

Integrative taxonomy approach to Indo-Pacific Olividae: new species revealed by molecular and morphological data

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ABSTRACT. Five new species of Olivoidea are described based on molecular and morphological evidence: four shallow subtidal *Ancilla* from Madagascar and Papua New Guinea, and one deep water (500–600 m) *Calyptoliva* from the Tuamotus. The sympatric – but not syntopic – *Ancilla morrisoni* and *A. kaviengensis*, from New Ireland province, are morphologically cryptic, differing mostly in shell colour, but are molecularly distinct. The sympatric – and possibly syntopic – *Ancilla atimovatae* and *A. lhaumeti*, belong to a species flock from southernmost Madagascar; *A. atimovatae* is conchologically nearly indistinguishable from *A. ventricosa*, but differs markedly in radular morphology. *Calyptoliva* was previously known only from the Coral Sea; *C. bbugae* is the first representative of the genus to yield molecular data. The new *Ancilla* are described based on sequenced holotypes; the type material of the new *Calyptoliva* includes a sequenced paratype.

Introduction

Gastropods of the superfamily Olivoidea Latreille, 1825 are common dwellers of shallow waters in tropical and subtropical zones of the World Ocean, rarely occurring in depths exceeding 1000 meters but reaching as deep as 1855 meters [“*Amalda*” *sibuetiae* – Kantor, Bouchet, 1999]. Olivoidea encompasses around 30 extant genera and 460 accepted Holocene species [WoRMS, 2016]. Attractive glossy and usually colourful shells make Olivoidea a popular group among shell collectors and amateur taxonomists.

Some of the genera of Olivoidea were recently revised and are commonly treated in the literature:

Oliva Bruguière, 1789 has been treated in several monographs, most recently those of Tursch and Greifeneder [2001] and Hunon *et al.* [2009]. However most of the genera have never been revised, and the descriptions and limited data on anatomy are scattered in various papers. The genus *Ancilla* Lamarck, 1799, reviewed by Kilburn [1981], remains taxonomically complex due to rather uniform shells devoid of distinct sculpture and shell colouration, which renders species delimitation especially difficult. The genus *Ancilla* comprises 40 living species and subspecies [WoRMS, 2016], reaching highest diversity off south-eastern Africa, Mozambique and Madagascar, some living at low tide level, others reaching 365 meters depth [Kilburn, 1981]. Only five new species from Madagascar and Oman have been described since Kilburn’s revision [Bozetti, 2006; Boyer, 2015].

Olivoidea in general and *Ancilla* in particular remain virtually untouched by molecular phylogenetic and advanced morphological studies, and even the radula is known for a limited number of species.

Currently, a work on the molecular phylogeny of Olivoidea is in preparation by the authors of this publication, where more than one hundred specimens of Olivoidea were sequenced for standard genetic markers (COI, 16S, 12S, H3), including 36 specimens of *Ancilla*. The analysis of this material in integrative taxonomy framework using both molecular data supported by a morphological approach revealed several undescribed species. Four species of the genus *Ancilla*, and one of *Calyptoliva* Kantor et Bouchet, 2007 were collected in sufficient num-

bers for formal description. The aim of this paper is to describe these five olivoidean species, revealed by molecular and morphological methods.

Material and methods

Material described here was collected during several biodiversity surveys (ATIMO VATAE and MIRIKY in Madagascar, KAVIENG 2014 and PA-PUA NIUGINI in Papua New Guinea, MAINBAZA in Mozambique, and TARASOC in French Polynesia) organized mainly by the Muséum National d'Histoire Naturelle, Paris (MNHN), Pro-Natura International (PNI) and the Institut de Recherche pour le Développement (IRD), as part of the *Our Planet Reviewed* and *Tropical Deep-Sea Benthos* programs [see Bouchet *et al.*, 2008 and the BasExp database at <http://expeditions.mnhn.fr/>]. In the field, living specimens were anaesthetized with MgCl₂ or removed from their shell using a microwave oven [Galindo *et al.*, 2014]. A piece of the head-foot was cut and preserved in 96–98% ethanol. Bodies were then separated from the shells, with shells kept dry to prevent deterioration by etching and carrying the same registration number as the corresponding body and tissue-clip in 96–98% ethanol. Material (shell, tissue and DNA) is vouchered in MNHN (<http://science.mnhn.fr>) (Table 1).

Shell terminology follows mostly Kilburn [1981] and Tursch and Greifeneder [2001].

Abbreviations and conventions: AL, aperture length; BWL, body whorl length; MNHN, Muséum national d'Histoire naturelle, Paris, France; SL, shell length; SW, shell width.

PCR amplification and DNA sequencing

Total genomic DNA was extracted from muscle tissue using NucleoSpinR 96 Tissues (Macherey–Nagel) and following the manufacturer's instructions. A fragment of the mitochondrial gene Cytochrome Oxidase I (COI) was sequenced (Table 1). All PCR reactions were performed following protocols described in detail earlier [Fedosov *et al.*, 2015]. Gene was sequenced for both directions to confirm accuracy of each sequence. Sequencing has been performed by Eurofins. Chromatograms were edited using CodonCode Aligner version 3.7.1.1.

Species delimitation and phylogenetic analysis

Sequences were aligned using MUSCLE [Edgar, 2004]: no indels were detected. Pairwise genetic distances (p-distances) were calculated with MEGA 6 [Tamura *et al.*, 2013]. The web version (<http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html>) of ABGD (Automatic Barcode Gap Discovery) [Puillandre *et al.*, 2012] was used to propose primary species hypotheses, with default parameters. In addition to the *Ancilla* specimens, five other Olivoidae were used as outgroups for the phylogenetic analyses: MNHN IM-2009-25009 *Entomoliva mirabilis*, MNHN IM-2007-31956 *Ancillina* cf. *sumatrana*, MNHN IM-2009-11968 *Amalda hilgendorffi richeri*, MNHN IM-2013-18534 *Benthobia* sp. and MNHN IM-2013-9727 *Fusulculus crenatus*. Each codon position of the COI was considered as independent partition, each following a GTR+I+G model. Bayesian Analyses (BAs) were performed running two parallel analyses in MrBayes 3.2.6 [Huelsenberg *et al.*, 2001] on XSEDE, as implemented on the CIPRES Science Gateway v.3.1 [Miller *et al.*, 2010]. Each run consisted of six Markov chains and 10,000,000 generations with 8 chains, 5 swaps, a sampling frequency of 1,000 and a temperature of 0.02. Convergence of each analysis was evaluated using Tracer1.4.1 [Rambaut *et al.*, 2014] to ensure that all ESS values exceeded 200. Consensus tree was calculated after omitting the first 25% trees as burn-in.

The radula was prepared following the standard protocol in Kantor and Puillandre [2012] and examined with scanning electron microscopes in MNHN and A.N. Severtzov Institute of Ecology and Evolution, Russian Academy of Sciences.

Results

Species delimitation, and phylogenetic analysis

Pairwise distribution of the genetic distances (Fig. 1) clearly show a gap between 2 and 4% and between 10 and 12%. ABGD systematically defines a partition of 11 species hypotheses, with genetic distances within species hypotheses (mean = 0.54%, max. = 1.3%) smaller than between species hypotheses (mean = 11.63%, min. = 3.9%), corresponding to the first gap observed in the pairwise distribution of genetic distances. In the phylogenetic tree, the 11 species hypotheses proposed by ABGD correspond to 11 independent lineages (of which five were represented by a single specimen), characterized by long branches between lineages and short branches within lineages (Fig. 2). Because they constitute independently evolving groups characterized by low intra-lineage genetic distances and high inter-lineage genetic distances, we consider that these lineages correspond to species. They were furthermore supported by morphological differences, as described below.

For one species described herein (*Ancilla atimovatae* sp. nov.), we failed to sequence the COI gene, but were able to amplify and sequence three other genes. In the molecular tree based on four genes (not reported here) [Kantor *et al.*, in prep.] it

Table 1. List of specimens analyzed with the Barcode of Life Data System (BOLD) and GenBank accession numbers.

Genus	Species	Inventory number	Expedition	Station	Locality	BOLD	COI
<i>Ancilla</i>	<i>adelphe</i> Kilburn, 1981	IM-2009-15475	ATIMO VATAE	BM06	South Madagascar, 25°27'55"S, 44°57'38"E, 0-1 m	OLIV014- 16	KX233283
<i>Ancilla</i>	<i>adelphe</i> Kilburn, 1981	IM-2009-15491	ATIMO VATAE	BM07	South Madagascar, 25°27'55"S, 44°57'38"E, 0-1 m	OLIV021- 16	KX233281
<i>Ancilla</i>	<i>adelphe</i> Kilburn, 1981	IM-2009-15510	ATIMO VATAE	BV16	South Madagascar, 25°25'33"S, 44°55'50.9953"E	OLIV030- 16	KX233282
<i>Ancilla</i>	<i>adelphe</i> Kilburn, 1981	IM-2009-15519	ATIMO VATAE	BP42	South Madagascar, 25°22.8"S, 44°51.1"E, 18-20 m	OLIV037- 16	KX233278
<i>Ancilla</i>	<i>adelphe</i> Kilburn, 1981	IM-2009-15524	ATIMO VATAE	BV16	South Madagascar, 25°25'33"S, 44°55'50"E	OLIV042- 16	KX233279
<i>Ancilla</i>	<i>adelphe</i> Kilburn, 1981	IM-2009-15535	ATIMO VATAE	BP41	South Madagascar, 25°22.9"S, 44°51.0-51.6"E, 19-21 m	OLIV052- 16	KX233277
<i>Ancilla</i>	<i>adelphe</i> Kilburn, 1981	IM-2009-15538	ATIMO VATAE	BP36	South Madagascar, 25°21'52"S, 44°50'13"E, 10-17 m	OLIV054- 16	KX233280
<i>Ancilla</i>	<i>aureocallosa</i> (Kilburn et Jenner, 1977)	IM-2007-39045	MAINBAZA	CP3143	Mozambique Channel, 23°32"S, 35°46"E, 264-277 m	OLIV007- 16	KX233284
<i>Ancilla</i>	<i>giaquintoi</i> Bozzetti, 2006	IM-2009-15526	ATIMO VATAE	BP22	South Madagascar, 25°23'26"S, 44°51'39"E, 20-22 m	OLIV044- 16	KX233285
<i>Ancilla</i>	<i>kaviengensis</i> sp. nov.	IM-2013-51964	KAVIENG 2014	KR82	Papua-New Guinea, 02°39.6"S, 150°39.9"E, 2-12 m	OLIV072- 16	KX233294
<i>Ancilla</i>	<i>kaviengensis</i> sp. nov.	IM-2013-55102	KAVIENG 2014	KS57	Papua-New Guinea, 02°38.9"S, 150°40.1"E, 7-9 m	OLIV075- 16	KX233297
<i>Ancilla</i>	<i>kaviengensis</i> sp. nov.	IM-2013-55130	KAVIENG 2014	KB62	Papua-New Guinea, 02°36.4"S, 150°42.4"E, 19 m	OLIV076- 16	KX233286
<i>Ancilla</i>	<i>kaviengensis</i> sp. nov.	IM-2013-55138	KAVIENG 2014	KD70	Papua-New Guinea, 02°38.3"S, 150°45.6"E, 10-15 m	OLIV077- 16	KX233305
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15481	ATIMO VATAE	BP21	South Madagascar, 25°23.1"S, 44°51.4"E, 20-23 m	OLIV016- 16	KX233303
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15482	ATIMO VATAE	BV16	South Madagascar, 25°25.6"S, 44°55.9"E, 9 m	OLIV017- 16	KX233299
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15503	ATIMO VATAE	BS11	South Madagascar, 25°28'36"S, 44°56'45"E, 8-11 m	OLIV025- 16	KX233296
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15506	ATIMO VATAE	BP42	South Madagascar, 25°22.8"S, 44°51.1"E, 18-20 m	OLIV027- 16	KX233288
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15507	ATIMO VATAE	BM06	South Madagascar, 25°27'55"S, 44°57'38"E, 0-1 m	OLIV028- 16	KX233300
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15513	ATIMO VATAE	BP37	South Madagascar, 25°22.4"S, 44°50.2"E, 19-20 m	OLIV033- 16	KX233301
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15515	ATIMO VATAE	BP37	South Madagascar, 25°22.4"S, 44°50.2"E, 19-20 m	OLIV034- 16	KX233302
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15523	ATIMO VATAE	BV16	South Madagascar, 25°25.6"S, 44°55.9"E, 9 m	OLIV041- 16	KX233291
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15528	ATIMO VATAE	BP42	South Madagascar, 25°22.8"S, 44°51.1"E, 18-20 m	OLIV046- 16	KX233293
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15533	ATIMO VATAE	BP21	South Madagascar, 25°23.1"S, 44°51.4-51.6"E, 20-23 m	OLIV050- 16	KX233298
<i>Ancilla</i>	<i>lhaumeti</i> sp. nov.	IM-2009-15550	ATIMO VATAE	BV16	South Madagascar, 25°25.6"S, 44°55.9"E, 9 m	OLIV060- 16	KX233292
<i>Ancilla</i>	<i>morrisoni</i> sp. nov.	IM-2013-55401	KAVIENG 2014	KS63	Papua-New Guinea, 02°45.2"S, 150°41.7"E, 10-12 m	OLIV078- 16	KX233290
<i>Ancilla</i>	<i>morrisoni</i> sp. nov.	IM-2013-55403	KAVIENG 2014	KS63	Papua-New Guinea, 02°45.2"S, 150°41.7"E, 10-12 m	OLIV079- 16	KX233289
<i>Ancilla</i>	<i>sp.</i>	IM-2007-36606	MAINBAZA	CP3133	Mozambique Channel, 25°11"S, 35°10"E, 200-201 m	OLIV005- 16	KX233304
<i>Ancilla</i>	<i>sp.</i>	IM-2009-15527	ATIMO VATAE	DW3523	South Madagascar, 24°22'57"S, 47°31'23.4012"E, 200-220 m	OLIV045- 16	KX233295
<i>Ancilla</i>	<i>sp.</i>	IM-2009-25001	MIRIKY	CP3262	Madagascar, 15°34'9.8"S, 45°43'40.8"E, 227-283 m	OLIV065- 16	KX233287
<i>Ancilla</i>	<i>thomassini</i> Kilburn, 1981	IM-2009-15460	ATIMO VATAE	TB13	South Madagascar, 25°01.5"S, 47°00.0"E, 2-4 m	OLIV011- 16	KX233307
<i>Ancilla</i>	<i>thomassini</i> Kilburn, 1981	IM-2009-15534	ATIMO VATAE	TS13	South Madagascar, 25°02.3"S, 46°59.6"E, 5-6 m	OLIV051- 16	KX233306
<i>Ancilla</i>	<i>ventricosa</i> (Lamarck, 1811)	IM-2009-15486	ATIMO VATAE	BP42	South Madagascar, 25°22.8"S, 44°51.1"E, 18-20 m	OLIV020- 16	KX233309
<i>Ancilla</i>	<i>ventricosa</i> (Lamarck, 1811)	IM-2009-15537	ATIMO VATAE	BP21	South Madagascar, 25°23.1"S, 44°51.4"E, 20-23 m	OLIV053- 16	KX233308
<i>Ancilla</i>	<i>ventricosa</i> (Lamarck, 1811)	IM-2009-15544	ATIMO VATAE	BP42	South Madagascar, 25°22.8"S, 44°51.1"E, 18-20 m	OLIV057- 16	KX233311
<i>Ancilla</i>	<i>ventricosa</i> (Lamarck, 1811)	IM-2009-15545	ATIMO VATAE	BV06	South Madagascar, 25°26.9"S, 44°55.9"E, 14-18 m	OLIV058- 16	KX233310
<i>Ancilla</i>	<i>ventricosa</i> (Lamarck, 1811)	IM-2009-15547	ATIMO VATAE	BP42	South Madagascar, 25°22.8"S, 44°51.1"E, 18-20 m	OLIV059- 16	KX233312
<i>Benthobia</i>	sp 2	IM-2013-18534	PAPUA NIUGINI	CP4038	Papua-New Guinea, 04°27"S, 145°34"E, 800-840 m	OLIV068- 16	KX233315
<i>Fusulculus</i>	<i>crenatus</i> Bouchet et Vermeij, 1998	IM-2013-9727	PAPUA NIUGINI	CP4008	Solomon Sea, 06°04"S, 148°10"E, 500-555 m	OLIV080- 16	KX233318
<i>Amalda</i>	<i>hilgendorffi richieri</i> Kilburn et Bouchet, 1988	IM-2009-11968	CONCALIS	DW2979	Northern New Caledonia, 18°16"S, 162°54"E, 350 m	OLIV010- 16	KX233273
<i>Entomoliva</i>	<i>mirabilis</i> Bouchet et Kilburn, 1991	IM-2009-25009	EXBODI	DW3906	New Caledonia, 19°50"S, 165°33"E, 490-580 m	OLIV066- 16	KX233317
<i>Ancillina</i>	<i>cf. sumatrana</i> (Thiele, 1925)	IM-2007-31956	PANGLAO 2005	CP2350	Philippines, Bohol Sea, 9°31'24"N, 124°03"E, 602-738 m	MITRI064- 15	KR087231

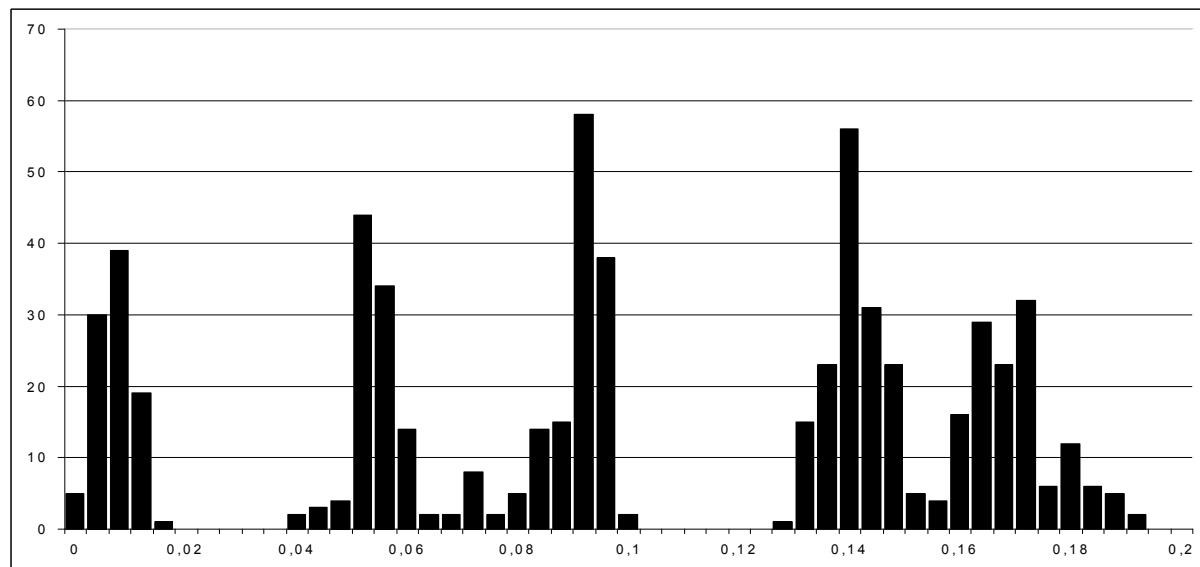


FIG. 1. Pairwise genetic distances histogram based on the COI sequences.

РИС. 1. Гистограмма попарных генетических расстояний гена COI.

constituted an independent lineage, placed as sister-group (with 100% support) of the clade uniting *A. ventricosa*, *A. adelpha* and *A. Ihaumeti* sp. nov. (node marked with an arrow on Fig. 2). Morphologically (radula) *A. atimovatae* is very distinct from all other analyzed herein species, and no similar radular type was ever recorded previously in *Ancilla* [Kilburn, 1981]. This leaves no doubts that *A. atimovatae* is a separate species, conchologically only superficially resembling *A. ventricosa*. Here we provide descriptions of the new species that were represented by several specimens in our material, allowing to evaluate the intra- and interspecific variation.

Taxonomy

Family Olividae Latreille, 1825

Type genus: *Oliva* Bruguière, 1789.

Ancilla Lamarck, 1799

Type species: *Ancilla cinnamomea* Lamarck, 1801; by subsequent monotypy.

Ancilla morrisoni sp. nov.

(Figs 3; 4 A-D; 5; 6)

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Type material: Holotype MNHN IM-2013-55401 and two paratypes from the same station MNHN IM-2013-55402, MNHN IM-2013-55403.

Type locality: Papua New Guinea, New Ireland Province, Kavieng Lagoon, S coast of Baudison Island, 02°45,2'S, 150°41,7'E, 10-12 m [KAVIENG 2014 Expedition, st. KS63].

Material examined: Type material (see above). Papua New Guinea, New Ireland, Kavieng Lagoon, KAVIENG 2014 Expedition, st. KB20, S coast of Baudison Island, 02°45,2'S, 150°41,7'E, 8 m (1 dd); st. KR57, E of Albatross Passage, wall with caves and ledges, 02°45,7'S, 150°44,5'E, 3-41 m (3 dd); st. KS63, S coast of Baudison Island, 02°45,2'S, 150°41,7'E, 10-12 m (1 dd), st. KB68, S coast of Baudison Island, 02°45,2'S - 150°41,7'E, 22-27 m (3 dd); st. KB70, E side of Wadei Island, 02°46,1'S, 150°45,2'E, 9-11 m, sand and rubble (3 dd); st. KR182 E of Albatross Passage, grit from floor of cave, 02°45,7'S, 150°44,5'E, 42 m (1 dd); st. KPS02, 02°45'S, 150°43'E, 14-32 m, (2 dd); st. KPS03, 02°45'S, 150°43'E, 14-16 m, sediment from a small cave (2 dd); st. KPR07, 02°45,4'S, 150°41,3'E, 22-27 m (4 dd).

Description (holotype). Shell oblong-ovate (Fig. 3 A-C), with evenly convex sides, maximum width median; spire short, rather blunt, with slightly convex whorls. Protoconch poorly delimited, of slightly less than 1.5 whorls, low, suture of first 0.75 whorls not overlaid by callus, diameter about 1.65 mm, exposed height about 0.8 mm. Teleoconch whorls about 1.5, most shell surface glossy, not microshagreened, but anterior part of the primary callus, plication plate, edge of siphonal fasciole and very narrow band along the outer lip heavily shagreened and mat. Primary callus of same colour as shell base.

Aperture with its greatest width slightly anterior to median, tapering adapically; siphonal canal wide, very shallowly notched. Olivoid groove narrow, well defined, terminating with denticle, and delimiting narrow, weakly convex, olivoid band. Anterior

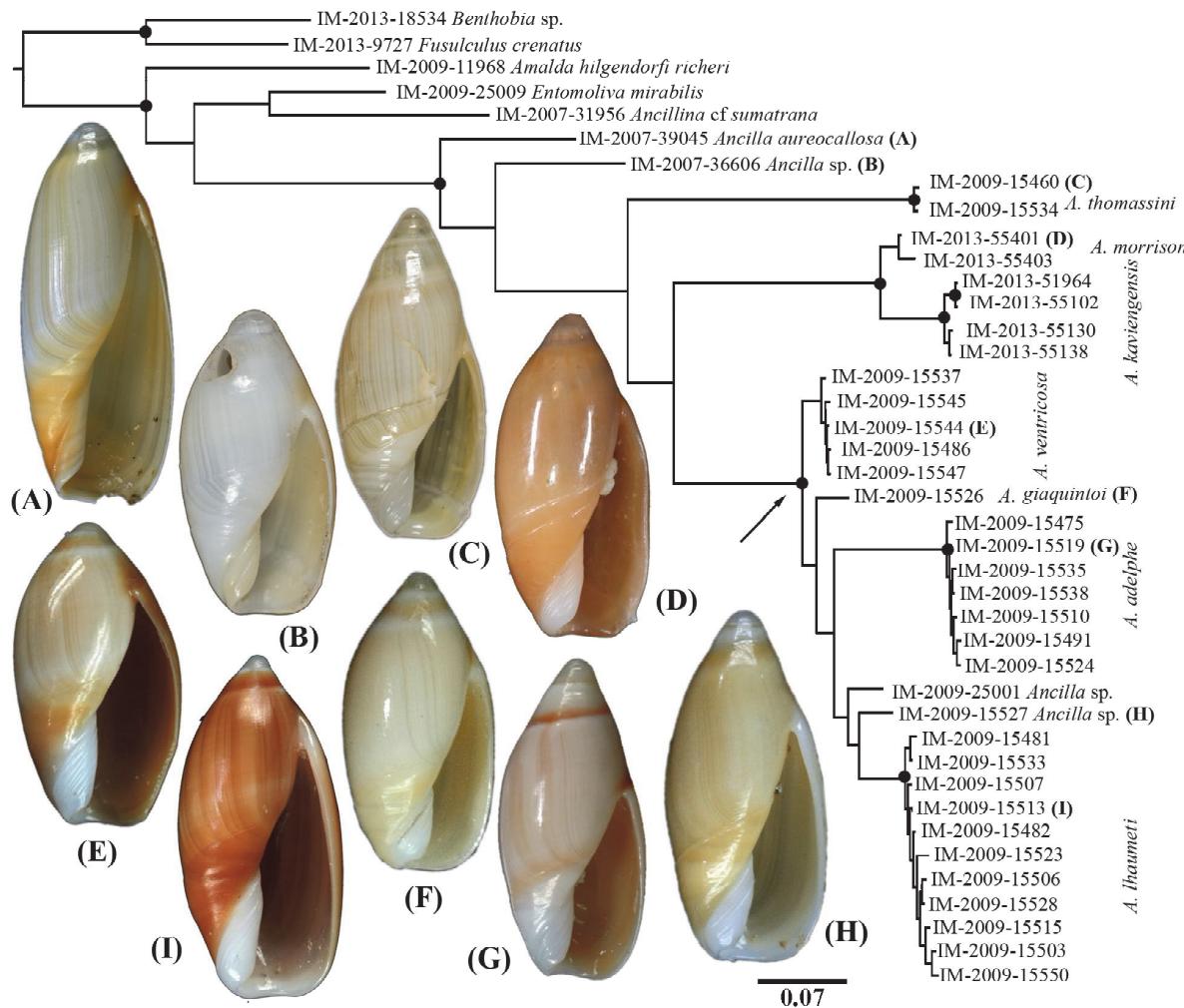


FIG. 2. Phylogenetic tree of *Ancilla* and outgroup olivoidean taxa obtained with Bayesian analysis of COI gene sequences. Only supported nodes with posterior probability values between 0.98 and 1.00 are marked on the tree with filled circles. (A). *Ancilla aureocallosa* (Kilburn et Jenner, 1977), MNHN IM-2007-39045, SL 21.7 mm. (B). *Ancilla* sp., MNHN IM-2007-36606, SL 5.6 mm. (C). *A. thomassini* Kilburn, 1981, MNHN IM-2009-15460, SL 6.3 mm. (D). *A. morrisoni* sp. nov., holotype, MNHN IM-2013-55401, SL 10.0 mm. (E). *A. ventricosa* (Lamarck, 1811), MNHN IM-2009-15544, SL 10.7 mm. (F). *A. glauqutoi* Bozetti, 2006, MNHN IM-2009-15526, SL 9.4 mm. (G). *A. adelphae* Kilburn, 1981, MNHN IM-2009-15519, SL 11.1 mm. (H). *A.* sp., MNHN IM-2009-15527, SL 12.7 mm. (I). *A. lhaumeti* sp. nov., holotype, MNHN IM-2009-15513, SL 15.3 mm. Arrow indicates the position of *A. atimovatae* in the multigene tree (see explanations in the text).

РИС. 2. Филогенетическое дерево видов *Ancilla* и аутгрупп, полученное с помощью Бэйесовского анализа последовательностей гена COI. На дереве кружками помечены узлы, имеющие уровень постериорной вероятности между 0,98 и 1,00. (A). *Ancilla aureocallosa* (Kilburn et Jenner, 1977), MNHN IM-2007-39045, SL 21.7 мм. (B). *Ancilla* sp., MNHN IM-2007-36606, SL 5.6 мм. (C). *A. thomassini* Kilburn, 1981, MNHN IM-2009-15460, SL 6.3 мм. (D). *A. morrisoni* sp. nov., голотип, MNHN IM-2013-55401, SL 10.0 мм. (E). *A. ventricosa* (Lamarck, 1811), MNHN IM-2009-15544, SL 10.7 мм. (F). *A. glauqutoi* Bozetti, 2006, MNHN IM-2009-15526, SL 9.4 мм. (G). *A. adelphae* Kilburn, 1981, MNHN IM-2009-15519, SL 11.1 мм. (H). *A.* sp., MNHN IM-2009-15527, SL 12.7 мм. (I). *A. lhaumeti* sp. nov., голотип, MNHN IM-2009-15513, SL 15.3 мм.

band slightly convex. Plication plate fairly narrow, not strongly twisted, with 5 lirae of about equal strength, the third abapical slightly broader than the others. Inner lip gently convex. Outer lip nearly straight in ventral and side views. Ground colour light orange. Protoconch slightly lighter than teleoconch. Plication plate off-white; anterior band slightly darker than adjacent surface, aperture light orange.

Measurements: holotype SL 10.0 mm, AL 7.5 mm, SW 4.5 mm.

[Описание (голотип). Раковина удлиненно-овальная (Рис. 3 А-С), с равномерно выпуклым профилем, максимальная ширина раковины приходится на середину высоты, завиток короткий, притулленный, со слабо выпуклыми оборотами. Протоконх слабо дифференцирован от телеконха, образован чуть менее 1,5 оборотами, низкий; шов первых 0,75 оборота протоконха не перекрыт каллусом. Диаметр протоконха около 1,65 мм, высота около 0,8 мм. Телеконх образован примерно 1,5 оборотами; большая часть поверхности раковины глянцевая, но передняя часть первичного каллуса, складчатая пластиинка, край сифональной фасциолы и очень узкая полоса вдоль внеш-



FIG. 3. Shells and live animals of *Ancilla morrisoni* sp. nov. A-D. Holotype, MNHN IM-2013-55401, SL 10.0 mm. D. Crawling animal. E-F. Paratype, MNHN IM-2013-55402, SL 9.4 mm. G-I. Paratype, MNHN IM-2013-55403, SL 4.8 mm, G. Shell at the same scale, as other specimens. H. Enlarged view of the shell. I. Crawling animal. D,I - photos of Laurent Charles.

РИС. 3. Раковины и живые экземпляры *Ancilla morrisoni* sp. nov. А-Д. Голотип, MNHN IM-2013-55401, SL 10.0 мм; Д. Ползущий моллюск. Е-Ф. Паратип, MNHN IM-2013-55402, SL 9.4 мм. Г-И. Паратип, MNHN IM-2013-55403, SL 4.8 мм. Г. Раковина в том же масштабе, что и остальные экземпляры. Н. Увеличенная раковина. И. Ползущий моллюск. Д,И - фотографии Laurent Charles.

ней губы устья матовые и покрыты густо расположеными микрогранулами. Первичный каллус имеет ту же окраску, что и поверхность раковины.

Устье имеет наибольшую ширину чуть впереди середины длины, сужается по направлению к вершине; сифональный канал широкий, с очень мелкой сифональной вырезкой. Оливоидный желобок узкий, четкий, завершается зубчиком на внешней губе и отделяет узкую, слабо

выпуклую оливоидную ленту. Передняя лента слабо выпуклая. Складчатая пластина сравнительно узкая, слабо изогнутая, с 5 складками примерно одинаковой выраженности. Третья сверху складка слегка шире остальных. Внутренняя губа устья слабо выпуклая. Внешняя губа почти прямая вентральном и латеральном виде. Раковина светло-оранжевая; протоконх чуть светлее остальной раковины; складчатая пластина беловатая; передняя лента

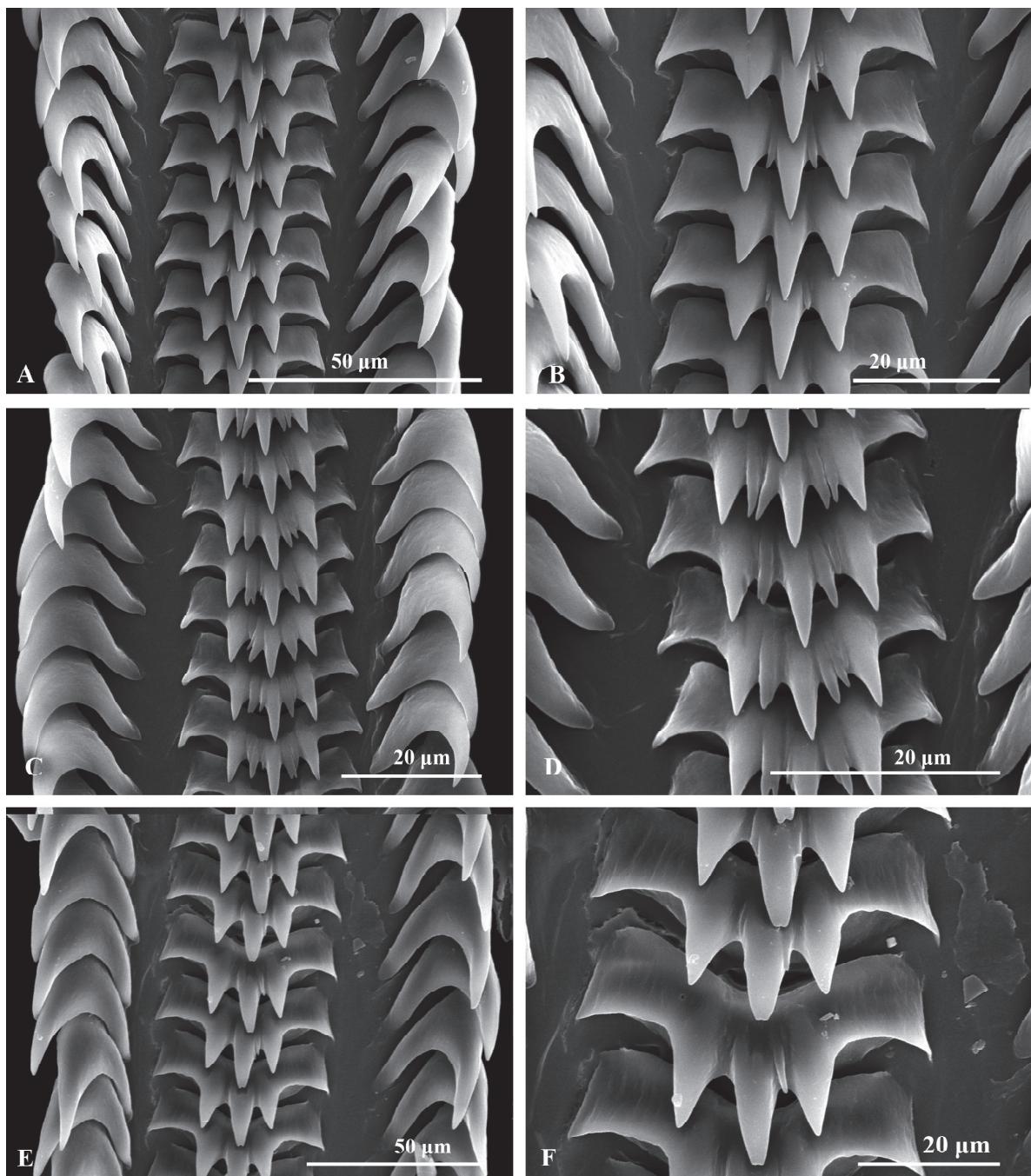


FIG. 4. Radulae of *Ancilla morrisoni* sp. nov. (A-D) and *A. kaviengiensis* sp. nov. (E-F). *Ancilla morrisoni* sp. nov. A-B. Holotype, MNHN IM-2013-55401. C-D. Paratype MNHN IM-2013-55403, SL 4.8 mm. *Ancilla kaviengiensis* sp. nov. E-F. Holotype, MNHN IM-2013-55130, SL 10.4 mm, shell on Fig. 21B).

Рис. 4. Радулы *Ancilla morrisoni* sp. nov. (A-D) и *A. kaviengiensis* sp. nov. (E-F). *Ancilla morrisoni* sp. nov. A-B. Голотип, MNHN IM-2013-55401. C-D. Паратип, MNHN IM-2013-55403, SL 4.8 мм. *Ancilla kaviengiensis* sp. nov. E-F. Голотип, MNHN IM-2013-55130, SL 10.4 мм, раковина на Рис. 21Б).

чуть темнее, чем прилежащие участки раковины; устье внутри светло-оранжевое.

Размеры: голотип SL 10.0 мм, AL 7.5 мм, SW 4.5 мм.]

Radula of the holotype (Fig. 4 A-B) rather long, consisting of 80 rows of teeth, of which around 10 are not fully formed. Length 0.9 mm (12% of AL), width of membrane about 85 μ m (0.85% SL, 1.1% AL). Rachidian with three large pointed cusps, cen-

tral cusp longest; an additional small denticle present between cusps in some rows. Lateral teeth flat, simple hook-shaped. Radula of subadult paratype (Fig. 4 C-D) similar to that of holotype, although the additional denticles between major cusps on the rachidian are relatively larger and there can be up to two denticles between cusps. Radular width around 60 μ m, but relatively wider (1.7% AL).

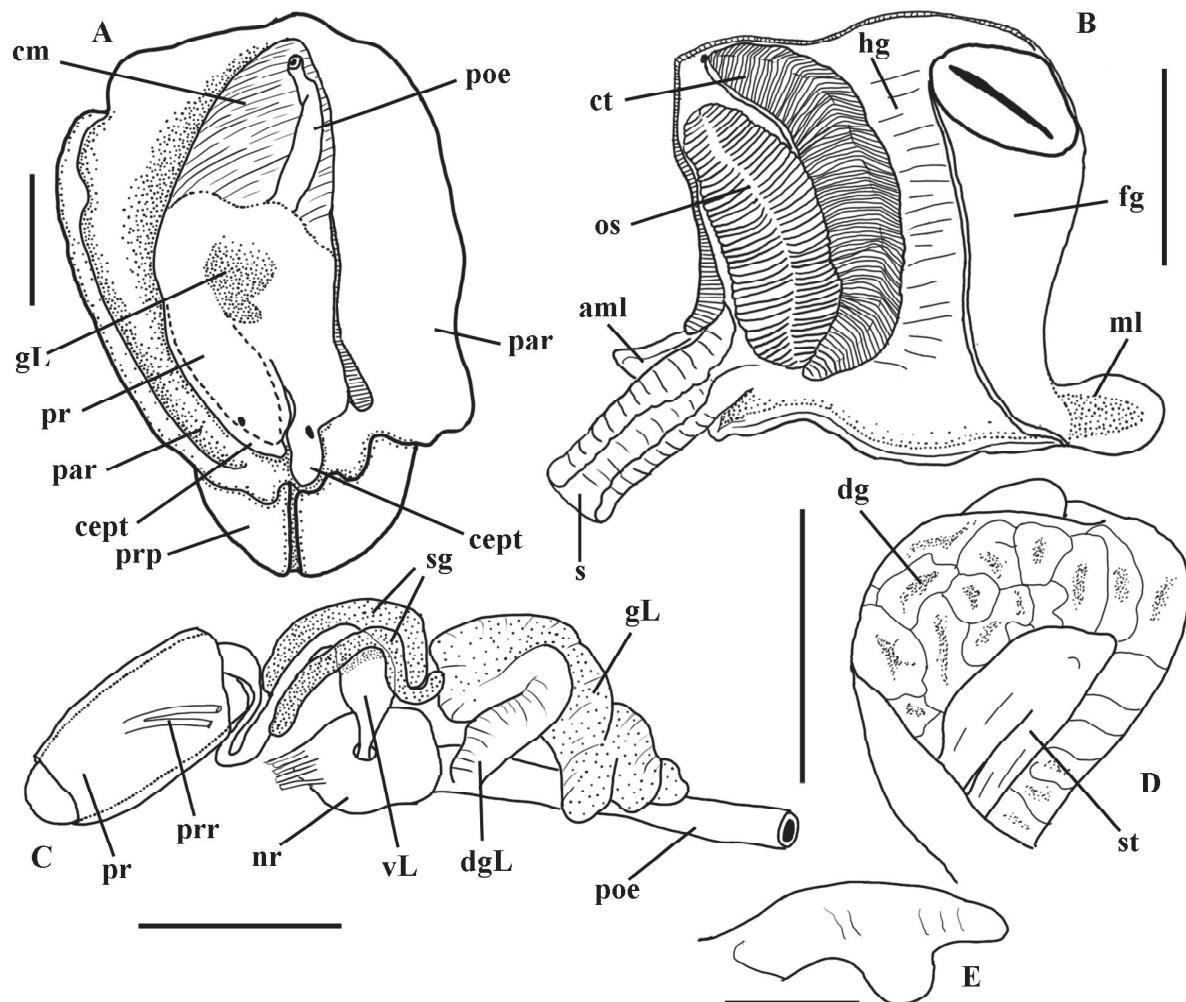


FIG. 5. Anatomy of *Ancilla morrisoni* sp. nov. (A-C – holotype, MNHN IM-2013-55401; D – juvenile paratype MNHN IM-2013-55403, E – paratype MNHN IM-2013-55402). A. Head-foot, dorsal view, mantle and visceral mass removed. B. Mantle. C. Anterior foregut, left lateral view. D. Visceral mass and stomach. E. Penis. Scale bars – 1 mm.
Abbreviations: aml – anterior mantle lobe; cept – cephalic tentacle; ct – ctenidium; dg – digestive gland; dgL – duct of gland of Leiblein; fg – female gonoduct; gL – gland of Leiblein seen through the body walls; hg – hypobranchial gland; ml – posterior mantle lobe; nr – circumoesophageal nerve ring; os – osphradium; par – parapodia; poe – posterior oesophagus; pr – proboscis seen through the body walls; prp – propodium; prr – proboscis retractors; s – siphon; sg – salivary gland; st – stomach; vL – valve of Leiblein.

РИС. 5. Анатомия *Ancilla morrisoni* sp. nov. (А-С – голотип, MNHN IM-2013-55401; Д – неполовозрелый паратип, MNHN IM-2013-55403, Е – паратип, MNHN IM-2013-55402). А. Цефалоподиум, дорсальный вид, мантия и туловищный мешок удалены. В. Мантия. С. Передний отдел пищеварительной системы, вид слева. Д. Туловищный мешок и желудок. Е. Пенис. Масштаб – 1 мм.

Base colour of living animal (Fig. 3 D) yellowish flesh, with irregularly shaped orange-brownish spots, covering major part of parapodia. Propodium and siphon speckled with small orange-brownish dots. Posterior foot edge with dense small whitish spots. In crawling snails, parapodia join on anterior band of the shell, covering the base of siphon. Dorsal longitudinal cleft of propodium able to be narrowed or widened, to form a wide and deep cleft, or a narrow line.

Anatomy (Fig. 5). Head-foot typical for the genus (Fig. 5A). Foot truncated posteriorly, nearly

straight, operculum absent. Parapodia strongly contracted, broad, propodium semi-circular, symmetrical, subdivided longitudinally by rather broad and deep cleft. Head strongly asymmetrical, with short flattened flaps contracted dorso-ventrally and small indistinct eyes seen as darker dots through the walls of the flaps. Rhynchostome positioned under the right flap.

Mantle nearly square (Fig. 5B). Siphon long and muscular, Mantle edge thickened, forming shallow fold, probably able to reflect over the lip. Osphradium large, with very narrow axis, ctenidium slightly

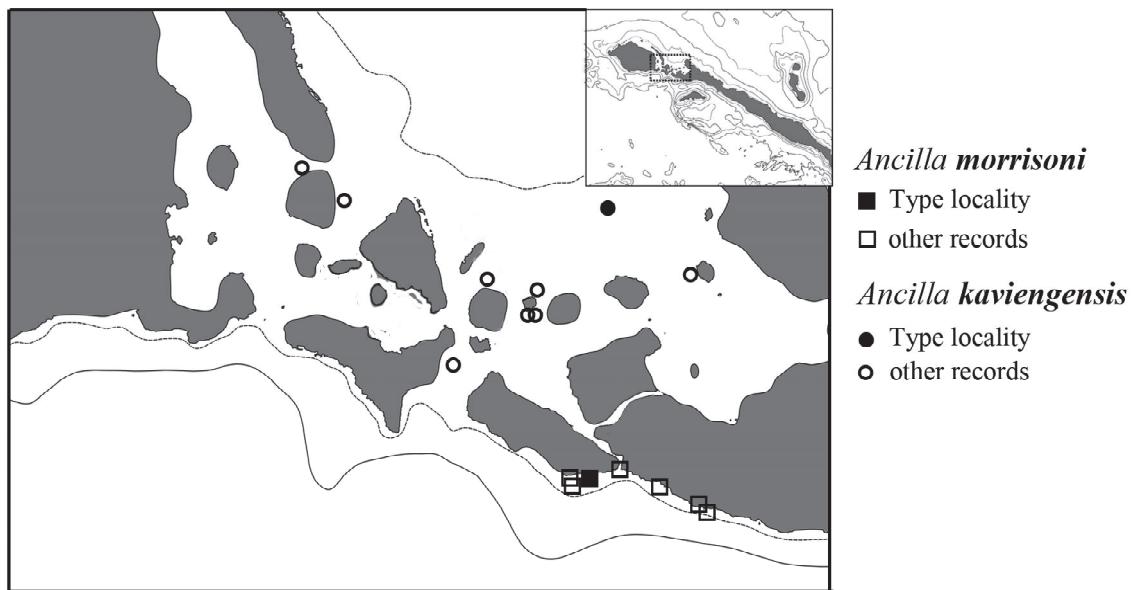


FIG. 6. Distribution of *Ancilla morrisoni* sp. nov. and *A. kaviengensis* sp. nov. in the lagoon between the tip of New Ireland and New Hanover.

РИС. 6. Распространение *Ancilla morrisoni* sp. nov. и *A. kaviengensis* sp. nov. в лагуне между окончностью Новой Ирландии и Новым Ганновером.

longer than osphradium, narrow, formed by tall subtriangular lamellae. Female pallial gonoduct swollen and occupying a significant part of mantle cavity volume, indicating that the specimen is mature. Hypobranchial gland of tall epithelium, not forming distinct folds. Posterior mantle lobe short, probably contracted, concave on inner surface. Anterior mantle lobe rather distinct, probably capable of extending through the siphonal notch.

Anterior foregut. All organs of body haemocoel are very compactly packed in natural position (significantly expanded on Fig. 5C). Proboscis short but broad, cylindrical, about 1 mm in length, gradually tapering to the tip. Rhynchodaeum thin, semi-transparent. Very weak, paired, lateral proboscis retractors attached symmetrically to the middle part of the rhynchodaeum. Rather large unpaired odontophoral retractor passing through the nerve ring to fuse with columellar muscle. Odontophore spanning about half of proboscis length, protruding backward from rear of retracted proboscis. Broad, paired, subradular cartilages fused in anterior part, but free along most length and connected with muscle. Salivary glands elongated, seemingly tubular, lying on both sides of anterior oesophagus. Salivary ducts fused with anterior oesophagus immediately after leaving the gland. In natural position anterior oesophagus together with the salivary glands are coiled and form nearly complete ring. Valve of Leiblein large, well defined. Gland of Leiblein long, strongly coiled, tubular, opening by a broad duct immediately posterior to the nerve ring. Posterior part of the gland pale-brownish, anterior whitish.

Contrary to other studied *Ancilla* species, the gland of Leiblein does not have muscular walls.

Stomach of a juvenile paratype (MNHN IM-2013-55403) with very short posterior mixing area (Fig. 5D).

Penis (Fig. 5E) of paratype MNHN IM-2013-55402 with smooth walls, short, significantly shorter than the mantle cavity, forming a relatively very large papilla, terminating in the seminal opening.

Remarks. In shell outline *Ancilla morrisoni* is extremely similar to *A. kaviengensis* sp. nov. with which it is broadly sympatric (for differences see under the description of the latter species). *Ancilla morrisoni* is also similar to *A. sarda* (Reeve, 1864), differing in the presence of the olivoid groove and a labral denticle. Another similar species is *Ancilla chrysoma* Kilburn, 1981, which differs from *A. morrisoni* by a broader aperture, a less constricted shell base, the presence of a diffuse white band below the suture on the last whorl, and a much larger size, attaining 40.9 mm versus 11 mm in *A. morrisoni*.

Ancilla species are most diverse in eastern Africa [Kilburn 1981, Boyer 2015], with few species reaching waters off India. The only species extending further eastward is *Ancilla ampla* Gmelin, 1791, with its subspecies *cylindrica* (G.B. Sowerby II, 1859) recorded as far east as the Coral Sea off Queensland [Kilburn, 1981] and the Philippines [Poppe, 2008]. *Ancilla morrisoni* together with *A. kaviengensis* extends the distribution of the genus further eastward, and is one of two species of *Ancilla* so far known from Papua New Guinea

(both described herein as new). No *Ancilla* species were found during the PAPUA NIUGINI expedition in Madang.

Etymology. The species is named after Hugh Morrison, diver, collector and dealer from Perth, who fruitfully participated in the PAPUA NIUGINI and KAVIENG 2014 expeditions to Papua New Guinea and collected the first live-taken specimen of this new species.

Distribution. All known specimens of the species were collected on the open exposed coast of the Bismarck Sea (southern coast of Baudison Island and New Ireland proper) (Fig. 6) at depths 8–41 m.

Ancilla kaviengensis sp. nov.
(Figs 4 E-F; 6; 7)

urn:lsid:zoobank.org:act:89E0F30B-9B60-4849-8B91-0B6BB0BE6848

Type material: Holotype MNHN IM-2013-55130 and 3 paratypes MNHN IM-2013-55138 (KAVIENG 2014, st. KD70), IM-2013-51964 (st. KR82), IM-2013-55102 (st. KS57).

Type locality: Papua New Guinea, New Ireland Province, Kavieng Lagoon, NW side of Ral Island, 02°36,4'S, 150°42,4'E, 19 m [KAVIENG 2014 Expedition, st. KB62].

Sequenced material (paratypes). Papua New Guinea, New Ireland Province, Kavieng Lagoon, KAVIENG 2014 Expedition, st. KD70, Eickstedt Passage W. of Usien Island, 02°38,3'S, 150°45,6'E, 10–15 m, coral rubble, sand (MNHN IM-2013-55138); st. KR82, SW of Ungon Island, 02°39,6'S, 150°39,9'E, 2–12 m, sand (MNHN IM-2013-51964); st. KS57, N point of Kaboteron Island, 02°38,9'S, 150°40,1'E, 7–9 m (MNHN IM-2013-55102).

Material examined. Type material (see above). Papua New Guinea, New Ireland Province, Kavieng Lagoon, KAVIENG 2014 Expedition. St. KB36, N side of Wadei Island, sand and rubble, 02°38,8'S, 150°38,4'E, 3–8 m slope (1 dd); st. KR116, Senta Channel, 02°34,6'S, 150°31,8'E, 9–11 m, sand (1 dd); st. KR124 E side of Tsoileunung Island, sand, rubble, some live coral, 02°36'S, 150°33,4'E, 6–21 m, (1 dd); st. KR170, SW point of Ungon Island, 02°39,5'S, 150°39,7'E, 1–8 m, sand and seagrass (1 dd); st. KPS09, 02°41,6'S, 150°37,2'E, 18–27 m, sediment in ledges, reef wall (2 dd); st. KPS10, 02°41,6'S, 150°37,2'E, 12–14 m, sediment between coral patches (1 dd).

Description (holotype). Shell oblong-ovate (Fig. 7 A-B), with evenly convex sides, maximum width median; spire short, blunt, with weakly convex whorls. Protoconch poorly delimited, its border can be deduced from the slight colour change – protoconch semitransparent; teleoconch whorls pale flesh colour and opaque. Protoconch diameter about 1.15 mm, exposed height about 0.75 mm, whorls about 1.75, suture of initial whorl not overlaid by callus. Teleoconch whorls about two, most shell surface

glossy, not microshagreened, but anterior part of the primary callus, plication plate, edge of siphonal fasciole and very narrow band along the outer lip heavily shagreened and mat. Primary callus of the same colour as shell base, visibly poorly separated from adjacent surface.

Aperture with its greatest width slightly anterior to median, tapering adapically; siphonal canal wide, very shallowly notched. Olivoid groove narrow, well defined, terminating with denticle, and delimiting narrow, weakly convex, olivoid band. Anterior band slightly convex. Plication plate fairly narrow, not strongly twisted, with 5 lirae of about equal strength and 6th very weak lowest one, the third abapical slightly broader than the others. Inner lip gently convex. Outer lip weakly convex. Shell of pale body colour, with slightly darker irregular patches along suture. Besides, there are irregularly spaced dense and very narrow lighter axial lines, corresponding to growth lines. Protoconch uniformly coloured, very slightly darker. Plication plate and anterior band of the same colour as adjacent surface, aperture interior same shade, slightly darker.

Measurements: holotype SL 10.4 mm, AL 7.4 mm, SW 4.7 mm.

[Описание (голотип). Раковина удлиненно-овальная (Fig. 7 A-B), с равномерно выпуклым профилем, максимальная ширина раковины приходится на середину высоты, завиток короткий, притупленный, со слабо выпуклыми оборотами. Протоконх слабо дифференцирован, его границу можно определить по слабому изменению цвета: протоконх полупрозрачный, обороты телеоконха бледно-телесного цвета, непрозрачные. Диаметр протоконха около 1,15 мм, высота около 0,75 мм, количество оборотов около 1,75; шов первого оборота протоконха не перекрыт каллусом. Телеоконх образован примерно двумя оборотами; большая часть поверхности раковины глянцевая, но передняя часть первичного каллуса, край сифональной фасциолы и очень узкая полоса вдоль внешней губы устья матовые и покрыты густо расположеннымными микрогранулами. Первичный каллус имеет ту же окраску, что и поверхность раковины и слабо дифференцирован от прилегающей поверхности раковины.

Устье имеет наибольшую ширину чуть впереди середины длины, сужается по направлению к вершине; сифональный канал широкий, с очень мелкой сифональной вырезкой. Оливоидный желобок узкий, четкий, завершается зубчиком на внешней губе и отделяет узкую, слабо выпуклую оливоидную ленту. Передняя лента слабо выпуклая. Складчатая пластина сравнительно узкая, слабо изогнутая, с 5 складками примерно одинаковой выраженности и шестой очень слабой. Третья сверху складка слегка шире остальных. Внутренняя губа устья слабо выпуклая. Раковина бледно-телесного цвета, с более темными нерегулярно расположенными пятнами вдоль шва; кроме того, имеются нерегулярно расположенные частые и очень тонкие осевые более светлые линии, соответствующие линиям роста. Протоконх чуть темнее остальной части раковины. Складчатая пластина и передняя лента того же цвета, что и остальная часть раковины, устье внутри того же оттенка, но темнее.

Размеры: голотип SL 10.4 мм, AL 7.4 мм, SW 4.7 мм.]



FIG. 7. Shells and live animal of *Ancilla kaviengensis* sp. nov. A-B. Holotype, MNHN IM-2013-55130, SL 10.4 mm (radula see Fig. 3 E-F). C-E. Paratype, MNHN IM-2013-51964, E. Crawling animal (photo of Laurent Charles). F. Specimen from st. KR116, SL 11.1 mm. Shells at the same scale.

РИС. 7. Раковины и живые моллюски *Ancilla kaviengensis* sp. nov. А-В. Голотип, MNHN IM-2013-55130, SL 10.4 мм (радула на Рис. 3 Е-Ф). С-Е. Параптип, MNHN IM-2013-51964, Е. Ползущий моллюск (фото Laurent Charles). F. Экземпляр, собранный на ст. KR116, SL 11.1 мм. Раковины в одной масштабе.

Radula of the holotype (Fig. 4 E-F) rather long, consisting of about 60 rows of teeth, of which around 20 are not fully formed. Length 1.0 mm (13.5% of AL), width of the membrane about 120 μm (1.15% SL, 1.6% AL). Rachidian with three large pointed cusps, central one the longest; an additional small denticle present between cusps in some rows. Lateral teeth flat, simple hook-shaped.

Living animal (Fig. 7E) white, with few irregularly shaped orange-brownish spots on parapodia.

Entire body with dense small distinct whitish spots. In crawling snails, parapodia join on anterior band of the shell, covering the base of the siphon.

Remarks. *A. kaviengensis* most closely resembles *A. morrisoni*, from which it differs in lighter coloured and slightly narrower shell. The darker axial narrow lines are better pronounced in *A. kaviengensis*, although they also can be observed on young specimens of *A. morrisoni*. The body of a live animal of *A. kaviengensis* is less marked with

orange-brown spots than that of *A. morrisoni*, it is lighter and with more obvious whitish spots. It should be noted that juveniles of both species are more similar than adults in body colouration. Some of the specimens, that we attribute here to *A. kaviengensis* on the basis of distribution, are intermediate in shape and colour between holotypes of both species and no clear morphological gap between two species can be determined.

The radulae of the holotypes of both species (having similar shell length) are similar in length and tooth morphology, although the radular ribbon of the holotype of *A. kaviengensis* is significantly broader with fewer rows of teeth. Since the degree of variability of radular morphology was not studied, it is impossible to conclude whether these differences can be attributed to inter- or intraspecific variability.

The molecular analysis (Fig. 2) supports the hypothesis that two species are present, even if the genetic distances between the two species are among the smallest between-species distances.

The ecological preferences of two species differ (Fig. 6). *A. morrisoni* was collected on the open exposed coast of Baudison Island and New Ireland proper, while *A. kaviengensis* was collected in the sheltered areas inside Lagoon.

Etymology. The species is named after the type locality – Kavieng Lagoon.

Distribution. All known specimens were collected in the sheltered areas inside Kavieng Lagoon at depths 1-27 m.

Ancilla atimovatae sp. nov.

(Figs 8 A-F; 9 A-C)

urn:lsid:zoobank.org:act:A5FD2E9B-EDEC-41BB-9E82-9402D8F3534B

Type material: Holotype: MNHN IM-2009-15511, paratypes MNHN IM-2000-32425 (Lavanono area, from local fishermen).

Type locality: South Madagascar: west of Cap Ste Marie near village of Lavanono, NW Rocher de l'Albatros, 25°28.2'S, 44°56.4'E, 12-14 m, [ATIMO VATAE st. BS01].

Description (holotype). Shell ovate, with evenly convex sides; spire short, rather blunt, with slightly convex whorls. Protoconch sharply delimited, of about 1.75 whorls, low, glossy, first whorl flattened above, remaining moderately convex, diameter about 1.7 mm, exposed height about 1.1 mm. On posteriormost half whorl of the protoconch callus gradually extending from abapical suture and posterior 0.2 of the protoconch whorl completely covered by thin primary spire callus. Teleoconch whorls about 2.25. Shell surface glossy, with few broadly spaced micropustules. Primary

spire callus of the same colour as shell base, its anterior border well defined due to slight elevation over cloak.

Aperture with its greatest width at median, tapering adapically; siphonal canal wide, very shallowly notched. Olivoid groove absent; anterior band slightly convex, not subdivided into upper and lower parts and not reaching the lip. Plication plate fairly narrow, medium twisted with 5 lirae, the second abapical strongest. Inner lip gently convex. Outer lip nearly straight in side view. Ground colour chestnut, interrupted by unevenly spaced bluish bands differing in width. Spire nearly uniformly bluish. Protoconch dark flesh-coloured, anterior band dark chestnut on apertural side of the shell and lighter on the dorsal side, with still lighter band along the rear edge of anterior band. Plication plate off-white; aperture light orange-brown.

Measurements: SL 15.0 mm, AL 10.7 mm, SW 7.9 mm.

[Описание (голотип). Раковина овальная, с равномерно выпуклым профилем; завиток короткий, притупленный, со слабо выпуклыми оборотами. Протоконх четко дифференцирован, примерно из 1,75 оборотов, низкий, блестящий, первый оборот уплощен сверху, оставшаяся часть протоконха умеренно выпуклая; диаметр протоконха около 1,7 мм, высота около 1,05 мм. На последней половине оборота протоконха каллус постепенно распространяется от нижнего шва в направлении вершины и самые последние 0,2 оборота протоконха полностью покрыты тонким первичным каллусом. Телеоконх образован примерно 2,25 оборотами. Поверхность раковины глянцевая, с редкими микрогранулами. Первичный каллус имеет ту же окраску, что и поверхность раковины, его передний край хорошо выражен благодаря возвышению на поверхностью последнего оборота.

Устье имеет наибольшую ширину в середине длины, сужается по направлению к вершине; сифональный канал широкий, с очень мелкой сифональной вырезкой. Оливовидный желобок отсутствует. Передняя лента слабо выпуклая, не подразделена на верхнюю и нижнюю части, не доходит до губы. Складчатая пластинка сравнительно узкая, умеренно изогнутая, с 5 складками, из которых вторая сверху самая выраженная. Внутренняя губа устья слабо выпуклая. Внешняя губа почти прямая вентральном и латеральном видах. Раковина каштановая, с неравномерно расположенными и различающимися по ширине голубоватыми полосами. Завиток почти равномерно голубоватый. Протоконх темно-телесного цвета, передняя лента темно каштановая на вентральной стороне раковины и более светлая на дорсальной, с более светлой полосой вдоль заднего края передней ленты. Складчатая пластинка беловатая, устье внутри светло оранжевое.

Размеры: голотип SL 15.0 мм, AL 10,7 мм, SW 7.9 мм.]

Radula of holotype (Fig. 9 A-C) rather long, consisting of 75 rows of teeth, of which 30 are not fully formed. Length 0.95 mm (8.9% of AL), width of the membrane about 140 µm (0.93% SL, 1.3% AL). Rachidian with numerous (11-17) narrow cusps, varying in number and shape, even in consecutive rows, outer and central cusps slightly longer

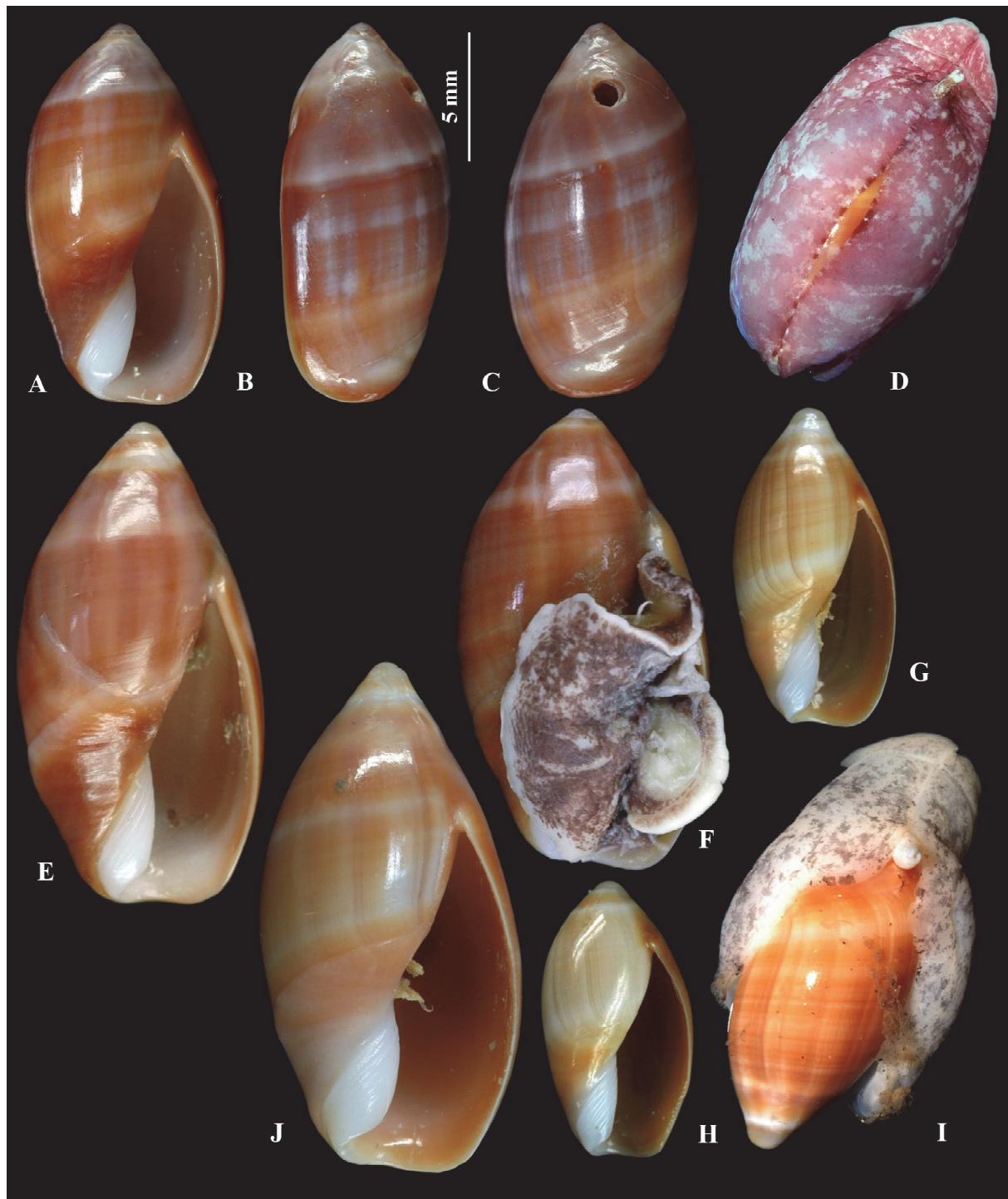


FIG. 8. Shells and live animal of *Ancilla atimovatae* sp. nov. (A-F) and *Ancilla ventricosa* (Lamarck, 1811) (G-J). *Ancilla atimovatae* sp. nov.: A-D. Holotype, MNHN IM-2009-15511, SL 15.0 mm. D – crawling live animal (photo P. Maestrati). E-F. Paratypes, MNHN IM-2000-32425, SL 18.9 and 18.0 mm. *Ancilla ventricosa*: G. MNHN IM-2009-15544, SL 10.7 mm (radula see Fig. 8D). H-I. MNHN IM-2009-15537, SL 12.4 mm; I. Crawling animal. J. MNHN IM-2009-15545, SL 20.0 mm.

РИС. 8. Раковины и живые моллюски *Ancilla atimovatae* sp. nov. (A-F) и *Ancilla ventricosa* (Lamarck, 1811) (G-J). *Ancilla atimovatae* sp. nov.: A-D. Голотип, MNHN IM-2009-15511, SL 15.0 mm. D. Ползущий моллюск (фото P. Maestrati). E-F. Паратипы, MNHN IM-2000-32425, SL 18.9 и 18.0 мм. *Ancilla ventricosa*: G. MNHN IM-2009-15544, SL 10.7 мм (радула на Рис. 8D). H-I. MNHN IM-2009-15537, SL 12.4 мм; I. Ползущий моллюск. J. MNHN IM-2009-15545, SL 20.0 мм.

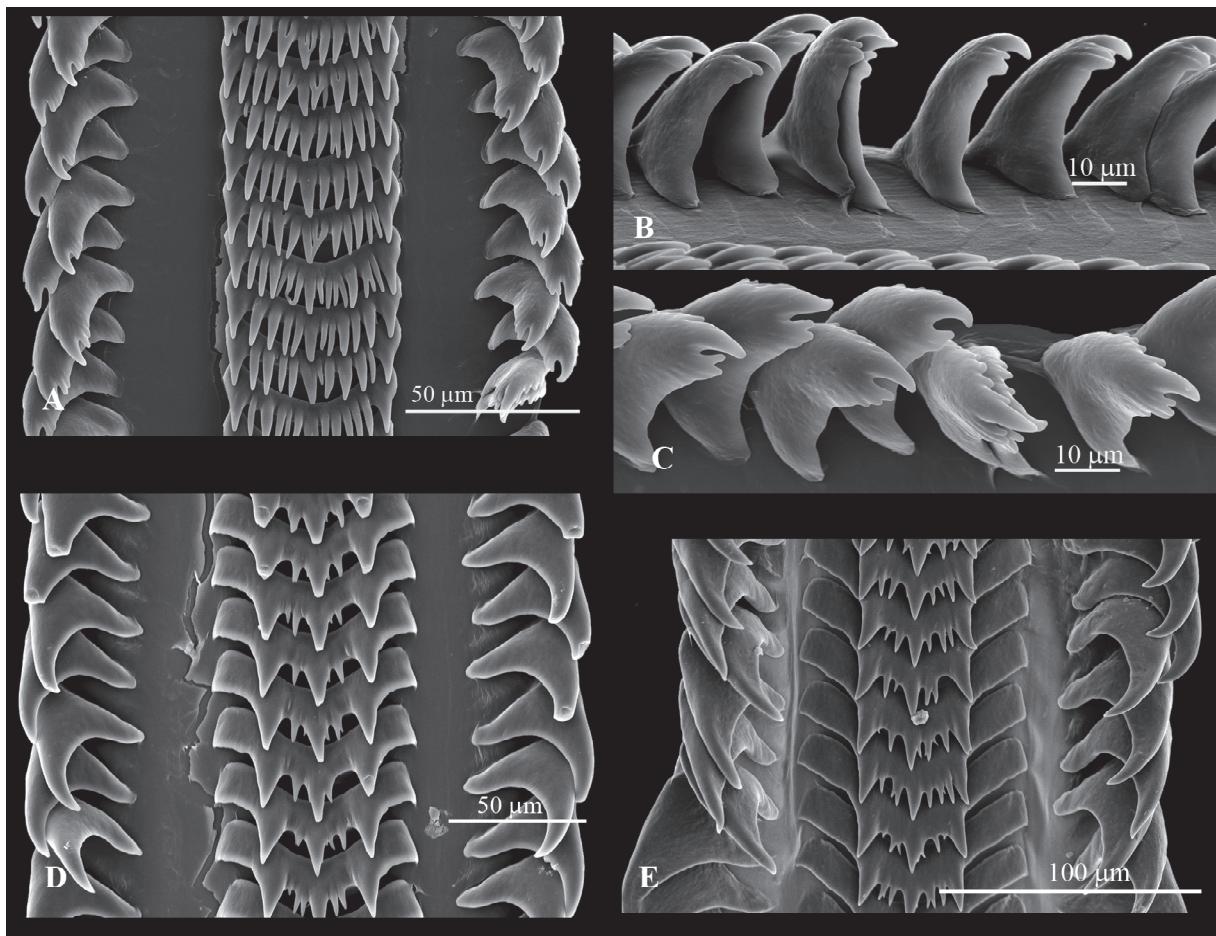


FIG. 9. Radulae of *Ancilla* spp. A-C. *Ancilla atimovatae* sp. nov., holotype, A. Dorsal view of the central part of the radula membrane; B, C. Lateral and dorsal views of the lateral teeth. D. *A. ventricosa* (Lamarck, 1811), MHN IM-2009-15544, SL 10.7 mm (shell see Fig. 7G). E. *A. ihaumeti* sp. nov., holotype, MHN IM-2009-15513, SL 15.3 mm.

РИС. 9. Радулы *Ancilla* spp. А-С. *Ancilla atimovatae* sp. nov., голотип, А. Вид центральной части радулярной мембранны с дорсальной стороны. Б, С. Вид латеральных зубов сбоку и с дорсальной стороны. Д. *A. ventricosa* (Lamarck, 1811), MHN IM-2009-15544, SL 10.7 мм (раковина на Рис. 7Г). Е. *A. ihaumeti* sp. nov., голотип, MHN IM-2009-15513, SL 15.3 мм.

and broader than intermediate cusps. Lateral teeth narrow and tall, bifurcating on the tip and with distinct serration both on inner and outer sides (Fig. 9 B-C).

In the crawling animal (Fig. 8D) parapodia covering completely the shell, with only the protoconch exposed between parapodia, which meet dorsally and embrace the siphon. Foot, including the sole, propodium and parapodia bright purple, with irregularly shaped lighter spots. Upper edge of parapodia with narrow longitudinal darker band. Siphon of similar colour, but lighter.

Remarks. The holotype is a sequenced specimen, two additional paratypes were obtained from local fishermen in Lavanono (Fig. 8 E-F). The largest paratype attains 18.9 mm, its radula appeared in all details similar to that of holotype. Operculum small, about 0.25 of aperture length, ovate, transparent, yellowish.

Ancilla atimovatae is very similar to the polymorphic species *Ancilla ventricosa* (Lamarck, 1822), which occurs sympatrically near Lavanono. The two species can hardly be distinguished in shell morphology (Fig. 8 G-J – *A. ventricosa* from Lavanono), but the colour of the shell of *A. atimovatae* is slightly more saturated. Also the primary callus on the spire whorls is thicker in *A. atimovatae*. Given that *A. ventricosa* is one of the most variable species of the genus [Kilburn 1981], these differences can hardly be considered significant. Nevertheless, the two species can be immediately recognized by the colour of the living animal (compare Fig. 8D and 8I) and their radulae. Among *Ancilla* species the radula of *A. atimovatae* is unique in the shape of rachidian, which is somewhat similar to that in *A. acuminata* (G.B. Sowerby II, 1859) and *A. eburnea* (Deshayes, 1830), which were classified by Kilburn [1981] in *Ancilla* (*Sparellina*).

Nevertheless, we think that the similarity is superficial. In *A. acuminata* and *A. eburnea*, the rachidian teeth have more or less pronounced lateral flaps, whereas in *A. atimovatae* there are no lateral flaps and the outer cusps are at the lateral edges of the teeth. The lateral teeth of *A. atimovatae* are unique in that they are serrated on the tip and along outer edge, unlike other studied *Ancilla* species in which the lateral teeth are simple, flat and hook-shaped. The radula of our specimen of *A. ventricosa* (Fig. 9D) resembles that illustrated by Kilburn [1981: figs 221–222]: the rachidian teeth are tricuspid with small additional denticles between the major cusps. We failed to sequence the COI gene for the holotype of *A. atimovatae*, but in the multigene analysis the two species *A. atimovatae* and *A. ventricosa* were clearly separate (see above), and not even sister species.

Judging from the large number of empty shells of *Ancilla* collected in vicinities of Lavanono, as well as purchased from local fishermen, the species is one of the most abundant ancillid in the area and outnumbers *A. ventricosa*.

Etymology. The species is named to commemorate the Atimo Vatae expedition to the “Deep South” of Madagascar, during which it was discovered.

Distribution: Known only from southernmost Madagascar near Lavanono, confirmed depth 12–14 m.

Ancilla lhaumeti sp. nov.
(Figs 9E; 10)

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Ancilla (Sparella) eloisae – Lhaumet, 2010: 7, Figs. 1–3 (unavailable name under Art. 16 of ICZN, since it was not declared to be intentionally new and there was no explicit fixation of the type material).

Type material: Holotype MHN IM-2009-15513, three paratypes (from different stations, see Material examined below) MHN IM-2009-15503, MHN IM-2009-15523, MHN IM-2009-15481.

Type locality: South Madagascar, near Cap Malaimpioka, 25°22.4–25°22.7'S, 44°50.2–44°50.6'E, 19–20 m [ATIMO VATAE St. BP37].

Material examined: Type material (see above). South Madagascar, ATIMO VATAE, st. BM06, Ambatobe, Bavarama, 25°27.9'S, 44°57.6'E, 0–1 m, 1 lv (sequenced specimen, MHN IM-2009-15507); st. BP21, west of Lavanono, 25°23.1–23.2'S, 44°51.4–51.6'E, 20–23 m, 2 lv (MHN IM-2009-15533, paratype MHN IM-2009-15481); st. BP42, west of Lavanono, 25°22.8–23.7'S, 44°51.1'E, 18–21 m, 2 lv (MHN IM-2009-15506, MHN IM-2009-15528); st. BS11, Rocher de l'Albatros, 25°28.6'S, 44°56.8'E, 8–11 m, 1 lv (paratype, MHN IM-2009-15503); st. BS13, Lavanono, 25°25.6'S, 44°55.9'E, 9 m, 3 lv (sequenced paratype MHN IM-2009-15523, sequenced specimens MHN IM-2009-

15482, MHN IM-2009-1550), st. BP37, near Cap Malaimpioka, 25°22.4–22.7'S, 44°50.2–50.6'E, 19–20 m (sequenced specimen MHN IM-2009-15515).

Description (holotype). Shell oblong-ovate, with evenly convex sides; spire short, rather blunt, with slightly convex whorls. Protoconch sharply delimited, of about 1.75 whorls, low, first whorl flattened above, remainder weakly convex, nearly flat-sided, diameter about 1.75 mm, exposed height about 1 mm. Less than one initial whorl of the protoconch free from callus, glossy, then callus gradually extending from abapical suture and posteriormost 0.25 of protoconch whorl before transition to teleoconch completely covered by thin primary spire callus. Teleoconch whorls about 2.5. Entire shell surface microshagreened, more densely so on anterior band and plication plate, anterior border of primary spire callus undefined.

Aperture with greatest width just anterior to median, tapering adapically; siphonal canal wide, very shallowly notched. Olivoid groove absent; anterior band slightly convex, not subdivided into upper and lower parts and not reaching the lip. Plication plate fairly narrow, not strongly twisted, with 6 lirae, the third abapical strongest. Inner lip gently convex. Outer lip nearly straight in side view. Ground colour light chestnut, with distinct, very narrow and irregularly spaced, darker axial lines, not seen on anterior band. Protoconch pale flesh-coloured, subsutural band lighter, of the same colour as protoconch, more pronounced on upper teleoconch whorls and nearly absent on last whorl. Plication plate off-white; anterior band slightly darker than body whorl cloak, of the same colour, aperture light orange-brown.

Measurements: (holotype largest available specimen): SL 15.3 mm, AL 11.8 mm, SW 7.3 mm.

[Описание (голотип).] Раковина удлиненно-овальная, с равномерно выпуклым профилем, завиток короткий, притупленный, со слабо выпуклыми оборотами. Протоконх хорошо дифференцирован, низкий, образован примерно 1,75 оборотами; первый оборот уплощен сверху, оставшаяся часть протоконха слабо выпуклая. Диаметр протоконха около 1,75 мм, высота около 1 мм. Первый оборот протоконха не покрыт каллусом, блестящий, затем каллус постепенно распространяется от нижнего шва в направлении вершины и самые последние 0,25 оборота протоконха перед границей с телооконхом полностью покрыты тонким первичным каллусом. Телооконх образован примерно 2,5 оборотами. Вся поверхность раковины покрыта микрогранулами, более плотно расположеными на передней ленте и складчатой пластинке. Передний край первичного каллуса не выражен.

Устье имеет наибольшую ширину чуть ниже середины длины, сужается по направлению к вершине; сифональный канал широкий, с очень мелкой сифональной вырезкой. Оливоидный желобок отсутствует. Передняя лента слабо выпуклая, не подразделена на верхнюю и нижнюю части, не доходит до губы. Складчатая пластинка сравнительно узкая, умеренно изогнутая, с 6 складками,



FIG. 10. Shells and live animal of *Ancilla ihaumeti* sp. nov. (A-H) and *Ancilla giaquintoi* Bozzetti, 2006 (I-K). A. *ihaumeti* sp. nov.: A-C. Holotype, MNHN IM-2009-15513, SL 15.3 mm. D. Paratype, MNHN IM-2009-15523, SL 13.2 mm. E-F. Paratype, MNHN IM-2009-15503, SL 11.8 mm; F. Crawling animal, approximately at the same scale. G-H. Paratype MNHN IM-2009-15481, SL 10.8 mm. A. *giaquintoi* Bozzetti, 2006: I-K. Holotype, MNHN IM-2000-9793, SL 19.9 mm.

РИС. 10. Раковины и живой моллюск *Ancilla ihaumeti* sp. nov. и *Ancilla giaquintoi* Bozzetti, 2006 (I-K). A. *ihaumeti* sp. nov.: A-C. Голотип, MNHN IM-2009-15513, SL 15.3 мм. D. Паратип, MNHN IM-2009-15523, SL 13.2 мм. E-F. Паратип, MNHN IM-2009-15503, SL 11.8 мм; F. Ползущий моллюск, примерно в том же масштабе. G-H. Паратип, MNHN IM-2009-15481, SL 10.8 мм. A. *giaquintoi* Bozzetti, 2006: I-K. Голотип, MNHN IM-2000-9793, SL 19.9 мм.

из которых третья сверху самая выраженная. Внешняя губа почти прямая в латеральном виде. Раковина светло-каштановая, с отчетливыми очень узкими и нерегулярно расположенными более темными осевыми линиями, незаметными на передней ленте, и светлой пришовной полосой бледно-телесного цвета, лучше выраженной на верхних оборотах телоонха и почти незаметной на последнем обороте. Протоонх бледного телесного цвета; складчатая пластинка беловатая, передняя лента темнее, чем остальная часть последнего оборота, но того же цвета, устье внутри светло-оранжевое.

Размеры: (голотип самый крупный из доступных экземпляров) SL 15.3 мм, AL 11,8 мм, SW 7.3 мм.]

Radula of holotype (Fig. 9E) rather long, consisting of 80 rows, of which 15 are not fully formed. Length 1.22 mm (10.4% of AL), width of the membrane about 220 μ m (1.43% SL, 1.86% AL). Rachidian with 3 major subequal cusps, between which 2-3 small cusps are situated, varying in size from row to row. Lateral teeth flat, broadly hook-shaped, height slightly exceeding the width of the base.

In the crawling animal (Fig. 10F), parapodia covering the shell laterally and anteriorly, meeting antero-dorsally, embracing the siphon. Foot truncated posteriorly. Body flesh-coloured, speckled with irregularly shaped brown spots, propodium lighter coloured, dorsal edge of parapodia brown.

Remarks. The holotype is the darkest of the available specimens, the others being significantly more pale, with the subsutural band paler and less contrasted but still obvious. The number of lirae on the columellar pillar seems to increase with shell length and only 4 are present in small specimens. The conspecificity of all specimens is confirmed by nearly identical COI sequences (Fig. 2).

The species is most similar to *Ancilla giaequintoi* Bozzetti, 2006 described on the basis of several empty shells collected in the Lavanono area (Fig. 10 I-K). *A. giaequintoi* has an orange shell, similar in shade to the holotype of *A. lhaumeti*, but significantly darker than the remaining specimens of the new species. The anterior band is distinctly lighter than the last whorl cloak in *A. giaequintoi*, but of the same colour in *A. lhaumeti*; in lateral view, the outer apertural lip is more strongly conchate in *A. giaequintoi* than in any of our specimens of *A. lhaumeti* (it is straight in the holotype). We do not have adult specimens available for sequencing that can be undoubtedly identified as *A. giaequintoi*, but one sequenced subadult (shell length 9.4 mm, MNHN IM-2009-15526) can be, judging from protoconch and upper teleoconch whorls, attributed to it; it is molecularly distinct from *A. lhaumeti* (Fig. 2).

The light specimens of *A. lhaumeti* are similar to *Ancilla adelphae*, differing in their relatively low spire and lighter spiral subsutural band, while *A. adelphae* has a contrasting dark suprasutural spiral band.

Etymology. The species is named after Gilbert Lhaumet, an olive enthusiast who first revealed this new species from southern Madagascar.

Distribution: Known only from southernmost Madagascar, intertidal to 23 m.

Calyptoliva Kantor et Bouchet, 2007

Type species: *Calyptoliva bolis* Kantor et Bouchet, 2007; OD.

Calyptoliva bbugae sp. nov.

(Figs 11, 12)

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Type material: Holotype, lv, MNHN IM-2007-38919, paratypes 1 lv, MNHN IM-2007-39266, sequenced and 3 dd, MNHN IM-2000-32413 (all from TARASOC, st. DW3380).

Type locality: Tuamotu Archipelago, off Kaukura, 15°41'S, 146°54'W, 507-607 m [TARASOC, st. DW3373].

Material examined: Type material (see above). TUA-MOTU, off Kaukura, TARASOC, st. DW3355, 15°57'S, 147°08'W, 530-710 m (1 dd); st. DW3373, 15°41'S, 146°54'W, 507-607 m (3 dd); st. DW3374, 15°39'S, 146°54'W, 703-790 m (1 dd); st. DW3380, 15°39'S, 146°56'W, 970-1060 m (4 paratypes and 2 dd).

Description (holotype). Shell solid, glossy, elongate-ovate, white (BWL/SL = 0.80, AL/SL = 0.63, D/SL = 0.50), with medium-wide aperture and low spire, with about one protoconch whorl and 3 teleoconch whorls. Protoconch large, low, evenly rounded, diameter 1.5 mm, exposed height 0.8 mm, smooth; protoconch-teleoconch transition indistinctly marked by the appearance of callus overlapping the suture on teleoconch whorls. Whorls profile moderately convex, evenly rounded. Suture shallowly impressed, overlaid by very narrow, thin, smooth callus. Aperture medium wide, tapering adapically. Outer lip thickened, convex adapically, nearly straight along most the length and rounded abapically. Plication plate narrow, slightly extending beyond the rear edge of anterior band, micro-shagreened, in its lower part bearing seven low but distinct spiral plicae. Anterior band separated by low, but distinct, step, and whiter colouration. Very indistinct, unevenly spaced, thin riblets visible on last whorl cloak in oblique light. Anterior band indistinctly subdivided by low ridge in upper and lower anterior band, the latter corresponding to the fasciole and approximately twice as broader as the former.

Dimensions: SL 8.7 mm, SW 4.2 mm, BWL 7.2 mm, AL 5.3 mm.

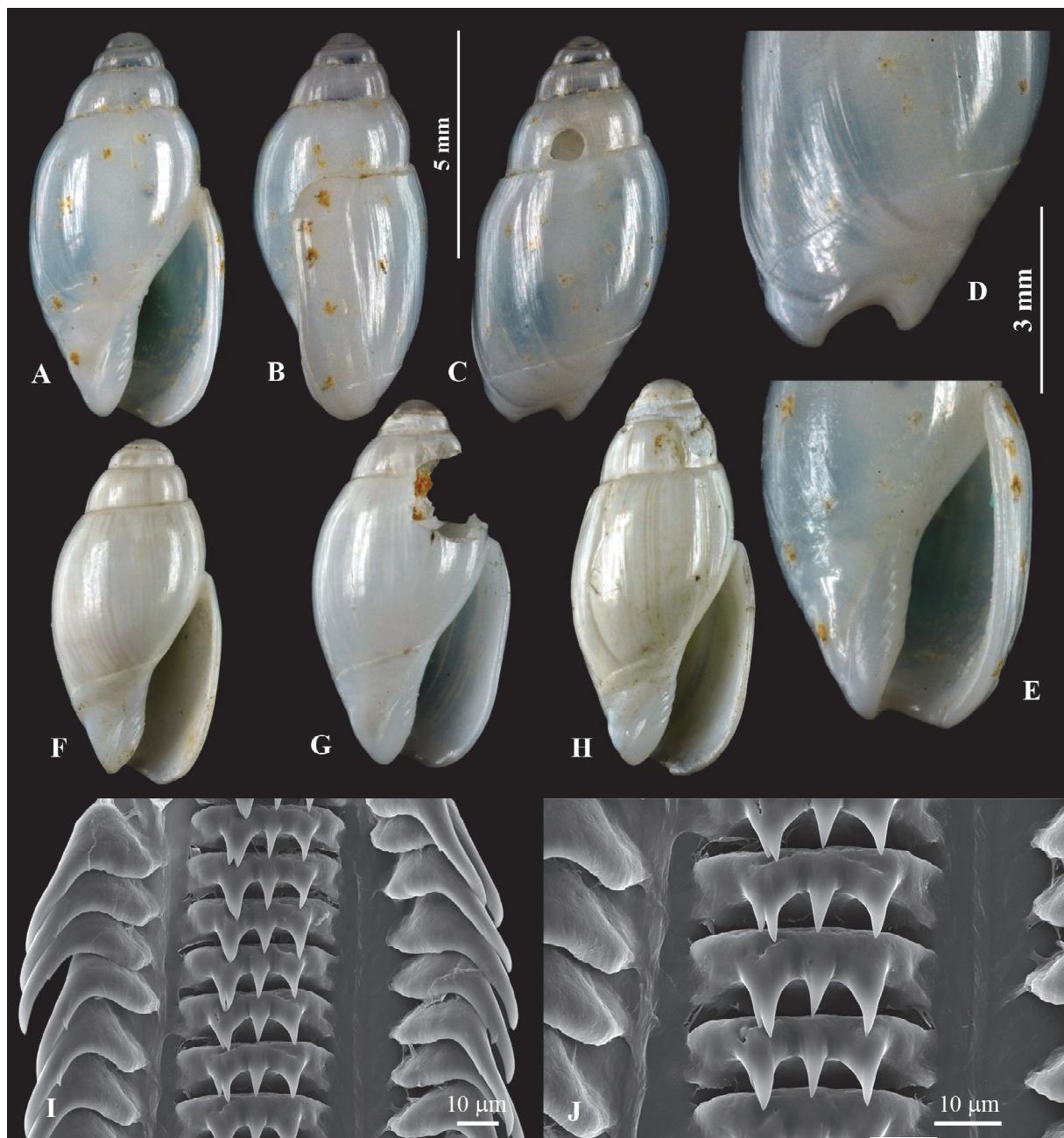


FIG. 11. Shells and radula of *Calyptoliva bbuieae* sp. nov. **A-D.** Holotype, MNHN IM-2007-38919, SL 8.7 mm. **D.** Latero-dorsal view of the anterior band. **E.** Enlarged aperture. **F-H.** Paratypes. **F.** SL 7.7 mm (MNHN IM-2000-32413). **G.** SL 8.2 mm (sequenced paratype, MNHN IM-2007-39266). **H.** SL 8.7 mm. **I-J.** Radula of holotype.

РИС. 11. Раковины и радула *Calyptoliva bbuieae* sp. nov. **A-D.** Голотип, MNHN IM-2007-38919, SL 8.7 мм. **D.** Латеро-дорсальный вид передней ленты. **E.** Увеличенное устье. **F-H.** Параптипы. **F.** SL 7.7 мм (MNHN IM-2000-32413). **G.** SL 8.2 мм (секвенированный параптип, MNHN IM-2007-39266). **H.** SL 8.7 мм. **I-J.** Радула голотипа.

[Описание (голотип). Раковина прочная, блестящая, удлиненно-ovalьная, белая ($BWL/SL = 0.80$, $AL/SL = 0.63$, $D/SL = 0.50$), с умеренно-широким устьем и низким завитком; состоит примерно из одного оборота протоконха и 3 дефинитивных оборотов. Протоконх крупный, низкий, равномерно округлый, диаметр 1,5 мм, высота 0,78 мм, гладкий. Граница протоконха и телоеконха неотчетливо определяется появлением каллуса, покрывающего шов на оборотах телоеконха. Профиль оборотов умерен-

но выпуклый, равномерно закругленный. Шов слабо прижатый, покрыт очень узким, тонким, гладким каллусом. Устье умеренно широкое, сужается по направлению к вершине. Складчатая пластинка узкая, слегка выдается за задний край передней ленты, покрыта микрогранулами, в нижней части с семью низкими, но отчетливыми спиральными складками. Передняя лента образует в задней части низкий, но отчетливый уступ и белее по окраске. Очень тонкие спиральные нерегулярно расположенные ребрыш-

ки видны на последнем обороте в косом свете. Передняя лента нечетко подразделена низким спиральным ребром на верхнюю и нижнюю зоны, последняя соответствует фасциоле и примерно вдвое шире передней зоны.

Размеры: SL 8.7 мм, SW 4.2 мм, BWL 7.2 мм, AL 5.3 мм.]

The holotype had dried soft parts, which were rehydrated for partial anatomical study. Operculum partially broken, transparent, yellowish, with few indistinct growth lines. Propodium crescent-shaped, folded along central longitudinal dorsal furrow (Fig. 12A). Cephalic flaps nearly symmetrical, with very short tapering remnants of tentacles on the tips. Eyes present, distinct, at mid-length of the cephalic flaps. Right flap split lengthwise (obviously teratological), each lobe having its own eye (Fig. 12D).

Mantle broad (Fig. 12B), with thin edge and short but broad siphon. Mantle filament absent, right anterior corner of the mantle extended into a small triangular mantle lobe. Mantle lobe and adjacent portion of the mantle slightly pigmented. Rectal gland not seen. Osphradium large, ovate, nearly symmetrical, brownish, with broad axis. Ctenidium curved and embracing osphradium posteriorly.

Proboscis short, rather broad, smooth, with large rounded mouth opening. Odontophore basal, protruding backward from retracted proboscis. Salivary glands rather large, oval in outline, ramified tubular. Gland of Leiblein large, compact, ovate, dark-brown. Valve of Leiblein relatively very large, pyriform.

Stomach with very long posterior mixing area (Fig. 12C).

Radula (Fig. 11 I-J) long, of about 75 rows, of which 23 not fully formed. Length 0.8 mm (15% of AL), width of the membrane about 100 µm (1.15% SL, 1.89% AL). Rachidian with 3 cusps (in some rows left lateral cusp bifurcated), central cusp about same width and slightly shorter than lateral cusps (Fig. 11J). Lateral teeth almost triangular with curved hook-like tips. On some teeth indistinct additional cusp at mid-length on inner side.

Remarks. The paratypes and additional specimens are very similar to the holotype, varying in relative shell width and the degree of division of the anterior band – from rather clearly demarcated by a ridge or groove to almost without division. The number of spiral plicae on the plication plate varies from 4 to 7. The largest empty shell has length 9.8 mm.

Calyptoliva bbugae is most similar in shape to *C. amblys* Kantor et Bouchet, 2007, differing by its broader, more ovoid shell shape. Its radula differs from that of *C. bolis* Kantor et Bouchet, 2007 [Kantor, Bouchet, 2007: fig. 29] – the only one known in the genus in this respect – in having shorter lateral flaps of the rachidian and a larger central cusp on the rachidian.

The new species is the only sequenced representative of the genus so far and therefore no comparison with other species is possible.

Etymology. The species is named after Barbara Buge in recognition of her efforts and dedication in the management of the MNHN molecular mollusc collection, and in acknowledgement for her consistently friendly assistance.

Distribution. *Calyptoliva bbugae* is known from a very restricted area of the Tuamotu Archipelago, alive in 507–607 m. The genus was previously known only from the Coral Sea.

Discussion

Among the *Ancilla* species treated here there are two pairs of conchologically very similar ones: *A. morrisoni* – *A. kaviengensis* and *A. atimovatae* – *A. ventricosa*. The first two species are sister ones in our phylogenetic analysis (Fig. 2) and are sympatric, but not syntopic, with clear ecological differences between their habitats (Fig. 6). Their shells, radulae and foregut anatomy are so similar that in the absence of molecular evidence they are scarcely separable. *A posteriori* some minor differences in shell shape can be notified: *A. morrisoni* is visually more oval and relatively broader than *A. kaviengensis*. Nevertheless, the width to length ratio is very similar: in the holotype of the former it is 0.48, while in the holotype of the latter it is 0.45. Slight difference in colouration remains the main character, allowing recognition of both species, but with the limited material the variability of this character remains to be established. Some of the empty, partially discoloured, shells were difficult to assign. Finding of two new species off New Ireland is more than 1000 km extension to east of the known range of the genus. Recently *Ancilla* was recorded from the Philippines by Poppe [2008, pl. 546, fig. 5], the species illustrated as *A. cylindrica* (G.B. Sowerby II, 1859) being rather similar to *A. kaviengensis* in shell shape and colouration. Taxonomic position of the specimens from the Philippines remains to be clarified with molecular methods. More images of the specimens of Philippine *Ancilla* can be found at www.conchology.be website [www.conchology.be/?t=66&family=OLIVIDAE&species=Ancilla%20cylindrica, last accessed on May 15, 2016]. Based on new insights on interspecific differences, it is possible to conclude that two species are probably present – one, conchologically similar to *A. cylindrica* (holotype illustrated by Kilburn, 1981: fig. 171) and another, similar to *A. kaviengensis*. Nevertheless in the absence of comparative molecular data no final conclusions can be drawn, but our data suggest the existence of a yet unrecorded radiation and potentially additional new species in that part of the Western Pacific.

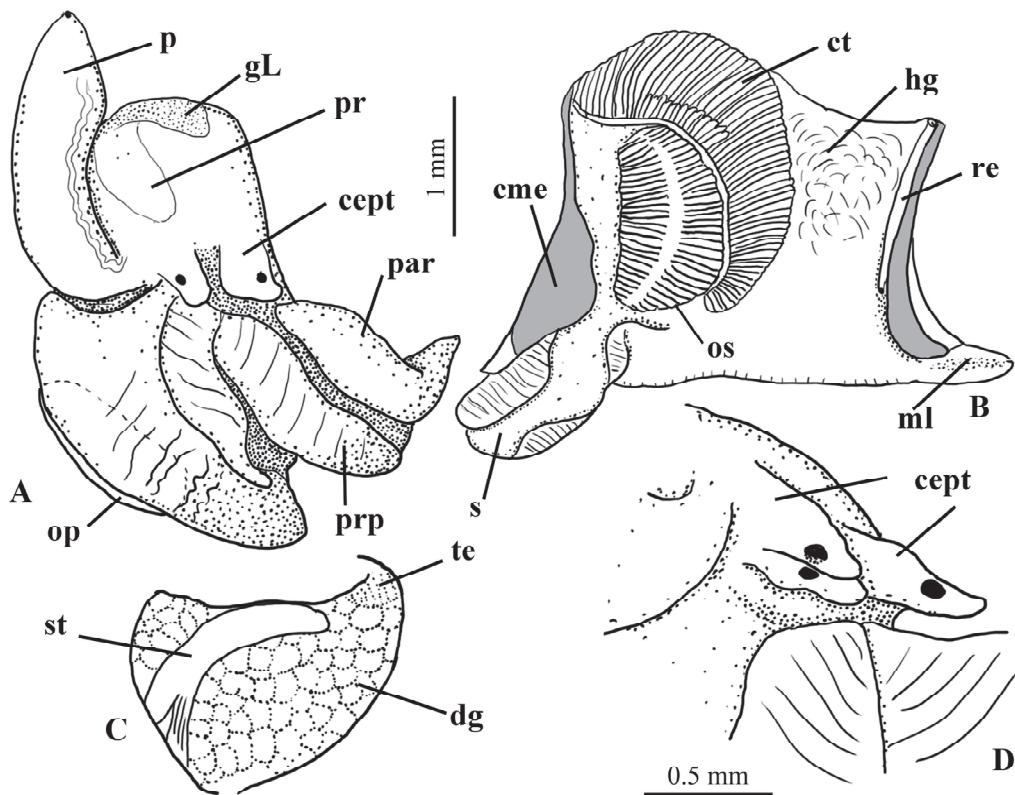


FIG. 12. Details of the soft body morphology of *Calyptoliva bbugae* sp. nov., holotype. A. Head-foot, mantle removed. B. Mantle. C. Visceral mass and stomach. D. Right lateral view of the head to show splitted right cephalic flap.

Abbreviations: cept – cephalic tentacle; cme – cut mantle edge; ct – ctenidium; dg – digestive gland; gL – gland of Leiblein seen through the body walls; hg – hypobranchial gland; ml – mantle lobe; op – operculum; os – osphradium; p – penis; par – parapodia; pr – proboscis seen through the body walls; prp – propodium; re – rectum; s – siphon; st – stomach; te – testis.

РИС. 12. Детали морфологии мягкого тела *Calyptoliva bbugae* sp. nov., голотип. А. Цефалоподиум, мантия удалена. В. Мантия. С. Туловищный мешок и желудок. Д. Вид головы справа, чтобы показать правую расщепленную головную лопасть.

On the contrary, the situation with *A. atimovatae* and *A. ventricosa* is quite different. The species have very similar shells, but are immediately separable by body colouration, and their markedly different radulae. With respect to *A. ventricosa*, Kilburn [1981: 440] concluded that “To some extent this variation is geographic, the result of the development of local morphs in various parts of its range”, but our results confirm the presence of at least two species, and additional species may well be involved. Therefore the problem of correct assignment of names still exists, since the holotype of *A. ventricosa* [illustrated by Kilburn, 1981: fig. 224] is an immature, badly worn specimen. The designation of the sequenced specimen as neotype may be a solution. Presently we adopted the Kilburn’s viewpoint that the radula of true *A. ventricosa* has a tricuspid central tooth with additional smaller cusps.

The presence in our material of several new species of *Ancilla*, some yet unnamed (represented by single specimens), most of them collected in

very restricted area off southern Madagascar, suggests that much remains to be discovered. It is already clear that conchological characters can be insufficient for species delimitation, and we would warn against description of new taxa in *Ancilla* without supporting molecular data.

The finding of the new species of *Calyptoliva*, *C. bbugae* was rather unexpected, since all three species of this genus known to date were described from the Coral Sea [Kantor, Bouchet, 2007]. The presence of additional species with lecithotrophic development at a distance of nearly 6,000 km is a very significant extension of the distributional range, suggesting that the genus may be present in intermediate localities. Anatomically only the type species of *Calyptoliva*, *C. bolis* has previously been examined in detail. Judging from fragmentary anatomy of *C. bbugae* (only a single dried body was available for study), it is similar to *C. bolis*, differing in less developed mantle lobe and morphology of the salivary glands, which are broad-tubular in *C. bolis* and ramified tubular in *C. bbugae*.

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РЕЗЮМЕ. На основании молекулярных и морфологических данных описано пять новых видов Olivoidea: четыре мелководных вида *Ancilla* с Мадагаскара и Папуа Новой Гвинеи и один глубоководный вид (500-600 м) *Calyptoliva* из архипелага Туамоту. Симпатрические, но не синтопические виды *Ancilla morrisoni* и *A. kaviengensis* с о. Новая Ирландия являются криптическими и различаются, главным образом, окраской раковины, но молекулярно отличны. Симпатрические и возможно синтопические *Ancilla atimovatae* и *A. lhaumeti* найдены у южного Мадагаскара; *A. atimovatae* конхологически почти неотличима от *A. ventricosa*, однако имеет разительно другую морфологию раковины. *Calyptoliva* была известна ранее только из Кораллового Моря; *C. bbugaeae* является первым видом рода, для которого получены молекулярные данные. Новые виды *Ancilla* описаны на основании секвенированных генотипов; типовой материал новой *Calyptoliva* включает секвенированный паратип.

Интегративный таксономический подход к Индо-Пацифическим Olividae: новые виды, выявленные по молекулярным и морфологическим данным

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