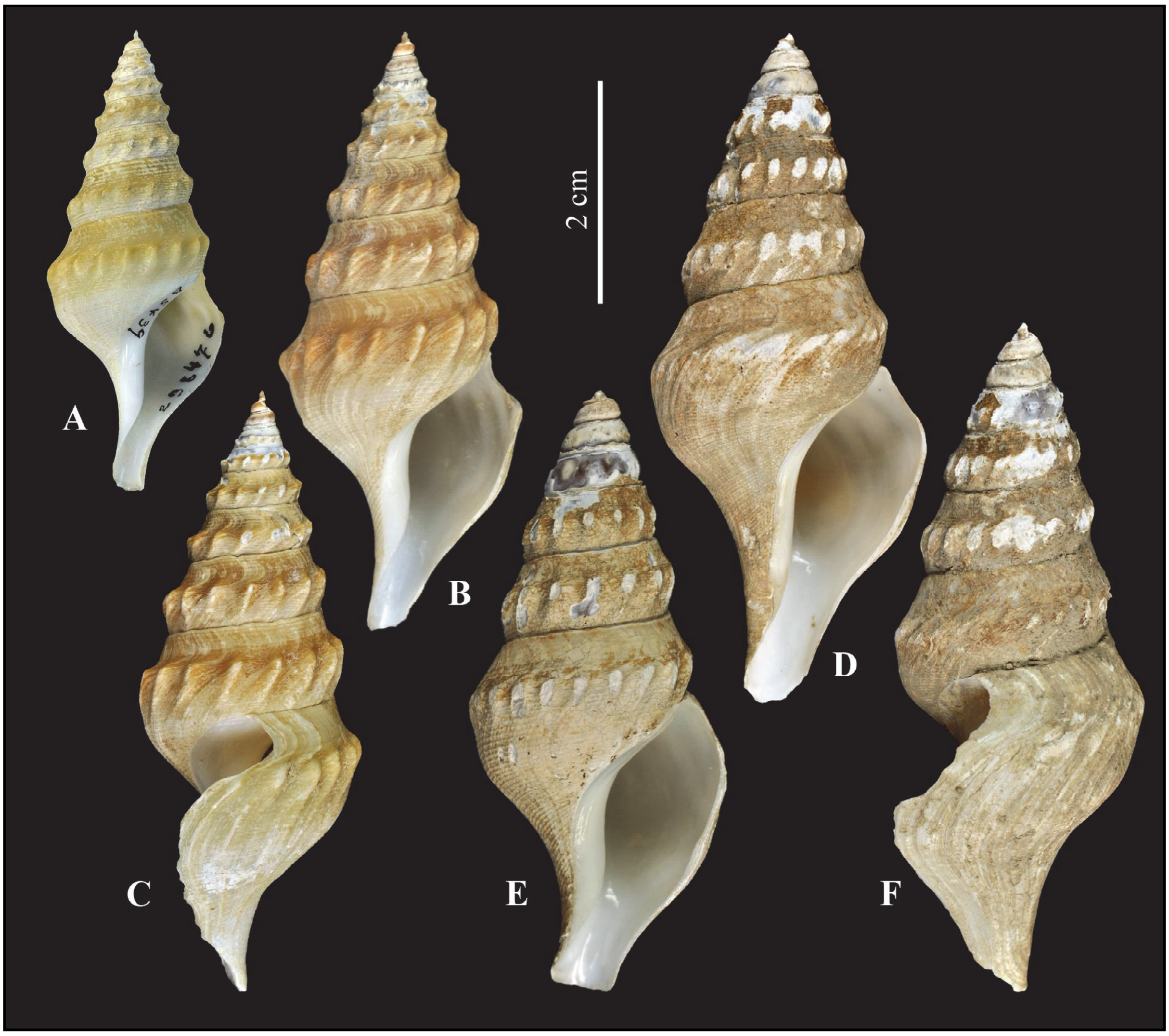

FIG. 21. Shells of *Leucosyrinx luzonica* (Powell, 1969). **A.** Holotype, USNM 238476, SL 41.5 mm. **B-C.** MNHN-IM-2013-44303, SL 54 mm. **D.** MNHN-IM-2013-59551, SL 59.7 mm. **E-F.** MNHN-IM-2013-59549, SL 53.8 mm. All shells at the same scale.

РИС. 21. Раковины *Leucosyrinx luzonica* (Powell, 1969). **A.** Голотип, USNM 238476, SL 41,5 мм. **B-C.** MNHN-IM-2013-44303, SL 54 мм. **D.** MNHN-IM-2013-59551, SL 59,7 мм. **E-F.** MNHN-IM-2013-59549, SL 53,8 мм. Все раковины в одном масштабе.

species of *Comitas* than to *Leucosyrinx*. It should be also stressed that the type species of *Comitas*, *Surcula oamarutica* Suter, 1917 (= *Drillia fusiformis* Hutton, 1877) is fossil and therefore there is no way we can confirm that the Recent species attributed to *Comitas* are congeneric with the type species. But as mentioned above in the remarks to the genus ***Comispira*** gen. nov., some species that are currently included in *Comitas* and never studied from the morphological and molecular perspectives may belong to ***Comispira.***

Nevertheless, all three mentioned genera are well distinguished by the radular morphology. In ***Comispira*** gen. nov. and *Sybogasyrinx* radulae have a well-defined central tooth with a distinct cusp. In *Comitas* and *Leucosyrinx*, there are weak remains of the central formation and central cusp is absent. Finally, morphology of the marginal teeth in the two latter genera is markedly different — they are very characteristically flat, broadly ovate, with thickened edges and the teeth tips, and without pronounced accessory limb in *Comitas* and lanceolate, duplex with distinct accessory limb in *Leucosyrinx* (Fig. 20).

It is noteworthy that the morphology of the marginal teeth in *Sibogasyrinx* ***sangeri*** sp. nov. is rather different from that in the *S. pyramidalis*. In both species the teeth are being folded lengthwise during the maturation (on Fig. 6A and D, not fully formed teeth are marked by white arrows). But in *S. pyramidalis* the posterior edge of the tooth (that becomes the accessory limb) is much more thick, while in *S.* ***sangeri*** sp. nov., the edges of the tooth are very weakly thickened, while the fully formed lengthwise folded tooth has a trough shape with a very narrow lumen.

Thus, in the mentioned cases the radular morphology appeared to be a reliable diagnostic character congruent with molecular phylogeny, despite the convergence of shell morphology,

Similar is the situation with *Lucerapex* and ***Pagodaturris*** gen. nov. The latter genus is conchologically rather similar to *Lucerapex* to the extent that the type species of ***Pagodaturris*** gen. nov. was previously attributed to *Lucerapex* (see above). Nevertheless, the radulae again allow discrimination of the two genera and, furthermore suggest similarity of ***Pagodaturris*** to *Makiyamaya*, a relationship confirmed by the exon-capture based phylogeny. In both genera, the marginal radular teeth have a characteristic morphology with the accessory limb subdivided longitudinally. In *Makiyamaya* the teeth clearly consist of three thickened limbs and can be called tripartite (Fig. 8 E-F). This peculiar radular morphology is confined at present to the two mentioned Clavatulidae genera.

Nevertheless we can equally provide many cases where very similar radulae are found in not closely related taxa, eg. in families Horaiclavidae and Pseudomelatomidae [Bouchet *et al.,* 2011].

Our data demonstrate once again the importance of combining molecular and morphological approaches to the taxonomy of Conoidea, in which many taxa do not withstand molecular phylogenetic tests, revealing numerous non-monophyletic taxa. Contrary to the family level taxa, which have already been revised and now correspond to robust major clades, there are still very few generic revisions based primarily on molecular results.

Finally, based on these results, together with all the systematic revisions performed in the last ten years using DNA data in the Conoidea, we would thus strongly recommend that any newly created taxa, as well as any attribution to higher level-taxa, should be supported by DNA data. In many Conoidea groups, not to do so would be equivalent to a more or less random partitioning.

## Acknowledgments

The material in this paper originates from numerous shore-based expeditions and deep sea cruises, conducted respectively by MNHN and Pro-Natura International (PNI) as part of the *Our Planet Reviewed* programme (SANTO 2006, INHACA 2011, PAPUA NIUGINI, GUYANE 2014, KAVIENG 2014; PI Philippe Bouchet) and/or by MNHN, Institut de Recherche pour le Dйveloppement (IRD) and other partners as part of the *Tropical Deep-Sea Benthos* programme (SALOMON 2, SALOMONBOA 3, EBISCO, CONCALIS, AURORA 2007, BIOPAPUA, EXBODI, KARUBENTHOS 2, MADEEP, DONGSHA 2014, NANHAI 2014, ZHONGSHA 2015; PIs Bertrand Richer de Forges, Philippe Bouchet, Sarah Samadi, Wei-Jen Chen, Tin-Yam Chan). In-country scientific partners included the University of Papua New Guinea (UPNG); National Fisheries College, Kavieng, Papua New Guinea; the Philippines Bureau of Fisheries and Aquatic Research, and the National Museum of the Philippines; Universidade Eduardo Mondlane, Maputo; Parc National de la Guadeloupe, and Universitй des Antilles; University of Taipei and University of Keelung, Taiwan. Funders and sponsors included the Total Foundation, Prince Albert II of Monaco Foundation, Stavros Niarchos Foundation, Richard Lounsbery Foundation, Vinci Entrepose Contracting, Fondation EDF, European Regional Development Fund (ERDF), the French Ministry of Foreign Affairs, Fonds Pacifique and the Government of New Caledonia; the Taiwan and South China Sea cruises were supported by bilateral cooperation research funding from the Taiwan Ministry of Science and Technology (MOST 102-2923-B-002-001-MY3, PI Wei-Jen Chen) and the French National Research Agency (ANR 12-ISV7-0005-01, PI Sarah Samadi). Additional field work included PANGLAO 2004-2005 (a joint project of MNHN, University of San Carlos, Cebu City, and the Philippines Bureau of Fisheries and Aquatic Research); sampling in Western Australia arranged by Hugh Morrison, with support of the Western Australian Museum; sampling in Congo arranged by Bernard Thomassin; and the CAML-CEAMARC cruises of RSV Aurora Australis and TRV Umitaka Maru (IPY project no.53) supported by the Australian Antarctic Division, the Japanese Science Foundation, the French Polar Institute IPEV (ICOTA and REVOLTA programmes), CNRS, MNHN and ANR (White Project ANTFLOCKs USAR no.07-BLAN-0213-01, PI Guillaume Lecointre). All expeditions operated under the regulations then in force in the countries in question and satisfy the conditions set by the Nagoya Protocol for access to genetic resources.

The study was conducted using Joint Usage Center «Instrumental methods in ecology» at the IEE RAS. We thank A.Neretina and A.Nekrasov for their friendly and helpful assistance with the SEM facilities. The contributions of Y.Kantor and A.Fedosov (morphological studies) were supported by the grant from the Russian Science Foundation RSF 16-14-10118.This project was partly supported by the Service de Systématique Moléculaire (UMS 2700 CNRS-MNHN) and by the CONOTAX project funded by the French ANR (grant number ANR-13-JSV7-0013-01).

We thank, among others, Virginie Héros, Philippe Maestrati, Barbara Buge, Dario Zuccon, Julien Brisset and Gilberto Marani for their role in specimens processing during the expeditions and their help in curating and sequencing the specimens. Our special thanks to Phil Fallon, who sorted and identified conoidean material from GUYANE 2014 expedition.

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# Новые и необычные глубоководные Conoidea, ревизованные на основании строения раковины, радулы и ДНК

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**РЕЗЮМЕ.** В процессе реконструкции новой молекулярной филогении Conoidea, основанной на методе exon-capture были выявлены новые виды и виды с примечательной морфологией. Обсуждается таксономия этих видов, для большинства впервые изображена радула. Описаны новые роды: ***Comispira*** gen. nov. (Cochlespiridae), типовой вид *Leucosyrinx mai* Li et Li, 2008; ***Pagodaturris* gen. nov.** (Clavatulidae), типовой вид *Pleurotoma molengraaffi* Tesch, 1915. Новые виды: ***Comispira compta*** gen. et sp. nov., *Sibogasyrinx* ***sangeri*** sp. nov. (оба относятся к Cochlespiridae), ***Pagodaturris philippinensis*** gen. et sp. nov. (Clavatulidae), *Horaiclavus* ***micans*** sp. nov., *Iwaoa* ***invenusta*** sp. nov. (оба относятся к Horaiclavidae), *Lucerapex* ***cracens*** sp. nov., *Lucerapex* ***laevicarinatus*** sp. nov. (Turridae), *Heteroturris* ***kanacospira*** sp. nov. (Borsoniidae). *Epideira* Hedley, 1918 перенесена из Pseudomelatomidae в Horaiclavidae. Впервые изображены радулы *Kuroshioturris nipponica* (Shuto, 1961) (Turridae), *Leucosyrinx verrillii* (Dall, 1881), *Leucosyrinx luzonica* (Powell, 1969), comb. nov.