

The anatomy and taxonomy of selected Neogastropoda (Gastropoda) of phylogenetic importance

Yuri I. KANTOR^{1,4}, Alexander FEDOSOV², Philippe BOUCHET³, Nicolas PUILLANDRE³

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

² Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, SWEDEN;

³ Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, 57 rue Cuvier, CP 26, 75005 Paris, FRANCE.

⁴ Corresponding author; E-mail: kantor.yuri1956@gmail.com

ABSTRACT. Recently the phylogeny of the order Neogastropoda based on exon-capture [Fedosov *et al.*, 2026], has confirmed the monophyly of the group and achieved high resolution for many deep nodes. Thorough examination of the sequenced species revealed novel and distinctive morphological characters, and in several cases highlighted unresolved taxonomic issues. Some sequenced species proved to be new to science, while others required reassessment of their generic or familial placement in light of the phylogenetic results. The anatomy of the anterior foregut of Enigmavasidae is described herein for the first time. A new species, *Egestas caledoniensis* (Costellariidae), is described from northern New Caledonia, representing the second extant species of the genus. The anatomy and radula of *Jaspidella jaspidea* (Olividae) are described for the first time, and it is suggested that the species may warrant recognition as a distinct subfamily. The unique radular anatomy of *Cyllene* (Cyllenidae) is described and illustrated in details for the first time, with the hypothesis that the teeth may function in toxin delivery. *Lachesiella*, a new genus of Columbellidae, is characterized by an unusual protoconch morphology and includes two new species: *Lachesiella kunie* and *Lachesiella apiceconica*. *Atlantamanaria*, new genus of Eosiphonidae based on the new species from the Caribbean is described, it closely resembles *Manaria* but is clearly distinct based on molecular data. Two new species of *Gaillea* (Eosiphonidae), *G. atlantica* and *G. crassa* are described from Guadeloupe. Finally, *Aforia bugae* (Cochlespiridae) is described as a new species from Papua New Guinea, marking the first record of the genus in this region.

[https://doi.org/10.35885/ruthenica.2026.36\(4\).1](https://doi.org/10.35885/ruthenica.2026.36(4).1)

Zoobank registration: [urn:lsid:zoobank.org:pub:366870F1-F95B-44F7-AB6A-617F9EE2D5BE](https://zoobank.org/pub:366870F1-F95B-44F7-AB6A-617F9EE2D5BE)

Анатомия и таксономия избранных Neogastropoda (Gastropoda), важных в филогенетическом аспекте

Юрий И. КАНТОР^{1,4}, Александр ФЕДОСОВ², Филипп БУШЕ³, Никола ПУЛЛЯНДР³

¹ Институт проблем экологии и эволюции им. А.Н.Северцова РАН, Ленинский проспект 33, 119071 Москва, РОССИЙСКАЯ ФЕДЕРАЦИЯ;

² Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, ШВЕЦИЯ;

³ Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, 57 rue Cuvier, CP 26, 75005 Paris, ФРАНЦИЯ.

⁴ Автор-корреспондент; E-mail: kantor.yuri1956@gmail.com

РЕФЕРАТ. Недавно опубликованная филогения отряда Neogastropoda, основанная на данных захвата экзонов [Fedosov *et al.*, 2026], подтвердила монофилию группы и разрешила топологию многих

глубоких узлов. Тщательное изучение секвенированных видов выявило новые и необычные морфологические признаки, а в ряде случаев высветило нерешенные таксономические проблемы. Некоторые секвенированные виды оказались новыми для науки, в то время как для других потребовался пересмотр родовой или семейственной принадлежности на основе филогенетических результатов. Впервые описана анатомия передней части пищеварительной системы Enigmavasidae. Новый вид *Egestas caledoniensis* (Costellariidae) описан с севера Новой Каледонии и представляет собой второй рецентный вид этого рода. Впервые описаны анатомия и радула *Jaspidella jaspidea* (Olividae), и высказано предположение, что этот вид может быть выделен в отдельное подсемейство. Уникальная морфология радулы *Cyllene* (Cyllenidae) впервые подробно описана и проиллюстрирована; выдвинута гипотеза, что зубы могут служить для доставки токсинов. *Lachesiella*, новый род Columbellidae, характеризуется необычной морфологией протоконха и включает два новых вида: *Lachesiella kunie* и *Lachesiella apiceconica*.

Описан *Atlantamanaria*, новый род Eosiphonidae из Карибского бассейна; он очень похож на *Manaria*, но четко отличается на основе молекулярных данных. Два новых вида *Gailllea* (Eosiphonidae), *G. atlantica* и *G. crassa* описаны из Гваделупы. Новый вид *Aforia bugeae* (Cochlespiridae) описан из Папуа–Новой Гвинеи, что является первой находкой этого рода в данном регионе.

Introduction

The order Neogastropoda Wenz, 1938 is a large and successful group of almost exclusively marine mollusks encompassing over 16,200 accepted Recent species [MolluscaBase, 2025]. According to the latest classification, there are 11 living neogastropod superfamilies and 64 families [Fedosov *et al.*, 2026]. Most neogastropod species are scavengers or active predators [Ponder, 1973; Taylor *et al.*, 1980; Kantor, 2002], while few lineages practice blood-sucking, parasitism, or have switched to herbivory (some Columbellidae) or suspension feeding (Olivellinae) [Marcus, Marcus, 1962; Troost *et al.*, 2012]. Neogastropods inhabit all oceans at all depths and often dominate deep-sea benthic communities in abundance and species richness [Taylor *et al.*, 1980].

Neogastropoda has a long and controversial history of taxonomic and phylogenetic studies. There have been several attempts to reconstruct the phylogeny of the group based on morphological characters [*e.g.*, Ponder, 1973; Kantor, 1996; Simone, 2011], which resulted in controversial hypotheses. This can be partially explained by high homoplasy in anatomical characters, with the origin of complex similar structures in non-closely related lineages [*e.g.*, tubular gland of Leiblein terminating in a muscular bulb in some Costellariidae, Marginellidae, and Conoidea]. Emerging molecular methods using Sanger sequencing have allowed researchers to resolve the phylogeny of some families, superfamilies and informal groups, but they generally failed to resolve deep nodes and obtain a robust phylogenetic hypothesis for the entire order.

A recent phylogenomic study [Fedosov *et al.*, 2024], combining comprehensive lineage sampling with broad genome representation based on exon-capture, recovered a generally well-supported phylogenetic backbone of the order. At the same time, it failed to either refute or support the monophyly of Neogastropoda as traditionally defined, as conflicting results were obtained regarding the placement of Cancellariidae. Finally, the analysis of a greatly expanded phylogenomic dataset comprising 677 taxa (a six-fold increase in species representation compared to Fedosov *et al.* [2024]) and covering all except two recognized neogastropod families allowed to confirm the monophyly of Neogastropoda and obtain better resolution for many deep nodes [Fedosov *et al.*,

2026], resulting in a new classification of the order, and an updated fossil record.

During the preparation of this new phylogeny, the species sequenced underwent thorough investigation, which in many cases uncovered novel and peculiar morphological characters and/or revealed taxonomic issues that needed to be resolved. Some sequenced species appeared to be new to science, while for others, generic or familial attribution needed to be revised based on their placement in the phylogeny. Most were previously unstudied with respect to radular morphology, and a few constituted independent lineages in the tree, corresponding to new families. The taxonomy of these taxa is discussed separately in the present paper, to avoid exaggerating the length of the phylogenetic study of Fedosov *et al.* [2026]. In most cases, the justification for including a species in a particular genus and family is based on the exon-capture tree, and we will refer to it wherever needed. However, here we include *cox1* phylogenies based on newly produced sequences. Although they may lack resolution at the family and sometimes even genus levels, these support the distinctiveness of the new species from close relatives, and allow evaluation of intraspecific variability.

Material and methods

Sampling

All the specimens treated in this paper were collected during cruises and shore-based expeditions organized between 2004 and 2016 by the Muséum National d'Histoire Naturelle, Paris (MNHN) and Institut de Recherche pour le Développement (IRD) (details are provided in Supplementary Table S1). Until 2012, live specimens for molecular analysis were anaesthetized with an isotonic solution of MgCl₂ 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 (Supplementary Table S1).

DNA sequences were produced using two different methodologies (Supplementary Table S1). Part of the specimens were included in a large dataset used to reconstruct a Neogastropoda phylogeny [Fedosov *et al.*, 2026] based on an exon capture approach. The details of DNA extraction, sequencing and phylogenetic analyses are provided in Fedosov *et al.* [2026]. For other specimens, only *cox1* sequences were produced, following the methodology described in Puillandre *et al.* [2017] for DNA extraction and

sequencing. After manual alignment of the *cox1* sequences, a Bayesian tree was reconstructed using Mr.Bayes 3.2.6 [Huelsenbeck, Ronquist, Hall, 2001]. Each of the two runs consisted of four Markov chains and 10 000 000 generations, with four chains, two swaps at each generation, a sampling frequency of one tree each 2000 generations and a chain temperature set at 0.02. Convergence of each run was evaluated using TRACER 1.6 [Rambaut, Drummond, 2014] to check that all effective sample size values exceeded 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. A GTR + I + G substitution model was used, and the *cox1* gene was divided into three partitions corresponding to the three codon positions.

Diagnostic combination of nucleotides was identified for *Atlantamanaria* in an alignment of barcode fragment of *cox1* comprising 15 other species of Eosiphonidae, of which 10 were members of the genus *Manaria* (supplementary data 1). To compile the diagnosis, we used MOLD v 1.4.3 [Fedosov *et al.*, 2022], with default settings for supraspecific taxa.

Shell morphology and radula

Radulae were prepared following a standard protocol detailed in Kantor and 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 – empty shell;
lv – live collected specimen;
MNHN – Muséum National d'Histoire Naturelle, Paris, France;
NMP – National Museum of Philippines, Manila, Philippines;
RGM – Nationaal Natuurhistorisch Museum, Leiden, Netherlands;
SL – shell length;
stn – station;
SW – shell width;
USNM – National Museum of Natural History, Smithsonian Institution, Washington DC, USA;
ZMHB – Zoological Museum, Humboldt University, Berlin, Germany.

Taxonomy

Superfamily Costellarioidea

MacDonald, 1860

Family Enigmavasidae Fedosov, Lemarcis, Bouchet, Harzhauser, Kantor, Kiel, Modica, Oliverio, Zaharias et Puillandre, 2026

Type genus: *Enigmavasum* Poppe et Tagaro, 2005; TS: *Enigmavasum enigmaticum* Poppe,

Tagaro, 2005; OD [= *Coralliophila* (Mipus) *tomlini* van Regteren Altena, 1950].

Remarks: This is so far a monotypical family. Both in shell shape and anatomy, *Enigmavasum* differs markedly from its closest relatives, the Ptychatractidae and Costellariidae, particularly in its relatively long proboscis with a very small radula situated apically in the proboscis. The radula is also very characteristic, and differs from those of the Ptychatractidae and Costellariidae in having tricus-pate, relatively narrow, robust, and deeply notched, rachidians with relatively very large cusps.

Enigmavasum tomlini (van Regteren Altena, 1950) (Figs 1A, 2)

Coralliophila (Mipus) *tomlini* van Regteren Altena, 1950: 217–218, fig. 10.

Mipus tomlini – Kosuge, 1986: 72, pl. 25, figs 7, 8 (holotype); Oliverio, 2008: 568, 573, figs. 141–144.

Enigmavasum enigmaticum Poppe, Tagaro, 2005: 133–134, pl. 1, **syn. nov.**

Type localities: *Coralliophila* (Mipus) *tomlini* – Jawa, Indonesia, “Poetjangan layers (volcanic facies): sheet 110B, C71, late Pliocene. *Enigmavasum enigmaticum* – Cotabato Province (Mindanao I.), 800 m, Philippines.

Holotypes: *Coralliophila* (Mipus) *tomlini* – RGM 46637, SL 44+ mm. *Enigmavasum enigmaticum* – NMP, Manila, SL 29.7 mm.

Material examined. PAPUA NEW GUINEA, S of Lae, Gulf of Huon, 6°51'S, 147°6'E, 613–652 m, BIOPAPUA, stn CP3631, 1 lv, MNHN-IM-2019-34814 (not sequenced, anatomy examined); 3°49'S; 144°39'E, 400–656 m, BIO-PAPUA, stn CP3704, 1 lv, MNHN-IM-2009-15307. Sequenced specimen (exon capture). W Rempi Area, 5°00'S; 145°50'E, 505–521 m, PAPUA NIUGINI, stn CP3961, 2 lv, MNHN-IM-2013-15967, MNHN-IM-2013-15968 (both sequenced for *cox1*).

Operculum relatively large, about 8 mm in length (0.8 of AL without canal), subtriangular, with rounded upper edge and tapering below to a terminal nucleus.

Digestive system (Fig. 2F). Proboscis medium-long, narrow, cylindrical. Proboscis retractors rather weak, on dorsal side of posterior half of rhynchodaeum directed backwards, on ventral side – anteriorly. Anterior oesophagus rather thin, leaving from posterior part of proboscis and following anteriorly being attached to rhynchodaeum. Salivary ducts paired, very thin, straight, seen as silvery lines attached to rhynchodaeum. Valve of Leiblein relatively very large, rounded. Mid oesophagus posterior to valve very narrow, but quickly enlarging and becoming muscular and obviously glandular, long, coiled. Gland of Leiblein massive, broadly tubular, tightly coiled, yellowish. Salivary glands fused without obvious border, irregularly shaped and embracing the

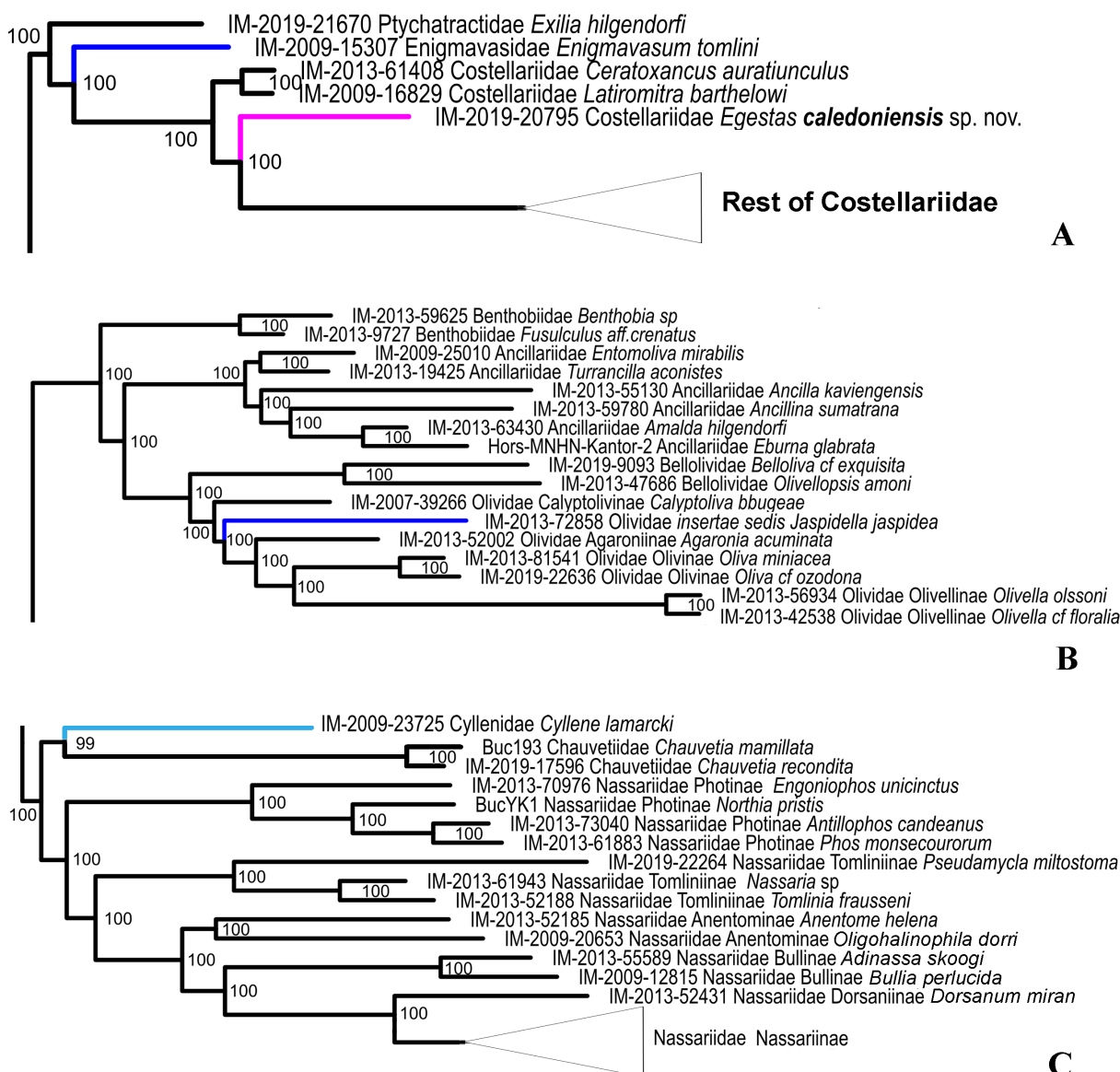


FIG. 1. Partial Posterior Mean Site Frequency (CAT-PMSF) exon-capture tree highlighting **A.** Costellarioidea; **B.** Olivoidea; **C.** Nassariidae, Chauvetiidae and Cyllenidae [after Fedosov *et al.*, 2026].

valve of Leiblein and nerve ring, acinous. Accessory salivary gland not found.

Radula (Fig. 2 G–H) small, occupying the anteriormost part of proboscis and spanning only about 1/5 of proboscis length, comprising about 55 rows of teeth, 1.56 mm in length (15.8% of AL), around 105 μm in width (1.1% of AL). Rachidian tooth robust, narrow, with narrow and deep notch on anterior edge, with three closely spaced large cusps spanning more than half of total tooth width, central cusp longest. Lateral teeth small, sickle-shaped.

Remarks. Enigmavasidae constitutes a separate lineage sister to Costellariidae in the exon-capture tree (Fig. 1A). The first offshoot of the latter is the clade uniting the genera *Ceratoxancus* Kuroda, 1952, *Latiromitra* Locard, 1897, and *Egestas* Finlay, 1926.

The superfamily Costellarioidea was recognized by Fedosov *et al.* [2026] to incorporate the families Ptychatractidae, Enigmavasidae, and Costellariidae.

Enigmavasum clearly differs from both Ptychatractidae (represented by *Exilia* Conrad, 1860) and *Ceratoxancus*+*Latiromitra*–*Egestas* in its shell characters and foregut anatomy. In the latter the proboscis is extremely short with odontophore and radula protruding backwards from proboscis base (vs relatively very long proboscis with a terminal radula in *Enigmavasum*) [Kantor, Bouchet, 1997; Bouchet, Kantor, 2000]. The proboscis retractors are relatively very large, paired, muscles attached to the anterior part of the rhynchodaeum (vs numerous smaller muscles attached to the posterior half of the rhynchodaeum in *Enigmavasum*); the salivary ducts

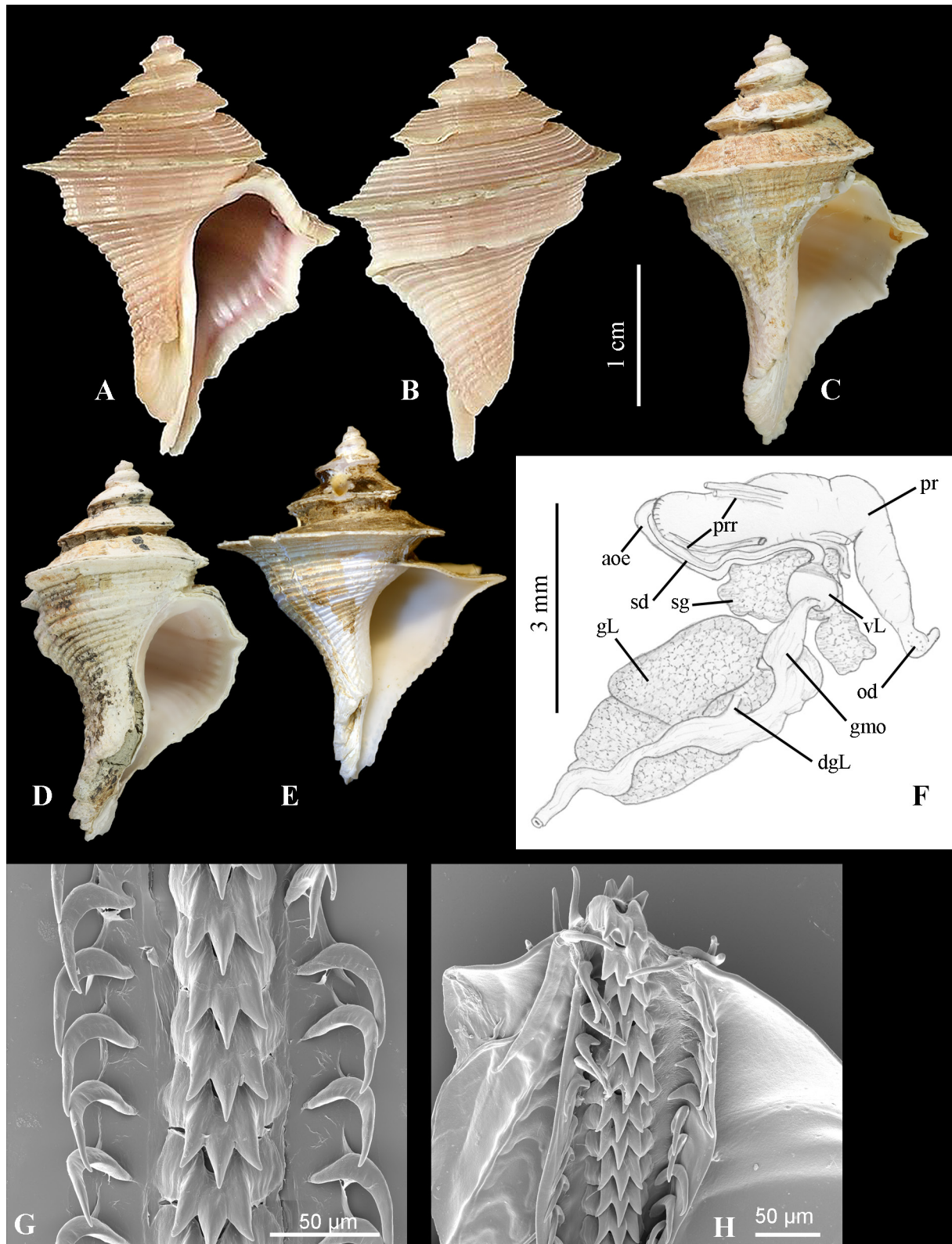


FIG. 2. *Enigmavasum tomlii* (van Regteren Altena, 1950). A–B. Holotype of *Enigmavasum enigmaticum* Poppe et Tagaro, 2005, SL 29.7 mm. C. MNHN-IM-2009-15307, SL 28.8 mm. D. MNHN-IM-2013-15967, SL 27 mm. E–H. MNHN-IM-2019-34814, SL 25.5 mm. F. Foregut anatomy. G–H. Radula. All shells at the same scale. Abbreviations: aoe – anterior oesophagus; dgL – duct of the gland of Leiblein; gL – gland of Leiblein; gmo – glandular mid-oesophagus; od – odontophore (position marked by dashed line); pr – proboscis; prr – proboscis retractors; sd – salivary duct; sg – salivary gland; vL – valve of Leiblein.

follow within the oesophagus walls (*vs* passing freely along oesophagus in *Enigmavasum*) and there is a medium-sized bulky or tubular and slightly coiled gland of Leiblein [Fedosov *et al.*, 2017] (*vs* massive gland of Leiblein in *Enigmavasum*). Rachidians in *Enigmavasum* bear a deep and narrow notch on the anterior edge and are shallowly arcuate, with very closely spaced, large and relatively long, cusps, thus very different from those in Costellariidae.

The shell of *Enigmavasum* with its dominating shoulder keel is unique for the superfamily. The fossil type species was described in the genus *Mipus* De Gregorio, 1885. Oliverio [2008] pointed out its similarity with *Enigmavasum enigmaticum*, but left the species in Coralliophilinae. The holotype of the latter species differs from *E. tomlini* in the presence of a distinct keel on shell periphery. The examined material demonstrates a gradual transition from specimens with an angular shell periphery to those with an evenly convex periphery, thus suggesting that we are dealing with the same species (Fig. 2).

Costellariidae MacDonald, 1860

Egestas Finlay, 1926

Type species: *Vexillum waitei* Suter, 1909 (OD).

Egestas caledoniensis sp. nov.

(Fig. 3 A–E)

Zoobank registration: urn:lsid:zoobank.org:act:9A405DB4-2C99-4F03-A7C4-C6C24EDFD5A8

Holotype (sequenced for exon capture): MNHN-IM-2019-20795, SL 4.8 mm, AL 2.5 mm.

Type locality. Northern New Caledonia, Atoll Pelotas, 18°27'S, 162°58'E, 613–623 m [SPAN-BIOS, stn DW5222].

Description (holotype). Shell small, turritiform, with medium-high spire and short siphonal canal, slightly bent abaxially. Shell comprising 3.75 teleoconch and slightly over 1.5 protoconch whorls. Protoconch paucispiral, dome-shaped, whorls glossy, microshagreened. Protoconch-teleoconch transition marked with three narrow and closely spaced, nearly orthocone, axial ribs. Suture distinct, shallowly impressed. Subsutural ramp narrow but distinct, deeply concave, with single convex spiral cord on later whorls. All teleoconch whorls with well pronounced axial ribs, 9 on first whorl, 8 on penultimate and last whorls. Ribs originate on shoulder and extend to lower suture on spire whorls and to shell base on last whorl. Spiral sculpture of equal, distinct cords on entire shell surface, including canal. Interspaces between cords about one cord width. Last whorl with 15 cords, including subsutural one.

Aperture irregularly oval. Inner lip with weak and narrow columellar and parietal callus, not seen in strict apertural view. Columella with three small but distinct and closely spaced columellar folds.

Colour uniformly off-white.

Radula (Fig. 3 D–E) long, comprising about 80 transverse rows of teeth, about 430 µm in length (17% of AL), radular membrane width about 45 µm (1.8% AL). Rachidian relatively broad but short, with medium-deep arcuate anterior edge. Three large, broadly spaced cusps, central slightly longer; interspaces with 1–4 smaller cusps, their number and shape varying even in adjacent rows. Lateral teeth with narrow base, simple sickle-shaped.

Etymology. The species is named after the type locality, New Caledonia.

Remarks. The new species is similar in shell outline to the type species, *E. waitei* (the only known Recent representative of the genus), but differs in having a stouter and relatively broader shell. Furthermore, the protoconch is conical in *E. waitei* (Fig. 3G), while it is lower and dome-shaped in *E. caledoniensis* sp. nov. The radulae are similar in both species (Fig. 3D, E, H), with the rachidian having additional cusplets between major cusps, that vary in shape and number from row to row.

Superfamily Olivoidea Latreille, 1825

Family Olividae Latreille, 1825

Jaspidella Olsson, 1956

Type species: *Voluta jaspidea* Gmelin, 1791, OD.

Jaspidella jaspidea (Gmelin, 1791)

(Fig. 4)

Material examined: MARTINIQUE, Lesser Antilles, 14°30'53"N, 60°49'48"E, 0 m, MADIBENTHOS, stn AM042, 1 spm, MNHN-IM-2013-72858 – sequenced for exon capture, anatomy and radula examined.

Anatomy. Propodium crescent-shaped, with deep central longitudinal dorsal furrow, separated from metapodium by narrow, but distinct and deep, furrow (Fig. 4C). Parapodia in contracted state short and thick, in live mollusc tightly embracing anterior part of shell, with tip of siphon and cephalic flap with eye protruding. Dorsal side of the foot, sole and parapodia with irregular, rather large, light brown, spots. Operculum large, narrow oval, completely transparent, yellow. Nucleus terminal, shifted adaxially. Cephalic flaps symmetrical, with short tapering tentacles on the tips. Eyes present, distinct, close to the tips of tentacles.

Mantle (Fig. 4D) length exceeding its breadth, with medium-long siphon. Mantle filament present, long, no distinct mantle lobe. Anterior mantle tentacle very reduced, hardly discernible from mantle edge. Rectal gland narrow, brownish. Osphradium medium-large, ovate, nearly symmetrical, light-orange, with very narrow axis, extending slightly over half of ctenidium length. Ctenidium anteriorly

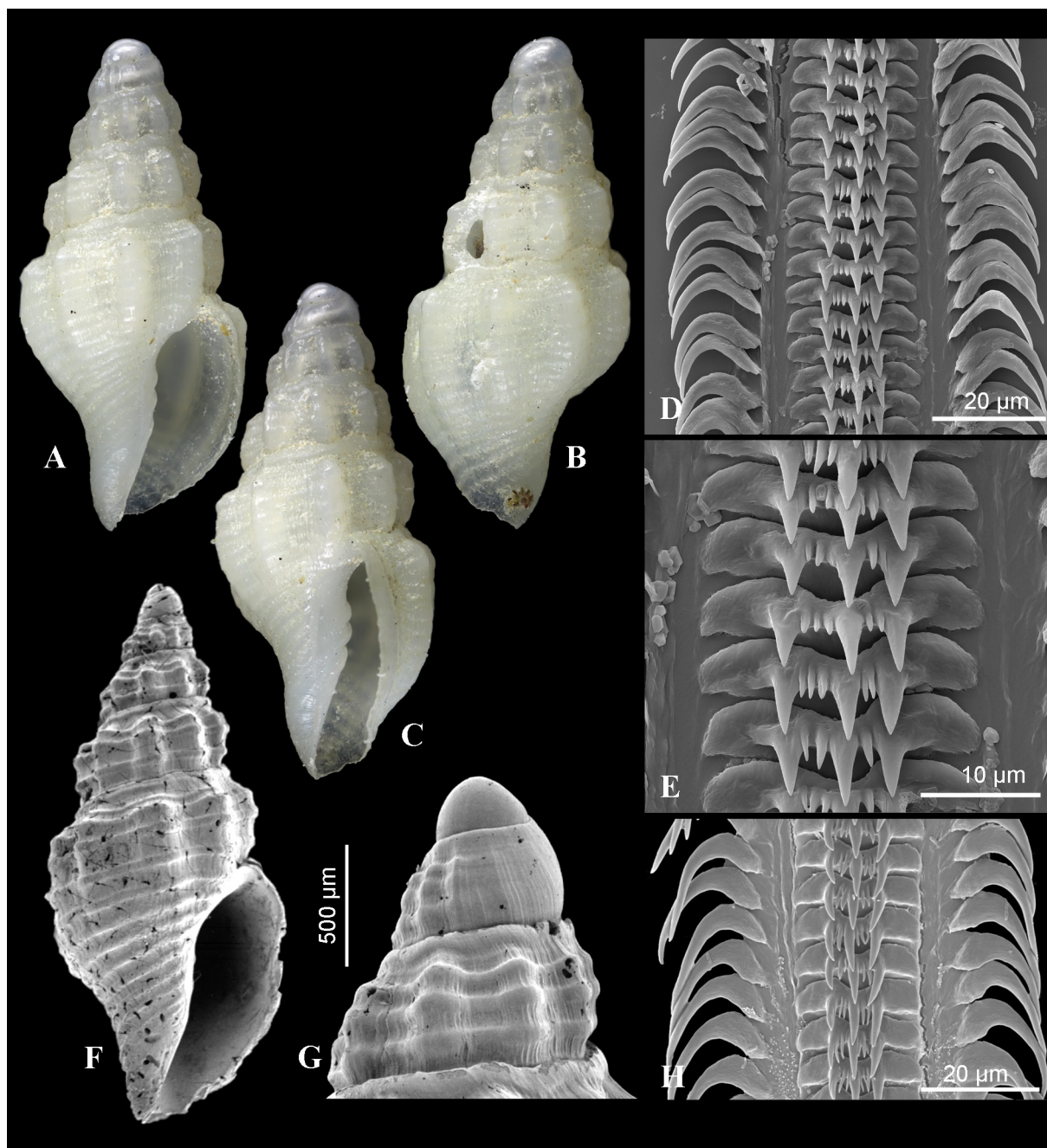


FIG. 3. **A–E.** *Egestas caledoniensis* sp. nov., holotype. **A–C** – shell, SL 4.8 mm; **D–E** – radula. **F–H.** *Egestas waitei* Suter, 1909, Te Papa Tongarewa, SL 6.8 mm. **G** – protoconch; **H** – radula.

narrow, broadening quickly, spanning about 4/5 of mantle length, of low, triangular lamellae.

Proboscis medium-long (Fig. 4 F–G), cylindrical, sharply narrowing towards the tip. Mouth opening rounded, very small. Few thin proboscis retractors attached laterally to posterior rhynchodaeum (Fig. 4 F–G – prr). Odontophore basal, protruding backwards from retracted proboscis. Medium-sized acinous salivary glands, oval in outline, right one covering relatively very large pyriform valve of Leiblein. Size of valve of Leiblein similar to the salivary gland. Powerful odontophore retractors passing through

the nerve ring. Gland of Leiblein medium-sized, compact, light-brown, coiled.

Radula (Fig. 4 H–I) long, comprising about 90 rows of teeth, 20 nascent. Lateral teeth leaf-shaped, concave posteriorly and convex anteriorly, with attenuated curved cusp directed from the center of the radula. Central teeth with three large cusps, central shortest, separated by distinct rather deep grooves.

Remarks. The genus *Jaspidella* was assessed with molecular approach for the first time by Fedosov *et al.* [2026] and formed either a sister group to *Calyptoliva* Kantor et Bouchet, 2007 (IQ-PMSF

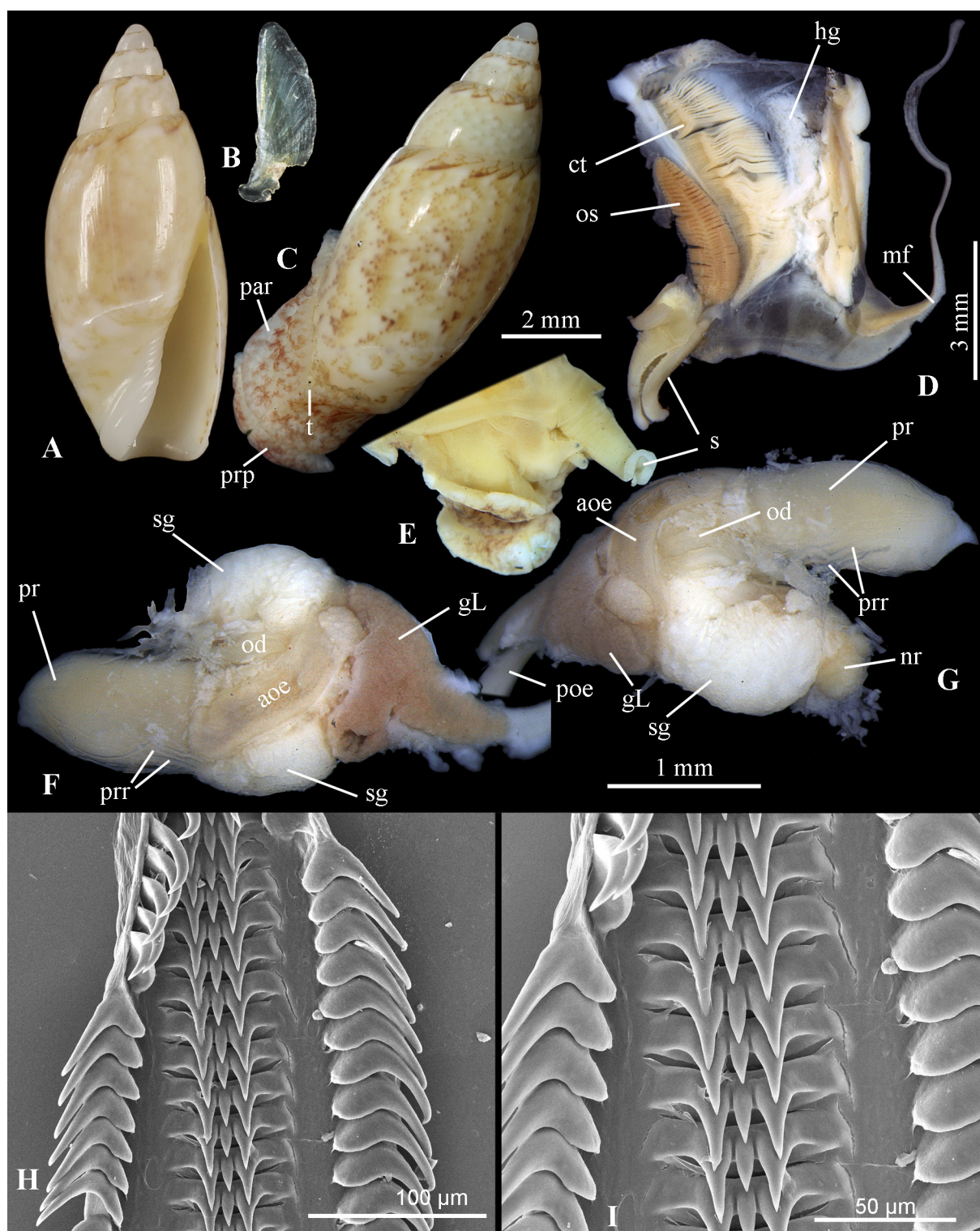


FIG. 4. *Jaspidella jaspidea* (Gmelin, 1791). A–C. MNHN-IM-2013-72858; A. Shell, SL 15.9 mm; B. Operculum; C. Living animal. D. Mantle. E. Anterior view of head and siphon. F–G. Anterior foregut, F, from dorsal side; G, from the right side. H–I. Radula. A–B at the same scale. Abbreviations: aoe – anterior oesophagus; ct – ctenidium; hg – hypobranchial gland; mf – mantle filament; nr – circumoesophageal nerve ring; od – odontophore; os – osphradium; par – parapodia; poe – posterior oesophagus; pr – proboscis; prp – propodium; prr – proboscis retractors; s – siphon; sg – salivary gland; t – head tentacle with eye.

analysis), or a separate deep lineage within Olivoidae (CAT-PMSF analysis) (Fig. 1 B). The anatomy (except the central tooth of the radula illustrated by line drawing by Olsson, 1956 – fig. 10) is described

herein for the first time. It differs from *Calyptoliva* in having a channelled suture of the shell and, correspondingly, in the presence of a mantle filament (Fig. 3D). These characters preclude including the genus

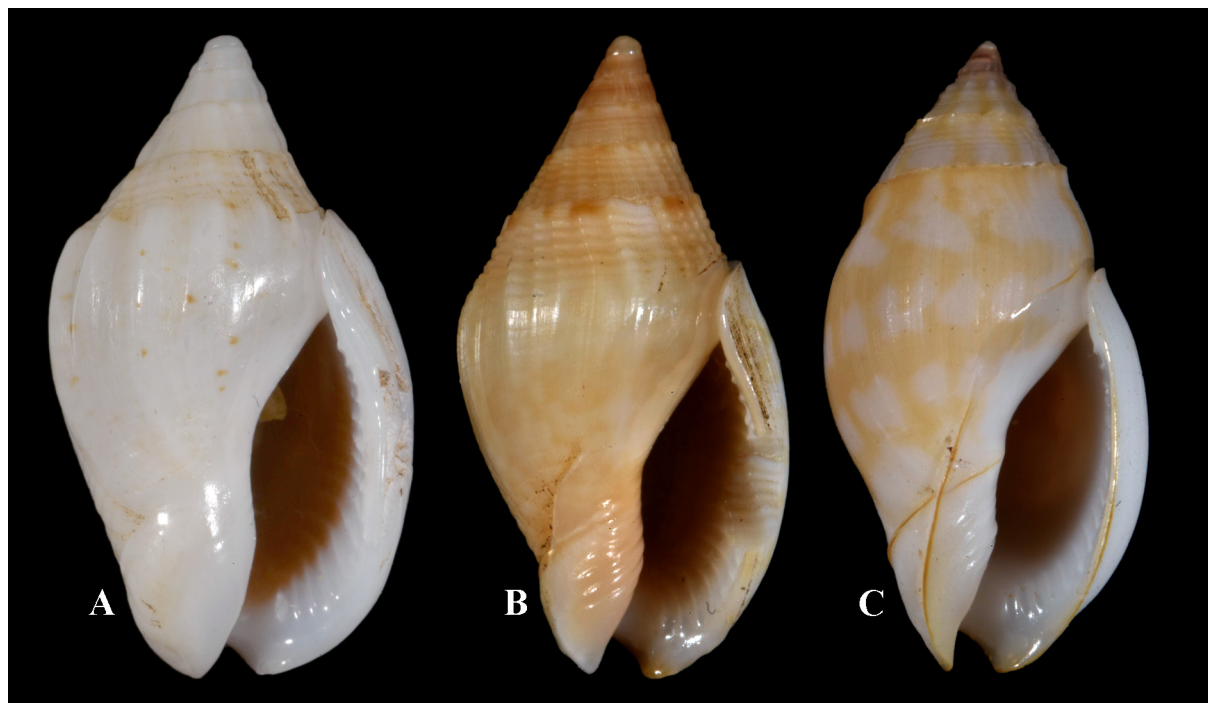


FIG. 5. **A.** *Cyllene lamarcki* Cernohorsky, 1975, MNHN-IM-2009-23725, Congo, Pointe-Noire, SL 14.7 mm. **B.** *Cyllene parvula* Bozzetti, 2004, MNHN-IM-2009-12763, South Madagascar, Lavanono, SL 11.8 mm. **C.** *Cyllene pulchella* A. Adams et Reeve, 1850, MNHN-IM-2013-58985, Papua New Guinea, New Ireland, SL 13.5 mm.

in Calyptolivinae, contrary to what is suggested by the IQ-PMSF analysis. The radula of *J. jaspidea* (Fig. 3 H–I) is most similar to that of Olivinae (see, e.g., Kantor *et al.* [2017]). The species possesses a large but thin chitinous operculum, a character shared with Calyptolivinae and Olivellinae, but not with Olivinae, Agaroniinae, and *Olivancillaria* d'Orbigny, 1841. Thus, the position of the genus remains uncertain. Previously it had been conditionally attributed to Belloliviidae [Kantor *et al.*, 2017], however, our recent analyses place it in Olividae, and it may represent a subfamily on its own. Due to both the very limited available material on *Jaspidella* and the fact that some genera of Olividae remain unstudied from either molecular or anatomical perspectives, despite they may belong to the same clade, we presently leave *Jaspidella* in Olividae *incertae sedis*.

Superfamily Buccinoidea Rafinesque, 1815
Family Cyllenidae Bellardi, 1882

Cyllene Gray, 1834
(Figs 1C, 5, 6)

Type species: *Cyllene owenii* J.E. Gray, 1834; by monotypy.

Material examined. *Cyllene lamarcki* Cernohorsky, 1975, MNHN-IM-2009-23725, Congo, Pointe-Noire, 4°43.0'S, 11°48.9' E, 8–9 m, Port ZANAGA, stn DW516 – exon-capture sequenced, radula examined; MNHN-IM-2009-21661, Mauritania, 8°18'N, 16°10'W, 0–13 m, N'DIAGO 1981, stn 147, 30.10.1981.

Cyllene parvula Bozzetti, 2004, MNHN-IM-2009-12763, South Madagascar, Lavanono, 25°26.9' S, 44°55.4' E, 24 m, ATIMO VATAE, stn BP09, 11.8 mm – radula examined.

Cyllene pulchella A. Adams et Reeve, 1850, MNHN-IM-2013-58985, Papua New Guinea, New Ireland, 2°25.4' 'S, 149°57.6' 'E, 112–140 m, KAVIENG 2014, stn DW4492 – radula examined.

Radula. Radulae morphologically rather similar in the three species examined. Radula long, comprising 75–90 transverse rows of teeth. Central tooth broad, with arcuate base and numerous (11–15) major cusps on posterior edge, increasing in length towards the central part and with indistinct serration laterally of the outer major cusp. Lateral teeth bicuspid, with large, strongly curved, outer cusp and very short, triangular inner one (Fig. 6 C). Outer cusp with a rather deep and narrow furrow running along its edge from the base to nearly the tip, producing a gutter-like structure; furrow ending short to the pointed tip (Fig. 6D). In *Cyllene pulchella*, outer cusps with a “blade” at least on the inner side, a low sharp fold spanning about 1/3 of the cusp length (Fig. 6F, white arrow). Radular membrane forming a crest between central and lateral teeth, tightly adhering to the low part of the inner side of lateral teeth, usually completely covering the inner cusp and adjacent parts of the tooth (Fig. 6F, black arrow).

Discussion. *Cyllene* forms a lineage sister to Chauvetiidae in the exon-capture based analysis, with maximal support in the CAT-PMSF analysis [Fedosov *et al.*, 2026]. However, the radulae are fundamentally different in the two groups, justify-

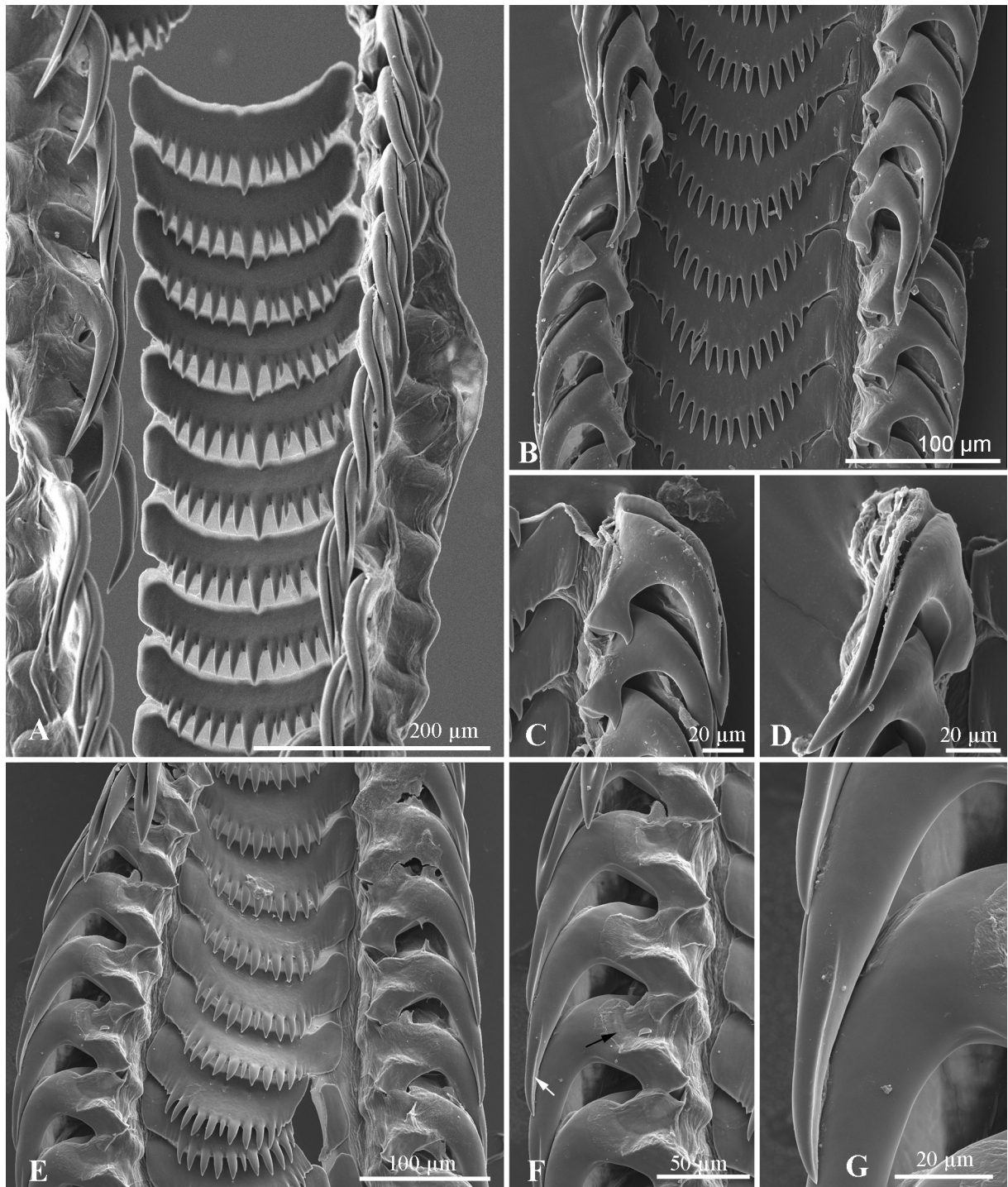


FIG. 6. Radula of *Cyllene* spp. **A.** *Cyllene lamarcki*, MNHN-IM-2009-23725 (shell on Fig. 5A). **B–D.** *Cyllene parvula*, MNHN-IM-2009-12763, shell on Fig. 5B. **E–G.** *Cyllene pulchella*, MNHN-IM-2013-58985, shell on Fig. 5C.

ing the placement of *Cyllene* to a family of its own, whereas it was previously ranked as a subfamily of Nassariidae [e.g. Cernohorsky, 1984; Kantor *et al.*, 2022].

The radula morphology is unique in at least two characters. First, the presence (at least in *Cyllene pulchella*) of a furrow and a blade on the outer cusps of the lateral teeth. A similar “gutter-shaped” morphology of the teeth is found in some Conoidea (e.g. in some *Xenuroturris* Iredale, 1929, Turridae

– Kantor *et al.*, 2024, fig. 9C; *Mangelia powisiana* (Dautzenberg, 1887), Mangeliidae – Bouchet *et al.*, 2011, fig. 8G, and *Ptychobela suturalis* (Gray, 1838), Pseudomelatomidae – Bouchet *et al.*, 2011, fig. 16D) and supposed to facilitate delivery into the prey of the toxins produced by the venom gland. The presence of a similar gutter in *Cyllene* suggests that it may also be used for injecting toxins into a prey, although in a way fundamentally different from Conoidea. In the latter, marginal teeth are dislodged from the

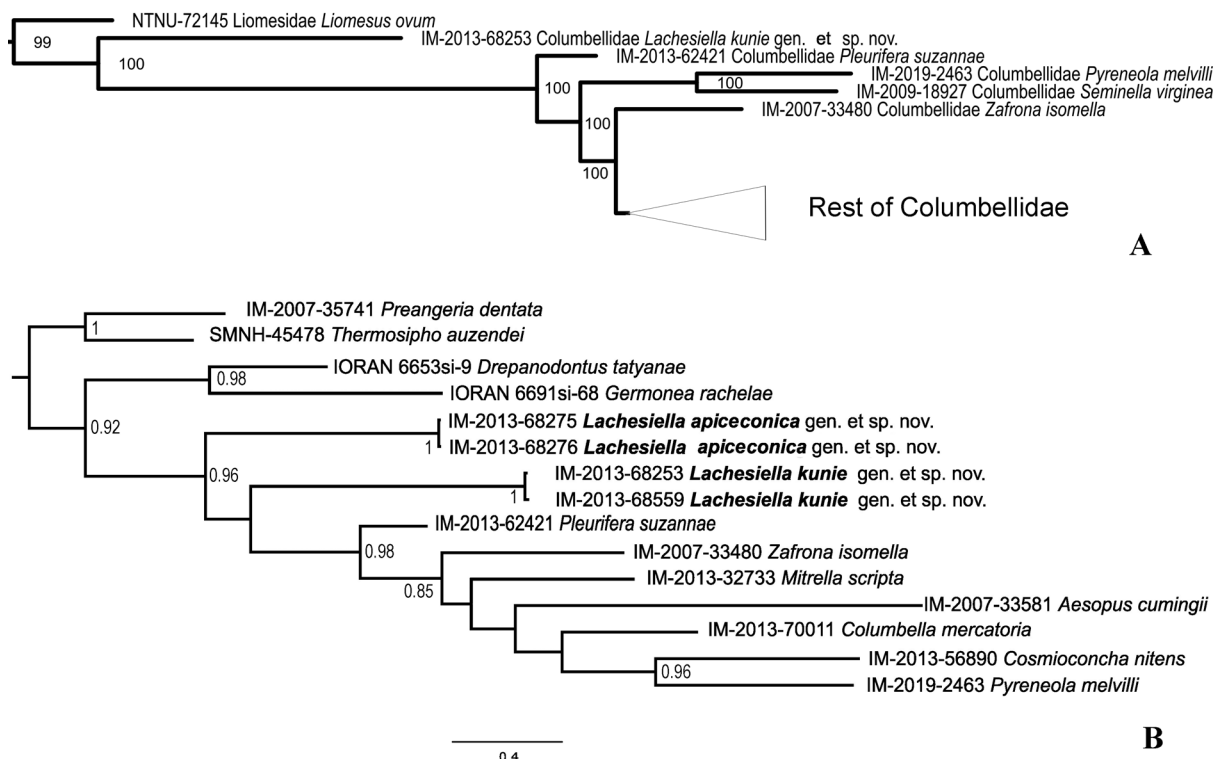


FIG. 7. **A.** Partial CAT-PMSF exon-capture tree depicting Columbellidae and *Lachesiella* gen. nov. [after Fedosov *et al.*, 2026]. **B.** *Cox1* based Bayesian tree depicting position of *Lachesiella* spp. in relation to other Columbellidae. Posterior probability nodal support is shown for values >0.85.

membrane, transferred to the tip of the proboscis and used one-at-a-time for wounding the prey and injecting the toxin. In *Cyllene*, the teeth obviously remain attached to the robust membrane and the injection may occur at the working surface (bending plane) of the radula. The unique crest of the membrane may seal the spaces between teeth thus preventing the diffusion of the toxins between teeth. This hypothesis would explain this remarkable case of convergence, but it needs confirmation since neither diet nor feeding mechanism have been described in Cyllenidae.

Family Columbellidae Swainson, 1840 *Lachesiella* gen. nov.

Zoobank registration: urn:lsid:zoobank.org:act:73172941-B90F-49C9-9749-67A5B2F03378

Type species: *Lachesiella kunie* sp. nov. (here designated).

Diagnosis: Shell small, up to 7.5 mm in length, relatively narrow, bucciniform, with cancellate sculpture of distinct spiral cords and weak axial ribs forming nodules of varying development at intersections. Protoconch with numerous, closely-set, axial ribs and a very small micro-shagreened nucleus lacking ribs.

Etymology: The genus name reflects its similarity to *Chauvetia* Monterosato, 1884 (Chauvetiidae), of which *Lachesis* Risso, 1826 is an invalid senior synonym.

Remarks: Currently, the genus *Lachesiella* contains two species from New Caledonia. Only one specimen of the type species was included in the exon-capture-based phylogeny, where it forms a very long branch, sister to all remaining Columbellidae with maximal support [Fedosov *et al.*, 2026] (Fig. 7A). A typical columbellid radula (Fig. 8 F–G) confirms placement of the genus in Columbellidae.

The genus is markedly distinct from all other Columbellidae in having a unique protoconch densely covered with axial ribs, whereas in other columbellids it is smooth. A similar protoconch is found in the genus *Falsitromina* Dell, 1990 (family Prosiphonidae), which is not closely related to Columbellidae. We therefore consider this similarity to be a convergence.

In general shell shape and sculpture, there is some resemblance to species of *Chauvetia* from the Atlantic. However, the latter can be immediately distinguished by protoconch morphology (protoconchs of several species are illustrated by Gofas and Oliver [2010]), which has a smooth, large nucleus and far fewer, stronger, and more widely spaced axial ribs. Additionally, the two genera differ markedly in radula morphology.

The family Columbellidae is an extremely diverse of Buccinoidea, with nearly 80 accepted Recent genera. At least two subfamilies have been proposed: Co-

lumbellinae Swainson, 1840 and Atiliinae Cossmann, 1901 (= Pyrenidae Suter, 1909; = Anachidae Golikov et Starobogatov, 1972). However, a recent molecular multilocus phylogeny of the family, analyzing 70 species from 31 genera [deMaintenon, Strong, 2022], did not support the separation of these subfamilies. The newly obtained phylogeny of Neogastropoda [Fedosov *et al.*, 2026] suggests that this new genus may constitute its own subfamily, but we refrain from formal description pending additional data on columbellid phylogeny in general.

***Lachesiella kunie* sp. nov.**

(Figs 7, 8, 10 A–B)

Zoobank registration: urn:lsid:zoobank.org:act:FF0DBC71-D0CB-4529-A58B-0FC64A670A3F

Holotype (sequenced for exon-capture): MNHN-IM-2013-68253.

Type locality. Southern New Caledonia, SW off Ile des Pins, 22°48'S, 167°7'E, 405–410 m [KANACONO, stn DW4661].

Other material:

SOUTHERN NEW CALEDONIA, SW off Ile des Pins, 22°48'S, 167°07'E, 405–410 m, KANACONO, stn DW4661 (1 lv – MNHN-IM-2013-68559, sequenced, SW off Ile des Pins, 22°49'S, 167°14'E, 410–440 m, KANACONO, stn DW4662 (1 lv – MNHN-IM-2013-68410); SW off Ile des Pins, 22°51'S, 167°15'E, 440–482 m, KANACONO, stn DW4663 (1 lv – MNHN-IM-2013-68336 – radula voucher); SW off Ile des Pins, 22°49'S, 167°25'E, 394–443 m, KANACONO, stn DW4714 (1 lv – MNHN-IM-2013-68296).

SOUTHERN NEW CALEDONIA, Norfolk Ridge, Eponge Bank, 24°55'S, 168°22'E, 508–532 m, SMIB 8, stn DW146-147 (ca 150 dd and lv); Norfolk Ridge, Stylaster Bank, 23°38'S, 167°43'E, 433–450 m, SMIB 8, stn DW166 (1 dd); Norfolk Ridge, Stylaster Bank, 23°38'S, 167°43'E, 430–452 m, SMIB 8, stn DW167 (9 dd); Norfolk Ridge, Stylaster Bank, 23°37'S, 167°42'E, 447–450 m, SMIB 8, stn DW169 (3 dd); Norfolk Ridge, Azteque Bank, 23°18'S, 168°05'E, 305–310 m, SMIB 8, stn DW190 (4 dd); Norfolk Ridge, Eponge Bank, 24°55'S, 168°22'E, 508–541 m, NORFOLK 1, stn. DW1684 (9 dd); Norfolk Ridge, Bank P, 23°17'S, 168°14'E, 190–212 m, NORFOLK 1, stn. DW1727 (8 dd). Norfolk Ridge, 24°53'S, 168°21'E, 565–600 m, BERYX 11, stn. DW10 (3 dd). Norfolk Ridge, 23°44'S, 168°16'E, 394–401 m, BATHUS 3, stn. DW818 (12 dd). SW off Ile des Pins, 22°47'S, 167°14'E, 440–450 m, BIOCAL, stn DW44 (118 dd).

Description (holotype). Shell small, bucciniform, with medium-tall spire and short siphonal canal. Shell comprising nearly 3 teleoconch and 1.75 protoconch whorls. Protoconch medium-high, dome-shaped, diameter about 0.8 mm, with distinctly micro-shagreened nucleus of about ½ whorl; later whorls sculptured with about 45 narrow, very distinct and closely spaced, orthocone axial ribs. Protoconch-teleoconch transition very distinct, marked by change in sculpture pattern. Axial sculpture on teleoconch whorls weak, of obtuse and low, regularly spaced, orthocone ribs disappearing below periphery on last whorl, 17 on last whorl. Spiral sculpture distinct,

of subequal cords, covering whole whorl height, including canal. Four cords on adapical whorls, adapicalmost immediately subsutural, smooth, lower three cords weakly crenulate at intersections with ribs. Last whorl with 11 cords, of which 10 on shell base and canal, gradually reduced in size, and lacking nodules. Intervals about twice as wide as cords.

Aperture low, subovate, columella bent at mid-height, smooth with very narrow callus, extending also to parietal wall. Outer lip simple.

Holotype SL 3.3 mm.

Operculum (not available in holotype, observed in other specimens) medium-sized, spanning about 1/2 of aperture, suboval, with terminal nucleus, lower narrower part of operculum clearly shifted adaxially.

Radula (Fig. 8 F–G) (MNHN-IM-2013-68336) very long, comprising about 120 transverse rows of teeth, 1.56 mm in length (130% of AL), narrow, typical for Columbellidae. Central tooth acusate, subrectangular, lateral teeth with narrow base, with large protruding basal secondary cusp (Fig. 8F, bsc) and distal secondary cusp (Fig. 8F, dsc), slightly smaller than the distal cusp (Fig. 8F, dc).

Etymology. The species is named after the type locality, Kunié – Ile des Pins in the local Kanak language. Used as noun in apposition.

Remarks. The species is quite variable, primarily in the prominence of the axial ribs, which range from very weak (resembling thickened growth lines) to distinct, becoming the dominant sculptural element. There is also variation in the development of nodules on the spiral cords, which can be weak to nearly obsolete (e.g., MNHN-IM-2013-68296). The species reaches up to 5 mm in shell length (SL), comprising approximately 3.5 teleoconch whorls. In both shell and protoconch morphology, this species is distinct from Columbellidae species in other genera, and no closely comparable species is known.

Lachesiella kunie sp. nov. is quite similar to *L. apiceconica* sp. nov., in shell characters and particularly in protoconch morphology: see under the Remarks section of the next species for diagnostic details.

***Lachesiella apiceconica* sp. nov.**

(Figs 7B, 9, 10 C–D)

Zoobank registration: urn:lsid:zoobank.org:act:ACE123F6-D898-4FDA-BFB8-FA694E8E4155

Holotype (sequenced for *cox1*), MNHN-IM-2013-68276, adult male.

Type locality. Southern New Caledonia. SW off Ile des Pins, 22°48'S, 167°15'E, 449–465 m [KANACONO, stn. DW4697].

Material examined (sequenced for *cox1*)

Southern New Caledonia. SW off Ile des Pins, 22°48'S, 167°15'E, 449–465 m, KANACONO, stn. DW4697, MNHN-IM-2013-68275.

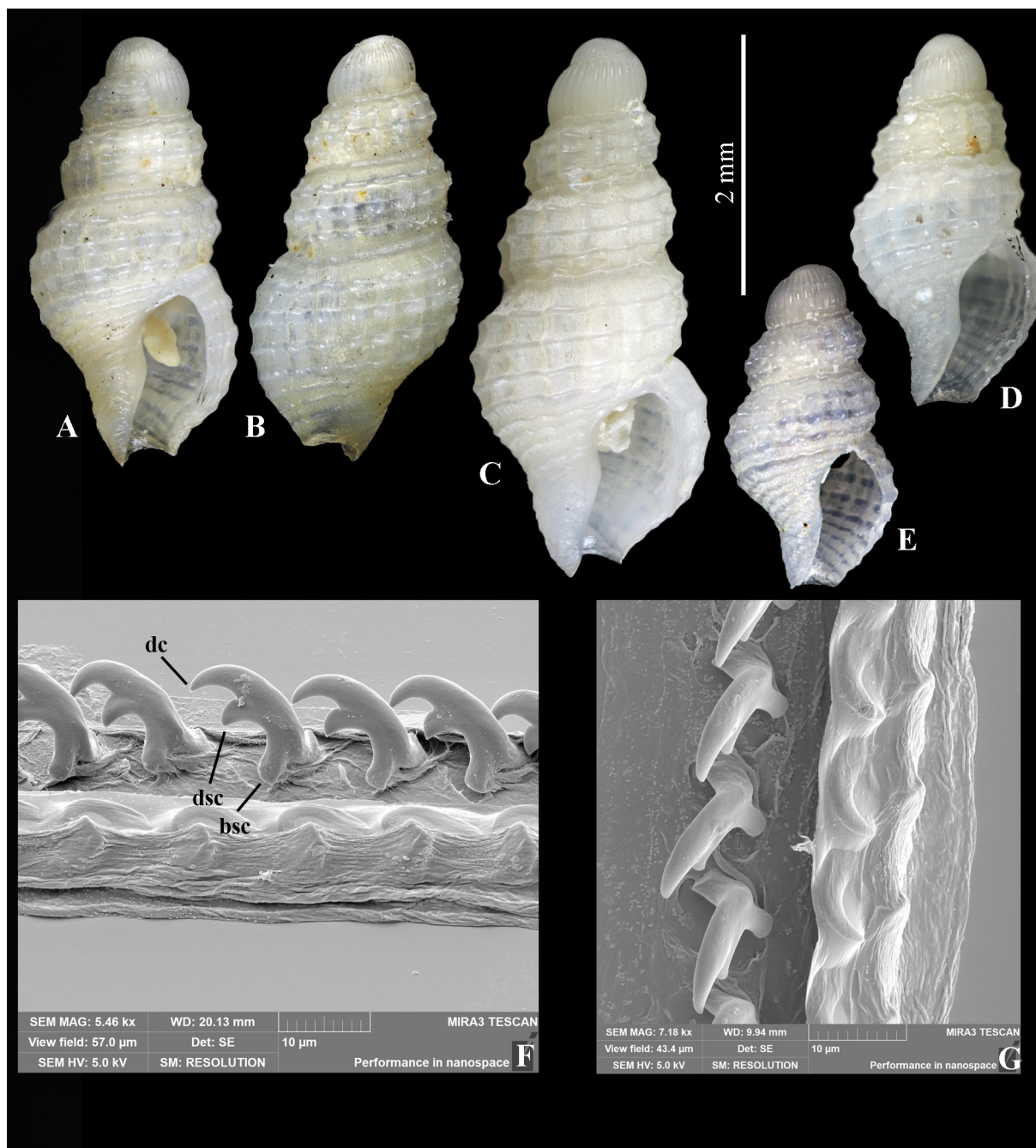


FIG 8. *Lachesiella kunie* sp. nov. A–B. Holotype, MNHN-IM-2013-68253, SL 3.3 mm. C. MNHN-IM-2013-68296, southern New Caledonia, SL 4.2 mm. D. MNHN-IM-2013-68336, SL 2.9 mm (radula voucher). E. MNHN-IM-2013-68559, SL 2.5 mm (sequenced spm). F–G. Radula of MNHN-IM-2013-68336; F – lateral view of the radula membrane; G – apical view. Shells at the same scale. Abbreviations on Fig. 8F: bsc – basal secondary cusp; dc – the distal cusp; dsc – distal secondary cusp.

Other material (not sequenced). Southern New Caledonia. SW off Ile des Pins, 23°10'S, 167°10'E, 675–680 m, BIOCAL, stn DW33 (2 dd). SW off Ile des Pins, 22°54'S, 167°17'E, 525–574 m, BATHUS 2, stn DW721 (20 dd). Ile des Pins, 23°09'S, 167°27'E, 1004–1009 m, NORFOLK 2, stn DW2144 (9 dd).

Northern New Caledonia. 18°49'S, 163°15'E, 600–615 m, BATHUS 4, stn DW914 (29 dd).

Description (holotype). Shell small, bucciniform, with tall spire and short siphonal canal. Shell com-

prising 4.25 teleoconch and 2.2 protoconch whorls. Protoconch medium-high, pointed, diameter about 0.75 mm. Protoconch distinctly micro-shagreened, sculptured with narrow, very distinct and closely spaced, orthocline axial ribs. Nucleus of about ½ whorl lacks axial ribs, protoconch II with about 55 ribs in total. Protoconch-teleoconch transition very distinct, marked by change in sculpture pattern. Axial sculpture on teleoconch whorls distinct, of obtuse and low, regularly spaced, orthocline ribs, disap-

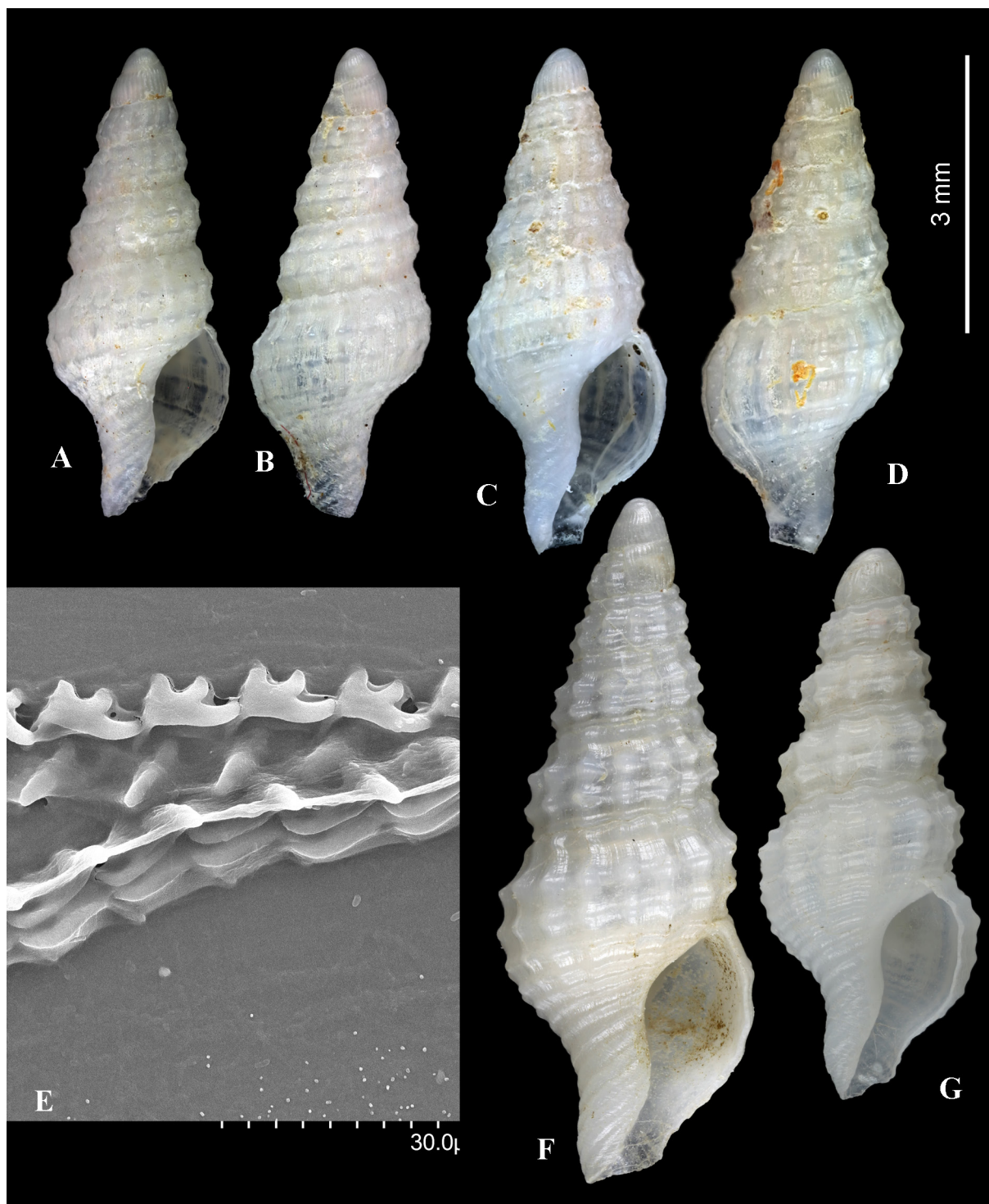


FIG. 9. *Lachesiella apiceconica* sp. nov. A–B. Holotype, MNHN-IM-2013-68276, SL 5.1 mm. C–D. Southern New Caledonia, MNHN-IM-2013-68275, SL 5.5 mm (sequenced spm). E. Radula of holotype. F. Southern New Caledonia, BIOCAL, stn DW33, SL 7.4 mm. G. Northern New Caledonia, BATHUS 4, stn DW914, SL 6.0 mm. Shells at the same scale.

pearing below periphery on last whorl, 18 on last whorl. Spiral sculpture of distinct, subequal cords, covering entire shell, including canal but absent on initial part of first teleoconch whorl. Three cords on adapical whorls, uppermost immediately subsutural. Last whorl with 15 cords, four adapical ones more pronounced and having distinct, rounded nodules at intersections with axial ribs. Intervals between cords

exceed cords width nearly three times on subsutural ramp and periphery, on shell base intervals gradually narrowing towards canal tip and on canal narrower than cords' width.

Aperture low, subovate, columella bent at its mid-height, smooth with very narrow callus, extending also to parietal wall. Outer lip simple.

Holotype SL 5.1 mm.

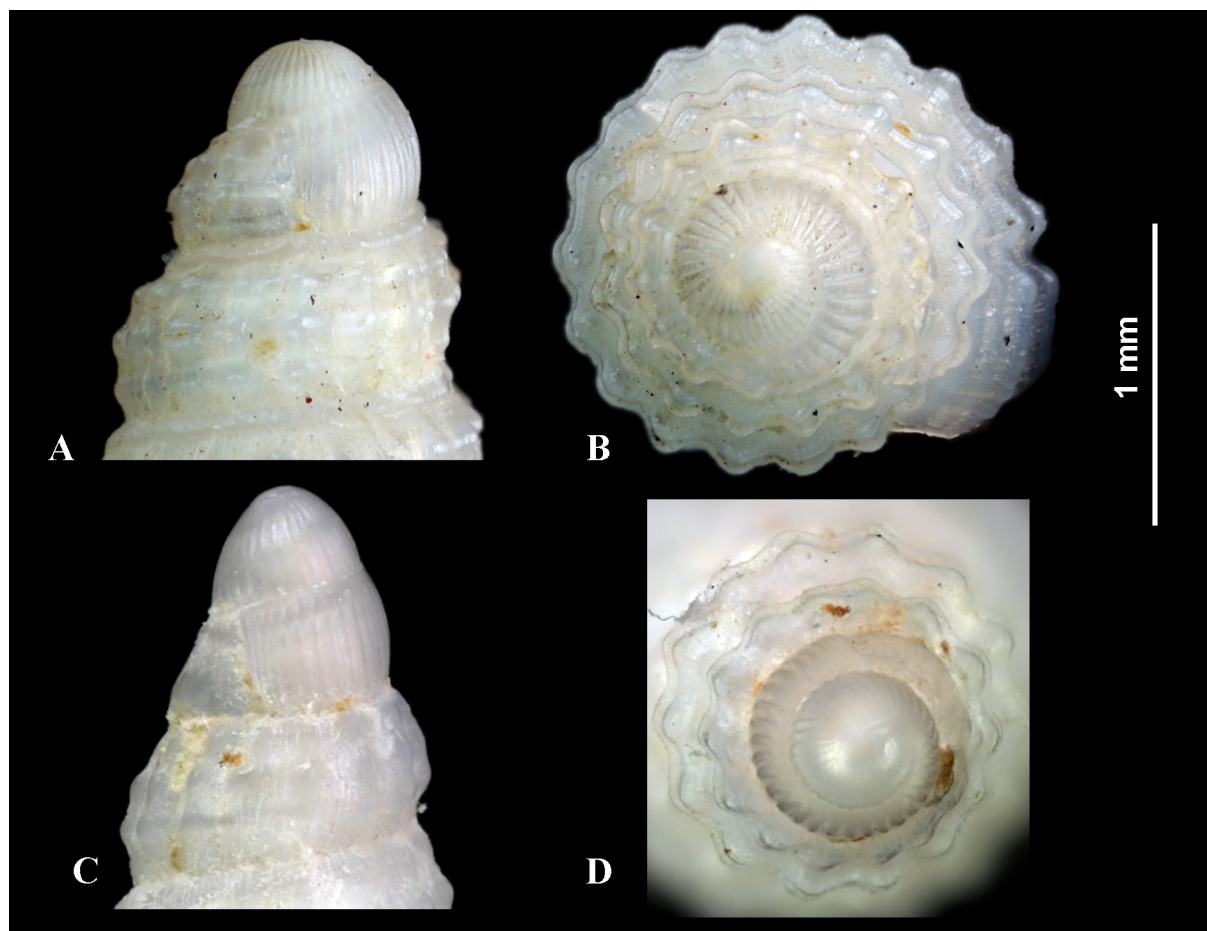


FIG. 10. Comparison of protoconchs of *Lachesiella* spp. A–B. *Lachesiella kunie* sp. nov., holotype, MNHN-IM-2013-68253. C–D. *Lachesiella apiceconica* sp. nov., holotype, MNHN-IM-2013-68276.

Operculum large, oval, transparent, yellowish, with terminal nucleus slightly shifted adaxially.

Radula (MNHN-IM-2013-68275) narrow, but very long, comprising about 90 transverse rows of teeth, about 0.94 mm in length (55% of AL), typical for Columbellidae. Central tooth an acusate subrectangular plate, lateral teeth with narrow base, large protruding basal secondary cusp and distal secondary cusp slightly smaller than the distal cusp.

Etymology: the species epithet is formed by combining *apex* (top) and the adjective *conic-us*, *-a*, *-um*, by reference to the conical shape of the protoconch.

Remarks. *Lachesiella apiceconica* sp. nov. is quite similar in shell characters, and particularly in protoconch morphology, to *L. kunie* sp. nov. It differs in the shape of the protoconch (Fig. 10), which is clearly conical, bullet-shaped of more than 2 whorls in *L. apiceconica* sp. nov., dome-shaped, vs of about 1.75 whorls in *L. kunie* sp. nov. *L. kunie* sp. nov. is also smaller (up to 5 mm in SL vs 7.5 mm in *L. apiceconica* sp. nov. and has a stouter shell with a shorter siphonal canal.

Two specimens were sequenced for partial *cox1* gene. In the *cox1* based tree they do not cluster with *L. kunie* sp. nov. (Fig 7B), but constitute a long

branch, sister to a clade including *L. kunie* sp. nov. and the rest of the Columbellidae, without statistically significant nodal support. This is questioning the congenericity of the two species, which share shell and protoconch characters unique for Columbellidae. Due to the limited sequenced material and a single genetic marker, we presently attribute *apiceconica* to *Lachesiella* with some reservation.

Most of the specimens of *L. apiceconica* sp. nov. were collected off Ile des Pins, where it is sympatric (albeit not syntopic) with *L. kunie* sp. nov. Nevertheless, one very similar and probably conspecific sample was collected in northern New Caledonia (Fig. 9G).

Prosiphonidae A.W.B. Powell, 1951

Met euthria Thiele, 1912

Type species. *Euthria martensi* Strebel, 1905, by original designation.

Met euthria fallax (Thiele, 1925)
(Fig. 11)

Euthria ? *fallax* Thiele, 1925: 147 [181], pl. 20, fig. 5.

Met euthria (?) *fallax* – Kilburn *et al.*, 2010: 45, text figs (syntype illustrated).



FIG. 11. *Meteuthria fallax* (Thiele, 1925), MNHN-IM-2009-6217.

Type material: 6 syntypes ZMHB, Agulhas Bank: off Cape Agulhas, 126 m, 35°19'S, 20°12'E, *Valdivia*, stn 109; S of Cape Point, 2750 m, 35°32,8'S, 18°20,1'E, *Valdivia*, stn 112.

Material examined (sequenced for *cox1*): MOZAMBIQUE CHANNEL, 25°58'S;34°47'E, 949-952 m, MAINBAZA, stn CC3170, 1 lv, MNHN-IM-2009-6217.

This species has never been collected since its original description. Due to this extreme rarity, and the very brief original description, we here provide a detailed re-description based on our specimen.

Description: Shell small, broad, stout, with low spire and short siphonal canal. Shell of 2.5 teleoconch whorls, distinctly angular on shoulder; shell base also distinctly angular at transition to siphonal canal. Protoconch of 2 whorls, first 1.25 whorl smooth, glossy, micro-shagreened, remaining part with narrow and closely spaced, thin and slightly prosocline, axial ribs, around 30 in total, each rib bearing a distinct protruding tubercle adapically. Protoconch-teleoconch transition indistinct, marked by appearance of definitive sculpture. Axial sculpture of strong, narrow, slightly sinuous ribs, rounded on top, 16 on last whorl, intervals twice as broad as ribs. Spiral sculpture of narrow, somewhat unevenly spaced, flattened cords, covering entire shell except siphonal canal, 8 on penultimate whorl and about 15 on last whorl. Aperture broad, oval, slightly constricted adapically. Shell uniformly off-white with slightly darker protoconch.

SL 5.0 mm.

Remarks. Our specimen is overall similar to Thiele's ones except for the angulation on shell base. This angulation may be the result of healed shell breakage. Our specimen is larger than those of Thiele (5 vs 3.5 mm).

Thiele [1925] was not able to find a radula in his live-collected specimen, and described an oval operculum, somewhat similar to that of *Pareuthria chlorotica* (von Martens, 1878). The drawing in Thiele [1925: pl. 35, fig. 25] is not clear and the operculum seems to have a subcentral nucleus.

Unfortunately, the body of our specimen was completely lysed for DNA extraction and neither radula, nor operculum were examined. Thus, the anatomical data cannot be used for attribution of the species to a particular genus. Molecular data also do not place it in any other Prosiphonidae genus sequenced to date. Therefore, the generic position of the species remains uncertain. Kilburn *et al.* [2010] placed it in *Meteuthria* with reservations. The type species of *Meteuthria*, *Euthria martensi*, is quite different in shell shape and sculpture, but has a more or less similar protoconch sculpture with numerous narrow axial cords [Pastorino, 2016: fig. 11 J-K]. We are not aware of any other Prosiphonidae genera where *M. fallax* could be placed based on its shell features. Therefore, pending additional data on anatomy, we retain it in *Meteuthria*.

Distribution. From Agulhas Bank, South Africa to Mozambique Channel, in 126-2750 m.

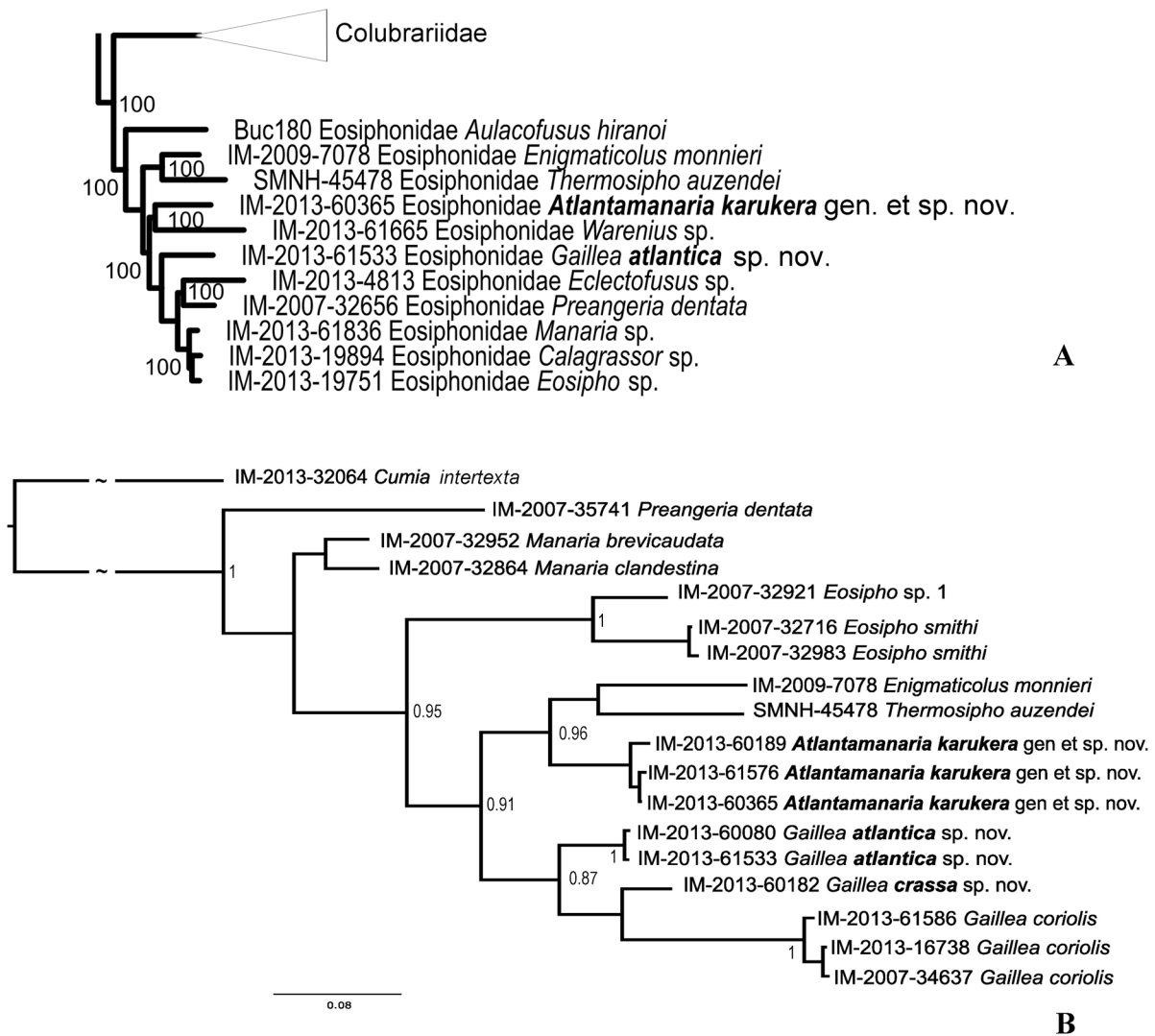


FIG. 12. **A.** Partial CAT-PMSF exon-capture tree depicting Eosiphonidae [after Fedosov *et al.*, 2026]. **B.** *coxI*-based Bayesian tree depicting selected Eosiphonidae. Posterior probability nodal support provided for values > 0.85.

Eosiphonidae Kantor, Fedosov, Kosyan,
Puillandre, Sorokin, Kano, R. Clark et
Bouchet, 2021

Atlantamanaria gen. nov.

Zoobank registration: urn:lsid:zoobank.org:act:
2735B012-36B7-4ED1-9D65-8C3F2071E0EB

Type species: *Atlantamanaria karukera* sp. nov.
(here designated).

Diagnosis: Shell medium-sized, reaching 35 mm in SL, fusiform, with high spire and medium-long siphonal canal. Axial sculpture strong, of broad axial folds. Spiral sculpture of distinct spiral cords covering entire shell surface.

Diagnosis (DNA) (3 spm): *Atlantamanaria* is unique among Eosiphonidae genera in having 'T' in the site 31, 'G' in the site 34, 'T' in the site 268, 'T' in the site 316 of the standard barcode fragment of *coxI*.

Etymology. While the genus is superficially very similar to *Manaria* E.A. Smith, 1906, the name

reflects its distribution in the Atlantic Ocean, while confirmed species of *Manaria* live in the Pacific.

Remarks. In shell characters *Atlantamanaria* is very similar to *Manaria* species and falls within the morphological range of the latter, as currently defined [Fraussen, Stahlschmidt, 2016]. Nevertheless, molecular trees based on both exon-capture and partial *coxI* sequences recover *Atlantamanaria* gen. nov. as a separate clade (Figs. 12 A–B). We identified 18 sites in the *coxI* alignment (available as a supplementary file), that are invariant in three sequenced specimens of *Atlantamanaria karukera*, and differentiate it from all species of *Manaria* for which DNA data was available (see supplementary data).

Fraussen and Stahlschmidt [2016] listed three species from the Atlantic Ocean that possibly belong to *Manaria*. One of them, *Eosipho atlanticus* Fraussen et Hadorn, 2005, is conchologically rather similar to *Atlantamanaria* and is probably conge-

neric (Fig. 13F). Two others, *Manaria burkeae* E. F. Garcia, 2008 and *Metula fusiformis* Clench et Aguayo, 1941 (= *Buccinofusus surinamensis* Okutani, 1982) are conchologically rather different from both *Manaria* and *Atlantamanaria* and probably belong to different genera.

***Atlantamanaria karukera* sp. nov.**

(Figs 12 A–B; 13 A–E)

Zoobank registration: urn:lsid:zoobank.org:act:82642370-CD2B-41B0-8723-361357CA5A65

Holotype (sequenced for *cox1*). MNHN-IM-2013-61576.

Type locality. GUADELOUPE, W of Marie-Galante, 16°3'N, 61°28'W, 368–388 m [KARUBENTHOS 2, stn CP4548].

Other material (all sequenced)

GUADELOUPE, N of Grande-Terre, 16°29'N, 61°42'W, 500–550 m, KARUBENTHOS 2, stn CP4524, 1 lv, MNHN-IM-2013-60189 (sequenced for *cox1*).; N of Grande-Terre, 16°40'N, 61°34'W, 385–399 m, KARUBENTHOS 2, stn CP4543, 1 lv, MNHN-IM-2013-60365 (sequenced for exon-capture and *cox1*).

Description (holotype). Shell up to 20 mm in SL, fusiform. Whorls convex, siphonal canal medium-long, slightly inclined adaxially. Suture distinct, impressed. Protoconch eroded, rendering whorl count impossible; better preserved protoconch in MNHN-IM-2013-60365 paucispiral, of about 1.75 seemingly smooth whorls. Protoconch-teleoconch transition marked by appearance of the definitive sculpture. Teleoconch of 6.25 convex whorls. Axial sculpture well-developed, of strong, broad, nearly orthocline, ribs with intervals equal or narrower than rib width. Ribs spanning suture to suture on spire whorls, fading on transition to shell base. First intact teleoconch whorl with 10 ribs, penultimate with 11, last with 10 ribs. Spiral sculpture well-developed, of distinct, subequal, rounded cords. Cords of even width on adapical teleoconch whorls, on penultimate and last whorl adapicalmost 3–4 cords slightly narrower than others. On last whorl additional smaller cordlets appearing on whorl periphery between some of the primary cords. On antepenultimate whorl 8 cords in total, on penultimate 10. Last whorl with 30 cords, 15 of which more closely spaced on shell base and canal.

Aperture ovate, slightly constricted adapically, lirate inside. Columella smooth, with narrow callus extending to parietal whorl. Outer lip thin; edge sharp, with 12 internal lirae, corresponding to interspaces between spiral cords. Aperture gradually passing into narrow siphonal canal. Periostracum thin, smooth.

Operculum oval with eroded terminal nucleus.

Measurements (holotype is the largest specimen): SL 19.3 mm, BWL 3.3 mm, AL (without canal) 6.8 mm, SW 8.2 mm.

Anatomy and radula studied in one female speci-

men (MNHN-IM-2013-60189 – Fig. 13D). Head with long cylindrical tentacles and small but distinct eyes at their base on small lobes. Long cylindrical proboscis, partly everted, length about 5.5 mm. Proboscis sheath very thin, semitransparent with several flat retractors attached at posteriormost part on the sheath. Salivary glands paired, acinous, situated on both sides of the nerve ring. Right gland tightly adjoins anterior gland of Leiblein. Gland of Leiblein relatively large, light brownish, compact. Valve of Leiblein rather large, pear-shaped. Odontophore spanning about half of proboscis length.

Radula (Fig. 13E) of 80 transverse rows of teeth, around 2.4 mm in length (46% of AL), 150 µm in width (2.9% of AL). Lateral teeth bicuspid, central with three cusps nearly equal in size.

Etymology. The species is named after the type locality, Karukera – Guadeloupe in the indigenous Arawak language. Used as noun in apposition.

Remarks. *Atlantamanaria karukera* is most similar to *Eosipho atlanticus* Fraussen et Hadorn, 2005, also from Guadeloupe, differing in its smaller adult shell (19.3 vs 34.6 mm), more delicate sculpture with more numerous spiral cords (30 vs 19 on the last whorl), and less convex whorls. *Eosipho atlanticus* was conditionally transferred to *Manaria* by Fraussen and Stahlsmidt [2016]. Due to its general shell similarity to *Atlantamanaria karukera* we here transfer *Eosipho atlanticus* to the new genus as *Atlantamanaria atlantica* (Fraussen et Hadorn, 2005) comb. nov.

Gaillea Kantor, Puillandre, Fraussen,
Fedosov et Bouchet, 2013

Type species: *Eosipho coriolis* Bouchet et Warén, 1986 (OD)

***Gaillea atlantica* sp. nov.**
(Figs 12; 14 A–E)

Zoobank registration: urn:lsid:zoobank.org:act:A9617A10-DB4B-4B87-B1F1-1C7B416DE2B5

Holotype (sequenced for exon-capture and *cox1*). MNHN-IM-2013-61533.

Type locality. GUADELOUPE, S of Marie-Galante, 15°49'N, 61°6'W, 835–898 m [KARUBENTHOS 2, stn CP4644].

Other material

GUADELOUPE, W of Grande-Terre, 16°13'N, 61°54'W, 406–644 m, KARUBENTHOS 2, stn CP4513, 1 lv, MNHN-IM-2013-60080 (sequenced for *cox1*), 1 lv, MNHN-IM-2013-60090 (non-sequenced). E of La Désirade, 16°14'N, 60°49'W, 618–632 m, KARUBENTHOS 2, stn CP4608, 1 lv, MNHN-IM-2013-61128 (non-sequenced).

Description (holotype). Shell small for the genus, broadly fusiform, with medium-tall spire. Whorls convex, weakly angulated on shoulder, siphonal canal rather long, slightly inclined adaxially. Suture

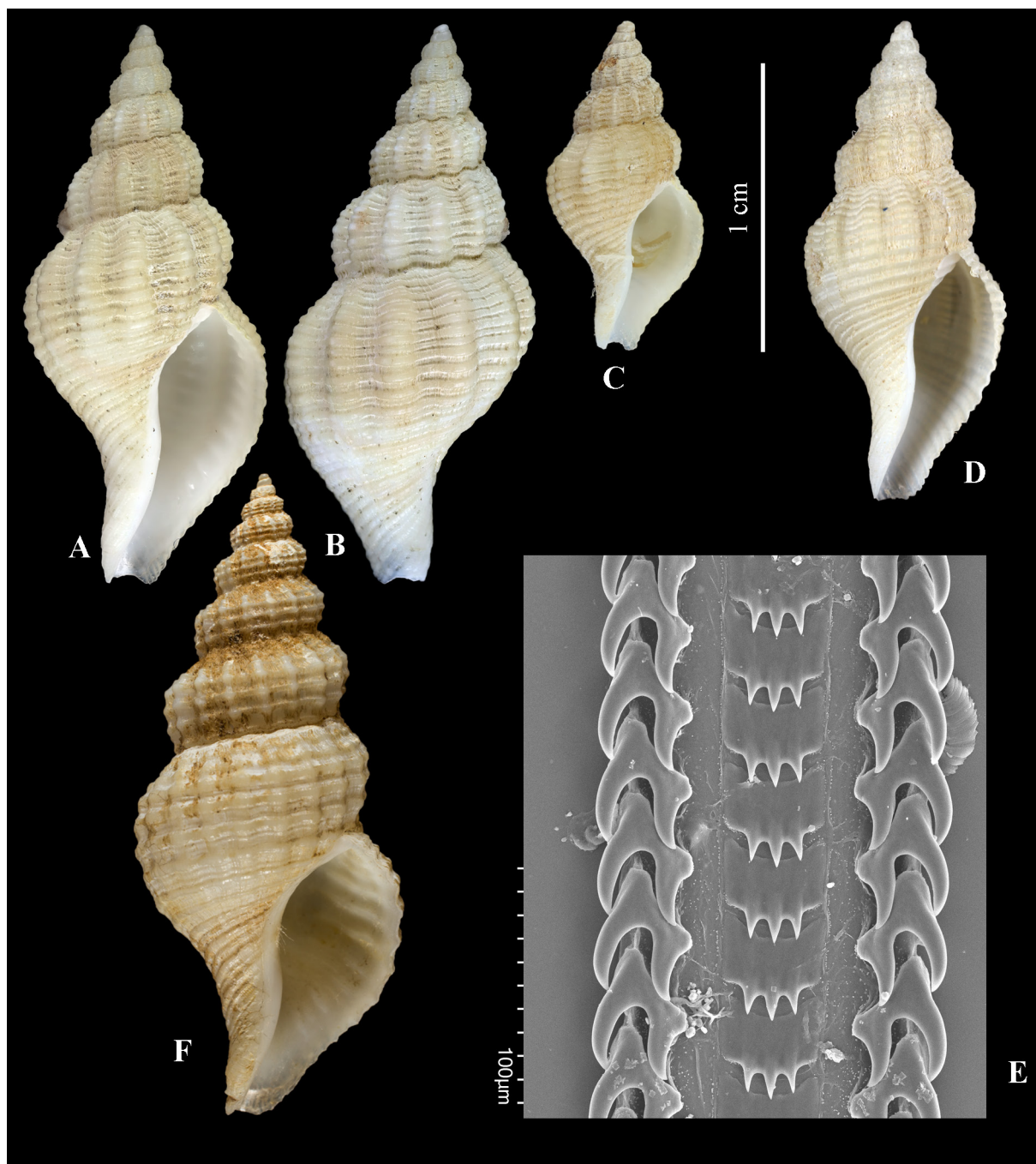


FIG. 13. A–E. *Atlantamanaria karukera* gen. et sp. nov., Guadeloupe. A–B. Holotype, MNHN-IM-2013-61576, SL 19.3 mm. C. MNHN-IM-2013-60365, SL 11.4 mm (sequenced for exon capture). D–E. MNHN-IM-2013-60189, SL 16.6 mm; E – radula. F. Holotype of *Eosipho atlanticus* Fraussen et Hadorn, 2005, MNHN-IM-2000-5996, SL 27.1 mm. A–D – at the same scale; E–F – reduced.

distinct, impressed. Protoconch eroded, rendering whorl count impossible. About 6 convex teleoconch whorls. Axial sculpture well-developed, of low but distinct, weakly prosocline, ribs present on all teleoconch whorls, with intervals equal or slightly broader than ribs width. Ribs spanning from suture to suture on spire whorls but weaker on subsutural ramp, fading below periphery on last whorl. First intact teleoconch whorl with 13 ribs, penultimate with 14, last with 16 ribs. Spiral sculpture of distinct,

well-developed cords, of uneven width, rounded on top; 5–6 narrow and weak, undulating cords on subsutural ramp; 5 stronger cords on periphery of last whorl, forming distinct nodules at intersection with axial ribs, with intervals 2–3 times cords width, 18 more closely spaced cords of uneven width on shell base and canal.

Aperture ovate, slightly constricted apically, with grooves inside, corresponding to spiral cords. Columella smooth, with narrow, rather thick callus

extending to parietal wall. Outer lip thin, edge sharp, Aperture gradually passing into narrow siphonal canal. Periostracum thin, forming closely spaced, axial lamellae with dense, short bristles.

Operculum yellowish, oval with terminal eroded nucleus in lower part shifted adaxially.

Measurements: SL 15.7 mm, AL (without canal) 6.5 mm, SW 7.4 mm.

Radula of MNHN-IM-2013-61128 was examined (Fig. 14 E). Lateral teeth bicuspid. Central teeth rather narrow, with nearly square base and three large cusps, central slightly longer than lateral ones.

Etymology: the specific epithet refers to the occurrence of the species in the Atlantic Ocean.

Remarks. *Gaillea atlantica* sp. nov. attains SL 20.6 mm (MNHN-IM-2013-60080, Fig. 14D). The other specimens examined are very similar to the holotype.

This species and *G. crassa* are the first molecularly confirmed records of the genus *Gaillea* in the Atlantic Ocean. In the *cox1* tree it falls – albeit with limited support – in the same clade as *Gaillea coriolis* (Bouchet et Warén, 1986), the type species of the genus. Kantor *et al.* [2013] suggested on morphological grounds that *Buccinum canetae* Clench et Aguayo, 1944 (off Cuba in 440–550 m) belongs to *Gaillea*, which is still not confirmed with molecular data. *Gaillea atlantica* differs from *G. canetae* in its much smaller size (holotype of the latter is 68.8 mm in SL), and by having fewer and less developed spiral cords.

Gaillea crassa sp. nov.
(Figs 12B; 14 F–H)

Zoobank registration: urn:lsid:zoobank.org:act:-67CE712F-813D-4659-A222-82743DAEC0B2

Holotype (sequenced). MNHN-IM-2013-60182.

Type locality. GUADELOUPE, N of Grande-Terre, 16°29'N, 61°62'W, 500–550 m [KARUBENTHOS 2, stn CP4524].

Other material

GUADELOUPE, N of Grande-Terre, 16°37'29"N, 61°47'W, 650–716 m, KARUBENTHOS 2, stn CP4522, MNHN-IM-2013-60159 (non-sequenced).

Description (holotype). Shell small for the genus, fusiform, with medium-tall spire. Whorls convex, very weakly angulated on shoulder, siphonal canal medium-long, nearly straight. Suture distinct, impressed. Protoconch eroded, rendering whorl count impossible, globose, with convex whorls. About 5 convex teleoconch whorls. Axial sculpture well-developed, of low, but distinct, weakly prosocline ribs on all teleoconch whorls, their intervals equal or slightly narrower than ribs width. Ribs spanning from suture to suture on spire whorls, fading on periphery of last whorl. First intact teleoconch whorl with 11 ribs, penultimate with 19, last with 18. Spiral sculpture of well-developed, distinct cords, of uneven

width, rounded on top. Subsutural ramp with 4 weak cords overlaid with thick periostracum, followed by 5 stronger cords on periphery of last whorl, forming distinct, rounded nodules at intersection with axial ribs, with quadrate interspaces of about cords width. Shell base and canal with 15 cords, closer spaced and of uneven width.

Aperture ovate, slightly constricted adapically, with grooves inside, corresponding to spiral cords. Columella smooth, with narrow, rather thick callus extending to parietal whorl. Outer lip thin; edge sharp, aperture gradually passing into narrow siphonal canal. Periostracum thick, forming closely spaced axial lamellae with dense short bristles, better seen in intervals between axial ribs.

Operculum yellowish, narrow oval with terminal nucleus in lower part shifted adaxially.

Measurements: SL 14.5 mm, AL (without canal) 5.4 mm, SW 6.3 mm.

Etymology. From the Latin adjective *crass-us*, *-a*, *-um*, thick, solid, stout, reflecting the stout shell shape with shorter canal than in other *Gaillea* species, and with rather coarse sculpture.

Remarks. Although molecularly clearly distinct from *Gaillea atlantica* sp. nov., *Gaillea crassa* sp. nov. is very similar to it and differs in having a more slender shell, more gradually passing into siphonal canal, shorter canal, more closely spaced and numerous axial ribs, and stronger spiral cords, giving an appearance of a coarser sculpture. The second available specimen (Fig. 14 H), not sequenced, is similar in shell shape to the holotype, but has fewer axial ribs with only 15 on the last whorl.

Superfamily Conoidea Fleming, 1822
Cochlespiridae Powell, 1942
Aforia Dall, 1889

Type species: *Pleurotoma circinata* Dall, 1873 (OD).

Aforia bugeae sp. nov.
(Figs 15 A–E, 16)

Zoobank registration: urn:lsid:zoobank.org:act:-7DEBEE12-BB7F-4B67-8FC9-77C8BB0D7378

Holotype (sequenced for *cox1*): MNHN-IM-2013-58238, subadult (Figs 15 A–D).

Type locality. Papua New Guinea, New Ireland, 2°18'S, 150°47'E, 1066–1200 m [KAVIENG 2014, stn. CP4434].

Other material

New Ireland, 2°16'S, 150°45'E, 1128–1135 m, KAVIENG 2014, stn. CP4436, MNHN-IM-2023-492, 2 dd.

Description (holotype). Shell fusiform, thin, with tall spire and very long, nearly straight siphonal canal. Protoconch eroded, of about 1.5 convex whorls, with indistinct transition to teleoconch. Teleoconch

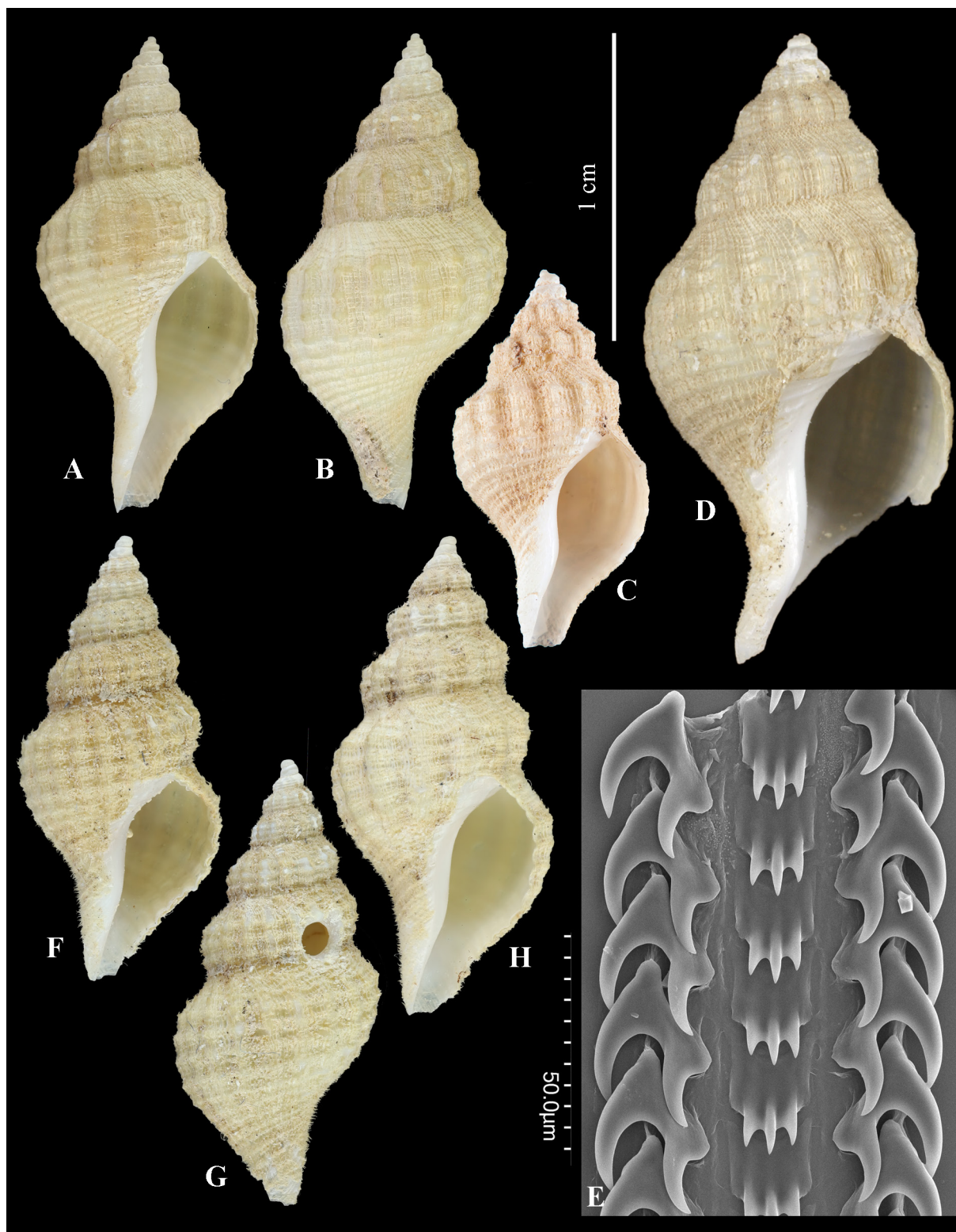


FIG. 14. *Gaillea* species. **A–E.** *Gaillea atlantica* sp. nov., Guadeloupe. **A–B.** Holotype, MNHN-IM-2013-61533, SL 15.7 mm. **C.** MNHN-IM-2013-60090, SL 12.4 mm. **D.** MNHN-IM-2013-60080, SL 20.6 mm. **E.** Radula, MNHN-IM-2013-61128. **G–H.** *Gaillea crassa* sp. nov., Guadeloupe. **F–G.** Holotype, MNHN-IM-2013-60182, SL 14.5 mm. **H.** MNHN-IM-2013-60159, SL 15.5 mm. All shells at the same scale.

of 6 whorls, strongly angulate at shoulder. Suture shallowly impressed. Subsutural ramp weakly concave, nearly flat. Axial sculpture limited to indistinct growth lines, thickened apically, producing row of

short, prosocline wrinkles, corresponding in shape to adapical part of anal sinus. Spiral sculpture of distinct cords of uneven width, 10 on subsutural ramp of penultimate and last whorl, 36 stronger cords

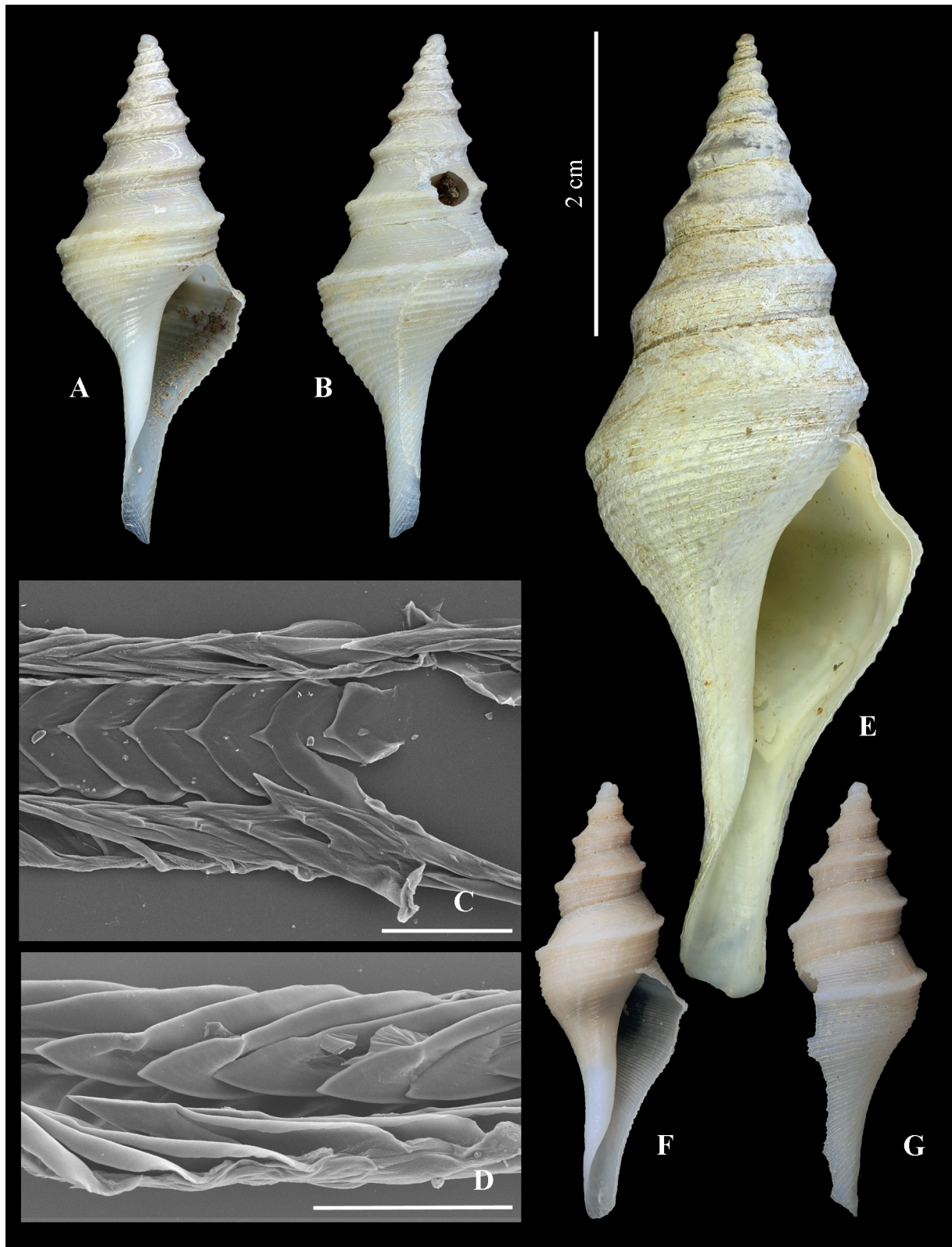


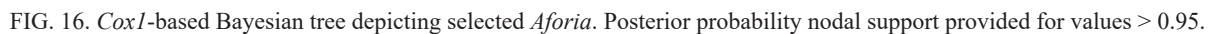
FIG. 15. *Aforia* species. A–E. *Aforia bugeae* sp. nov. . A–D. Holotype, MNHN-IM-2013-58238, SL 35.2 mm; C–D – radula. E. MNHN-IM-2023-492, New Ireland, SL 65.9 mm. F–G. *Aforia goniodes* (Watson, 1881), South Africa, 47°40'4.8'' S, 4°16'48'' E, 4579 m, ZSM 20050868, SL 30.1 mm, sequenced specimen. Scale bars for C–D 100 µm. Shells at the same scale.

below shoulder on last whorl, including about 20 on canal. Intervals between cords 1–2 times cords width. Strong keel on shoulder bearing 3 smaller cords.

Anal sinus, judging from growth lines, deep,

wide, rounded, occupying the entire subsutural ramp, its apex situated approximately at mid-height of ramp.

Aperture wide and oval, outer lip simple, par-



Specimens were obtained during research cruises and expeditions organized by the MNHN and ProNatura International as part of the Our Planet Reviewed programme and by the MNHN and the Institut de Recherche pour le Développement as part of the Tropical Deep-Sea Benthos programme (ZhongSha 2015 in the South China Sea; PANGLAO 2005 and AURORA 2007 in the Philippines), KAVIENG 2014 ([dx.doi.org/10.17600/14004400](https://doi.org/10.17600/14004400)), MADEEP ([dx.doi.org/10.17600/14004000](https://doi.org/10.17600/14004000)) and PAPUA NIUGINI ([dx.doi.org/10.17600/18000841](https://doi.org/10.17600/18000841)) in Papua New Guinea; KANACONO ([dx.doi.org/10.17600/16003900](https://doi.org/10.17600/16003900)), KOUMAC 2.3, in New Caledonia; SANTO 2006 in Vanuatu, SALOMON 2 ([dx.doi.org/10.17600/4100090](https://doi.org/10.17600/4100090)) in the Solomons, MIRIKY in Madagascar; KARUBENTHOS 2 ([dx.doi.org/10.17600/15005400](https://doi.org/10.17600/15005400)) in Guadeloupe, MADIBENTHOS in Martinique, GUYANE 2014 in French Guiana. We are grateful to numerous cruise leaders and co-PIs: Wei-Jen Chen, Laure Corbari, Stephane Hourdez, Peter Ng, Karine Olu-Le Roy, Bertrand Richer de Forges and Sarah Samadi (more information can be found

at expeditions.mnhn.fr). These 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 authors thank Virginie Héros, Philippe Maestrati, and Barbara Buge (MNHN) for their help in curating the vouchers.

We want to thank the reviewer, Dr. Marco Oliverio for valuable corrections and suggestions.

This study was conducted using Joint Usage Center 'Instrumental methods in ecology' at the IEE RAS. We thank R.M. Hatsaeva, S. Kolchev, D. Zaikin and A. Neretina for their friendly and helpful assistance with the SEM facilities. This work was supported by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 865101) to N.P.

Supplementary data.

Table S1. List of samples sequenced for *Cox1* and included in the molecular analyses. New sequences are highlighted in **bold**.

Input files for identification of the DNA diagnosis for the genus *Atlantomanaria*, and the output files generated by MOLD are available at 10.5281/zenodo.18805182.

References

- Bouchet P., Kantor Yu.I., 2000. The anatomy and systematics of *Latiromitra*, a genus of tropical deep-water Ptychatractinae (Gastropoda: Turbinellidae). *Veliger*, 49(1): 1–23.
- Bouchet P., Kantor Yu.I. 2004. New Caledonia: the major centre of biodiversity for volutomitrid molluscs (Mollusca: Neogastropoda: Volutomitridae). *Systematics and Biodiversity*, 1: 467–502. <https://doi.org/10.1017/s1477200003001282>
- Cernohorsky W. O. (1984). Systematics of the family Nassariidae (Mollusca: Gastropoda). *Bulletin of the Auckland Institute and Museum*. 14: i–iv, 1–356. Available online at <https://www.biodiversitylibrary.org/page/59858109>
- deMaintenon M., Strong E.E. 2022. Molecular phylogeny of Columbellidae (Gastropoda: Neogastropoda). *PeerJ*, 10: e13996. DOI:10.7717/peerj.13996
- Fedosov A.E., Puillandre N., Herrmann M., Dgebuadze P., Bouchet P. 2017. Phylogeny, systematics, and evolution of the family Costellariidae (Gastropoda: Neogastropoda). *Zoological Journal of the Linnean Society*, 179: 541–626.
- Fedosov A., Achaz G., Gontchar A., Puillandre N. 2022. MOLD, a novel software to compile accurate and reliable DNA diagnoses for taxonomic descriptions. *Molecular Ecology Resources*, 22(5): 2038–2053. DOI: 10.1111/1755-0998.13590.
- Fedosov A.E., Zaharias P., Lemarcis T., Modica M. V., Holford M., Oliverio M., Kantor Yu.I., Puillandre N. 2024. Phylogenomics of Neogastropoda: the backbone hidden in the bush. *Systematic Biology*, 73(3): 521–531. <https://doi.org/10.1093/sysbio/syae010>
- Fedosov A.E., Lemarcis T., Bouchet P., Harzhauser M., Kantor Yu.I., Kiel S., Modica M.V., Oliverio M., Zaharias P., Puillandre N. 2026. Phylogeny, classification, and evolutionary history of Neogastropoda. *Zoological Journal of the Linnean Society*, 207(3): zlag058. DOI: 10.1093/zoolinnean/zlag058.
- Fraussen K., Stahlschmidt P. 2016. The extensive Indo-Pacific deep-water radiation of *Manaria* E. A. Smith, 1906 (Gastropoda: Buccinidae) and related genera, with descriptions of 21 new species. In: Héros V., Strong E., Bouchet P. (Eds). *Tropical Deep-Sea Benthos*, 29. Muséum national d'Histoire naturelle, Paris : 363–456 (*Mémoires du Muséum national d'Histoire naturelle*, 208).
- Galindo L.A., Puillandre N., Strong E.E., Bouchet P. 2014. Using microwaves to prepare gastropods for DNA barcoding. *Molecular Ecology Resources*, 14: 700–705. DOI: 10.1111/1755-0998.12231
- Gofas S., Oliver J.D. 2010. Las especies del género *Chauvetia* (Gastropoda, Neogastropoda, Buccinidae) del área ibero-marroquí, con descripción de cuatro especies nuevas. *Iberus*. 28(1): 23–60.
- Huelsenbeck J.P., Ronquist F., Hall B. 2001. MrBayes: Bayesian inference of phylogeny. *Bioinformatics*, 17: 754–755.
- Kantor Yu.I. 1996. Phylogeny and relationships of Neogastropoda. In: Taylor J.D. (Ed.): *Origin and evolutionary radiation of Mollusca, Centenary Symposium of the Malacological Society of London*. Oxford University Press: 221–230.
- Kantor Y.I. 2002. Morphological prerequisites for understanding neogastropod phylogeny. *Bollettino Malacologico*, Supplement 4: 161–174.
- Kantor Yu.I., Bouchet P., 1997. The anatomy and systematics of *Ceratohancus*, a genus of deep-water Ptychatractinae (Gastropoda: Turbinellidae) with labral spine. *Veliger*, 40(2): 101–120.
- Kantor Yu.I., Fedosov A.E., Puillandre N., Bonillo C., Bouchet P. 2017. Returning to the roots: morphology, molecular phylogeny and classification of the Olivoidea (Gastropoda: Neogastropoda). *Zoological Journal of the Linnean Society*, 180(3): 493–541. DOI: 10.1093/zoolinnean/zlw003
- Kantor Yu.I., Harasewych M.G., Puillandre N., 2016. A critical review of Antarctic Conoidea (Neogastropoda). *Molluscan Research*, 36(3): 153–206. DOI: 10.1080/13235818.2015.1128523
- Kantor Y.I., Puillandre N. 2012. Evolution of the radular apparatus in Conoidea (Gastropoda: Neogastropoda) as inferred from a molecular phylogeny. *Malacologia*, 55: 55–90. DOI: 10.4002/040.055.0105
- Kantor Yu.I., Puillandre N., Fraussen K., Fedosov A.E., Bouchet P. 2013. Deep-water Buccinidae (Gastropoda: Neogastropoda) from sunken wood, vents and seeps: molecular phylogeny and taxonomy. *Journal of the Marine Biological Association of the United Kingdom*, 93(8), 2177–2195. DOI: 10.1017/s0025315413000672
- Kantor Yu.I., Fedosov A.E., Kosyan A. R., Puillandre N., Sorokin P. A., Kano Y., Clark R., Bouchet P. 2022. Molecular phylogeny and revised classification of the Buccinoidea (Neogastropoda). *Zoological Journal of the Linnean Society*, 194, 789–857. DOI: 10.1093/zoolinnean/zlab031
- Kantor Yu.I., Bouchet P., Fedosov A.E., Puillandre N., Zaharias P. 2024. Generic revision of Recent Turridae (Conoidea). *Journal of Molluscan Studies*, 90(5): eyae032. DOI: 10.1093/mollus/eyae032
- Kantor Yu. I., Sysoev A.V. 2006. *Marine and brackish-water Gastropoda of Russia and adjacent countries: an illustrated catalogue*. KMK Scientific Press Ltd., 371 p., 140 col. plates.

- Kilburn R.N., Marais J.P., Fraussen K. 2010. Buccinidae. In: Marais A.P., Seecombe A.D. (Eds). *Identification guide to the seashells of South Africa*. Volume 1. Groenkloof: Centre for Molluscan Studies: 16–52.
- Kosuge S. 1986. Some considerations on the family Coralliophilidae with descriptions of four new species. *Bulletin of the Institute of Malacology, Tokyo*, 2(4): 70–75.
- Marcus E., Marcus E. 1962. Studies on Columbellidae. *Boletim da Faculdade de Filosofia, Ciências e Letras. Universidade de São Paulo*, 261, *Zoologia*, 24: 335–402.
- MolluscaBase eds. 2025. MolluscaBase. Accessed at <https://www.molluscabase.org> on 2025-08-08. DOI:10.14284/448
- Oliverio M. 2008. Coralliophilinae (Neogastropoda: Muricidae) from the southwest Pacific. In: *Héros V. et al. (Ed.) Tropical Deep-Sea Benthos*, 25. *Mémoires du Muséum national d'Histoire naturelle*, 196: 481–585.
- Olsson A.A. 1956. Studies of the genus *Olivella*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 108: 155–225.
- Pastorino G. 2016. Revision of the genera *Pareuthria* Strebel, 1905, *Glypteuthria* Strebel, 1905 and *Meuthria* Thiele, 1912 (Gastropoda: Buccinulidae) with the description of three new genera and two new species from Southwestern Atlantic waters. *Zootaxa*, 4179 (3): 301–344.
- Ponder W.F. 1973. The origin and evolution of the Neogastropoda. *Malacologia*, 12: 295–338.
- Poppe G.T., Tagaro S. 2005. *Enigmavassum enigmaticum*, a new species from Cotabato, the Philippines. *Visaya*, 1(5): 133–135.
- Puillandre N., Fedosov A.E., Zaharias P., Aznar-Cormano L., Kantor Yu.I. 2017. A quest for the lost types of *Lophiotoma* (Gastropoda: Conoidea: Turridae): integrative taxonomy in a nomenclatural mess. *Zoological Journal of the Linnean Society*, 181(1): 243–271. <https://doi.org/10.1093/zoolinnean/zlx012>
- Rambaut A., Drummond A. J. 2014. *Tracer v1.6*. Available at: <http://beast.bio.ed.ac.uk/Tracer>
- Regteren Altena, C. O. van. 1950. The marine Mollusca of the Kendeng beds (East Java). Gastropoda part V (Families Muricidae - Volemidae inclusive). *Leidsche Geologische Mededelingen*, 15: 205–240.
- Simone L.R.L. 2011. Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology. *Arquivos de Zoologia*, 42: 161–323.
- Taylor J.D., Morris N.J., Taylor C.N. 1980. Food specialization and the evolution of predatory prosobranch gastropods. *Palaeontology*, 23: 375–409.
- Thiele J. 1925. Gastropoden der Deutschen Tiefsee-Expedition. II Teil. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899*, 17(2): 35–382, pls 13–46 [reprints paginated 1–348, pls 1–34]. Available online at <https://www.deutsche-digitale-bibliothek.de/item/3NJJP6TFO3ZWXZDRTI2CZV66VP76UDWR>
- Troost A.I., Rupert S.D., Cyrus A.Z., Paaadino F.V., Dattilo B.F., Peters W.S. 2012. What can we learn from confusing *Olivella columellaris* and *O. semi-striata* (Olivellidae, Gastropoda), two key species in Panamic sandy beach ecosystems? *Biota Neotropica*, 12: 101–116.

