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## Review of the *Nassarius pauperus* (Gould, 1850) complex (Nassariidae): Part 3, reinstatement of the genus *Reticunassa*, with the description of six new species

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**Abstract.** In this review (third part), several species within the *Nassarius pauperus* complex from the eastern Indian Ocean and western Pacific are treated, including a revised concept of *Nassa paupera* Gould, 1850, type species of the genus *Reticunassa* Iredale, 1936. In the most recent taxonomic revision, several species had been synonymized with *Nassarius pauperus* (Gould, 1850), despite distinctive differences among these species in shell morphology. We sequenced a fragment of the mitochondrial *COI* and the nuclear 28S genes of all available *Nassarius pauperus* complex species. Automatic barcode gap discovery and reciprocal monophyly were applied to propose species delimitation hypotheses and to support a new concept of the genus. Using morphological and molecular characters, *Reticunassa* is elevated to full genus rank. Six new species are described: *Reticunassa visayaensis* sp. nov., *R. poppeorum* sp. nov., *R. annabolteae* sp. nov., *R. goliath* sp. nov., *R. intrudens* sp. nov. and *R. thailandensis* sp. nov., while *R. tringa* (Souverbie, 1864) is recognized as a valid species.

**Keywords.** *Nassarius pauperus* complex, taxonomy, species delimitation, neotype, barcoding.

Galindo L.A., Kool H.H. & Dekker H. 2017. Review of the *Nassarius pauperus* (Gould, 1850) complex (Nassariidae). Part 3, reinstatement of the genus *Reticunassa*, with the description of six new species. *European Journal of Taxonomy* 275: 1–43. <http://dx.doi.org/10.5852/ejt.2017.275>

### Introduction

In his systematic revision of the species of Nassariidae, Cernohorsky (1984) treated 16 taxa as junior synonyms of *Nassarius (Hinia) pauperus* (Gould, 1850) (as “*Hima*”). All these nassariids are rather

similar and the small morphological differences were interpreted by Cernohorsky (1984) as representing intraspecific variation. Kool & Dekker (2006, 2007) discussed, in parts 1 and 2 of this ongoing review, whether many of these synonyms should not be considered valid species. DNA data obtained from live specimens collected during several MNHN expeditions were used here as evidence to support species hypotheses originally based solely on morphological features.

Kool & Dekker (2006, 2007) defined some informative morphological characters for the species included in the *Nassarius pauperus* complex (often as “*pauper*-complex”). Among these characters are the type and sculpture of the protoconch, the morphology of the spiral cords, the sculpture on the surface between the spiral cords, and the shape and sculpture of the columellar callus. Using molecular characters, Galindo *et al.* (2016) demonstrated that species attributed to the *Nassarius pauperus* complex clustered together in a clade separate from the genus *Nassarius* Duméril, 1805 s. str.

In part 1 of the *Nassarius pauperus* complex review, Kool & Dekker (2006) described six species with intercardal axial sculpture. In part 2, Kool & Dekker (2007) treated four species with intercardal spiral sculpture, from the western Indian Ocean to the central Pacific Ocean. In this third review, we treat eight species (of which six are new to science) from the eastern Indian Ocean and the Western Pacific, all with intercardal spiral sculpture. The new taxonomic scheme is supported by a species tree based on molecular data.

On the basis of the molecular analysis presented here, *Reticunassa* Iredale, 1936 is elevated to full genus status to include the species formally considered as constituting the *Nassarius pauperus* complex.

## Material and methods

Material was obtained from various natural history museums and private collections, listed in the acronyms section. Live-collected specimens used for molecular studies were anesthetized with MgCl<sub>2</sub> or microwaved (see Galindo *et al.* 2014). The bodies, preserved in 95% ethanol, were removed from the shells in the laboratory to prevent progressive deterioration of the shells by etching. The shells are kept dry and have been assigned the same registration number as the corresponding body or tissue in ethanol.

A stereo microscope was used to observe shell morphology and color patterns. A digital caliper (accurate to 0.1 mm) was used for measurements. Shells of the new species were photographed in dorsal, ventral and lateral views, using a Canon EOS 60D camera. Scanning electron microscope (SEM) images were obtained by backscattered electron diffraction on a VEGA II LSU TESCAN, under conventional high vacuum at 20 kV acceleration voltage (12 to 15 Pa chamber pressure) at the SEM-EDS of the ‘Direction des Collections’ at MNHN. In general, the terms and methods used for the morphological analysis follow part 1 of the review (Kool & Dekker 2006).

### Acronyms

- ABGD = Automatic Barcode Gap Discovery
- AMD = Aart M. Dekkers, Blokker, the Netherlands
- BOLD = Barcode of Life Database
- CP = beam trawl
- DW = Warén dredge
- GH = Glad M. Hansen, Lathlain, Australia
- HD = Henk Dekker, Winkel, the Netherlands
- HK = Hugo H. Kool, Dieren, the Netherlands
- HUJ = Hebrew University, Jerusalem, Israel
- JGMR = J.G.M. (Han) Raven, the Hague, the Netherlands

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MCZ	=	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
NHMUK	=	The Natural History Museum, London, United Kingdom
MHNBx	=	Muséum d'Histoire naturelle, Bordeaux, France
MNHN	=	Muséum national d'Histoire naturelle, Paris, France
MUZEE	=	Muzee Scheveningen, Scheveningen, the Netherlands
NBC	=	Naturalis Biodiversity Center, Leiden, the Netherlands
PS	=	P. Stahlschmidt, Rohrbach, Germany
RMNH	=	Rijksmuseum voor Natuurlijke Historie, collection incorporated in NBC
USNM	=	United States National Museum, Smithsonian Institution, Washington DC, USA
ZMA	=	Zoölogisch Museum Amsterdam, collection incorporated in NBC

### Abbreviations

l	=	length
lv	=	live-collected specimen
spm	=	specimen(s), in Material examined sections
stn	=	station
w	=	width

Molecular sequencing was carried out at the Service de Systématique Moléculaire (MNHN UMS 2700). Procedures from the Consortium for the Barcode of Life barcoding protocols ([www.barcodeoflife.org](http://www.barcodeoflife.org)) adapted to large biodiversity collections were followed (see Puillandre *et al.* 2012a). A piece of muscle from the foot, sufficient for approximately five DNA extractions, was stored in a 2D barcode tube as a reference tissue collection. Extraction was done with the NucleoSpin® 96 Tissue Core Kit adapted to a NucleoSpin® 96 Plasmid Binding Plate (Macherey-Nagel) using a liquid handling workstation (epMotion® 5075 VAC, Eppendorf). Purified DNA was stored in a second 2D tube. PCR reactions were performed in 20 µl, containing 2 µl of DNA, 1× reaction buffer, 2.5 mM MgCl<sub>2</sub>, 0.26 mM dNTP, 0.3 µM of each primer, 1 µl DMSO, 1 µl BSA (10 mg/l) and 1.5 units of Q-Bio Taq DNA polymerase (QBiogene, Carlsbad, California, USA). A fragment of 658 bp of the cytochrome oxidase I (*COI*) mitochondrial gene was amplified, using the universal primer set (LCO1490 and HCO2198) (Folmer *et al.* 1994) and a primer set specific for Nassariidae (5COIF: 5'ACAAATCATAAAGAYATTGGAAC-3', 492COIR: 5'CGCTCAAATTGTATTCCTCG-3' and 492COIRD: 5'CGYTCRAATTGTATYCCCTCG-3') (Galindo *et al.* 2016). Annealing temperature was 50°C for 35 seconds. The first subunit of the 28S gene was amplified using the C1' and D2 primers of Chisholm *et al.* (2001). Annealing temperature was 58°C for 40 seconds or a touchdown gradient from 66°C to 56°C for 8 seconds (plus 58°C for 30 seconds) whenever double bands were present. Sequencing was carried out by the Centre National de Séquençage, Genoscope (Évry, France) and Eurofins Genomics (Paris, France). In all cases, both directions were sequenced to confirm the accuracy of each haplotype.

Sequence cleaning and alignment was done by using Codon Code Aligner software. GenBank accession numbers for all the sequences obtained are included in Table 1. We compiled a dataset of sequences available for several closely related species, identified in a phylogenetic tree, based on a large dataset of Nassariidae (Galindo *et al.* 2016) to compare with our new species hypotheses. The analysis involved 89 *COI* sequences: 72 of them belong to the *Nassarius pauperus* complex, 16 sequences to other species of Nassariidae and one to a distant outgroup. The Automatic Barcode Gap Discovery (ABGD) method using the default parameters (Puillandre *et al.* 2012b) was employed. It automatically detects, when present, a threshold (the barcode gap) in the pairwise distribution of the genetic distances calculated between each pair of specimens.

To test whether the species hypotheses proposed by ABGD corresponded to monophyletic groups, Bayesian analyses, consisting of two Markov chains (35 million generations each with a sampling

**Table 1.** GenBank accession numbers for sequenced specimens of *Reticunassa* included in this paper. H = holotype; Hg = hologenophore; N = neotype; P = paratype; PNG = Papua New Guinea. [continued on next two pages]

Species	Region	Expedition	Station	ID number	Voucher	COI GenBank	28S GenBank
<i>R. compacta</i> (Angas, 1865)	Australia	WESTERN AUSTRALIA	WE03	IM200922545	Hg	KY499760	–
<i>R. crenulicostata</i> (Shuto, 1969)	PNG	PAPUA NIUGINI	PS29	IM201315398	Hg	KY499789	–
<i>R. hanraveni</i> (Kool & Dekker, 2006)	PNG	PAPUA NIUGINI	PB28	IM201312305	Hg	KY499782	–
<i>R. hanraveni</i> (Kool & Dekker, 2006)	PNG	PAPUA NIUGINI	PB28	IM201312307	–	KY499783	–
<i>R. hanraveni</i> (Kool & Dekker, 2006)	PNG	PAPUA NIUGINI	PS22	IM201314647	–	KY499788	–
<i>R. neoproducta</i> (Kool & Dekker, 2007)	Mozambique	INHACA 2011	MR20	IM200922676	–	KY499761	KY489523
<i>R. neoproducta</i> (Kool & Dekker, 2007)	Mozambique	INHACA 2011	MR20	IM200922701	–	KY499762	KY489524
<i>R. neoproducta</i> (Kool & Dekker, 2007)	Mozambique	INHACA 2011	MB7	IM200923969	Hg	KY499777	KY489537
<i>R. neoproducta</i> (Kool & Dekker, 2007)	Mozambique	INHACA 2011	MB7	IM200923970	–	–	KY489538
<i>R. neoproducta</i> (Kool & Dekker, 2007)	Mozambique	INHACA 2011	MB7	IM200923971	–	KY499778	KY489539
<i>R. neoproducta</i> (Kool & Dekker, 2007)	Mozambique	INHACA 2011	MB7	IM200923972	–	KY499779	KY489540
<i>R. neoproducta</i> (Kool & Dekker, 2007)	Mozambique	INHACA 2011	MB7	IM200923973	–	KY499780	KY489541
<i>R. neoproducta</i> (Kool & Dekker, 2007)	Mozambique	INHACA 2011	MB7	IM200923974	–	KY499781	–
<i>R. paupera</i> (Gould, 1850)	Vanuatu	SANTO 2006	DB12	IM200731782	N	KY499731	–
<i>R. poppeorum</i> sp. nov.	Vanuatu	SANTO 2006	DR03	IM200732742	P	KY499733	–
<i>R. poppeorum</i> sp. nov.	Vanuatu	SANTO 2006	FB61	IM200731779	H-Hg	KY582567	KY489493
<i>R. poppeorum</i> sp. nov.	Philippines	PANGLAO 2004	S2	IM200731937	P	KY582569	KY489495
<i>R. poppeorum</i> sp. nov.	Philippines	PANGLAO 2004	S2	IM200731938	P	KY499732	–
<i>R. poppeorum</i> sp. nov.	PNG	PAPUA NIUGINI	PM22	IM201313185	–	KY499785	–
<i>R. poppeorum</i> sp. nov.	PNG	PAPUA NIUGINI	PR202	IM201317555	–	KY499790	–
<i>R. poppeorum</i> sp. nov.	PNG	PAPUA NIUGINI	PB48	IM201317567	–	KY499792	–
<i>R. poppeorum</i> sp. nov.	PNG	PAPUA NIUGINI	PB47	IM201317574	–	KY499793	–
<i>R. rotunda</i> (Melvill & Standen, 1896)	PNG	PAPUA NIUGINI	PD27	IM201313211	Hg	KY499787	–
<i>R. silvardi</i> (Kool & Dekker, 2006)	Vanuatu	SANTO 2006	DS04	IM200731740	–	KY499728	–

Species	Region	Expedition	Station	ID number	Voucher	COI GenBank	28S GenBank
<i>R. silvardi</i> (Kool & Dekker, 2006)	Vanuatu	SANTO 2006	DS04	IM200731741	-	KY499729	KY489491
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	-	IM200923703	-	KY499763	-
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	MQ13-GR	IM200923704	-	KY499764	-
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	MQ13-GR	IM200923954	-	KY499765	KY489525
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	MQ13-GR	IM200923955	Hg	KY499766	KY489526
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	-	IM200923956	-	KY499767	KY489527
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	-	IM200923957	-	KY499768	KY489528
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	-	IM200923958	-	KY499769	KY489529
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	-	IM200923959	-	KY499770	KY489530
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	-	IM200923960	-	KY499771	KY489531
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	-	IM200923961	-	KY499772	KY489532
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	MQ13-GR	IM200923962	-	KY499773	KY489533
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	MQ13-GR	IM200923963	-	KY499774	KY489534
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	MQ13-GR	IM200923964	-	KY499775	KY489535
<i>R. silvardi</i> (Kool & Dekker, 2006)	Marquesas I.	PAKAIHI I TE MOANA	-	IM200923965	-	KY499776	KY489536
<i>R. simoni</i> (Kool & Dekker, 2007)	Madagascar	ATIMO VATAE	TS17	IM200912896	Hg	KY499754	KY489517
<i>R. simoni</i> (Kool & Dekker, 2007)	Madagascar	ATIMO VATAE	TS04	IM200913086	-	KY499759	KY489522
<i>Reticunassa</i> sp.	Vanuatu	SANTO 2006	FB61	IM200731778	Hg	KY499730	KY489492
<i>Reticunassa</i> sp.	PNG	PAPUA NIUGINI	PS45	IM201317562	Hg	KY499791	-
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM09	IM200912228	-	KY499734	-
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TM05	IM200912306	-	KY499735	-
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BS14	IM200912329	-	KY499736	KY489496
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM02	IM200912772	-	KY499737	KY489497
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912778	-	KY499738	KY489498
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912783	-	KY499739	KY489499
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912812	P	KY499740	KY489500

Species	Region	Expedition	Station	ID number	Voucher	COI GenBank	28S GenBank
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912825	–	KY499741	KY489501
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TS09	IM200912834	–	KY499742	KY489502
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912841	–	KY499743	KY489503
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912843	H	KY499744	KY489504
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912844	–	KY499745	KY489505
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912849	P	–	KY489506
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912855	–	–	KY489507
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912862	P	KY499746	KY489508
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BB03	IM200912865	–	KY499747	KY489509
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM06	IM200912868	P	–	KY582570
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	BM10	IM200912873	–	KY499748	KY489510
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TS09	IM200912881	–	KY499749	KY489511
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TV07	IM200912885	–	KY499750	KY489512
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TM05	IM200912888	–	KY499751	KY489513
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TM05	IM200912889	–	KY499752	KY489514
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	CP3547	IM200912893	–	–	KY489515
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TM08	IM200912894	–	KY499753	KY489516
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TM05	IM200912897	–	KY499755	KY489518
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TV07	IM200912898	–	KY499756	KY489519
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TM05	IM200912899	–	KY499757	KY489520
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TM05	IM200912905	–	KY499758	KY489521
<i>R. annabolteae</i> sp. nov.	Madagascar	ATIMO VATAE	TM05	IM200913087	–	–	KY582571
<i>R. tringa</i> (Souverbie, 1864)	Vanuatu	SANTO 2006	AT52	IM200731753	Hg	KY582566	–
<i>R. visayaensis</i> sp. nov.	Philippines	PANGLAO 2004	M40	IM200731912	H	KY582568	KY489494
<i>R. visayaensis</i> sp. nov.	PNG	PAPUA NIUGINI	PM22	IM201313184	–	KY499784	–
<i>R. visayaensis</i> sp. nov.	PNG	PAPUA NIUGINI	PM22	IM201313192	–	KY499786	–

frequency of one tree for every hundred generations) run in eight parallel analyses, was performed using MrBayes v. 3.2.6 (Ronquist & Huelsenbeck 2003) run on XSEDE. When the log-likelihood scores were found to stabilize, a consensus tree was calculated after omitting the first 25% trees as burn-in. The analyses were performed using the CIPRES Science Gateway (Miller *et al.* 2010). Kimura 2-parameter (K2P) distances, estimated with MEGA v. 6 (Tamura *et al.* 2011), were used to compare each new species with its relatives as defined above.

For type specimen selection, we attributed more importance to the sequenced specimens (genophores *sensu* Pleijel *et al.* 2008) than to shell features. All the material (type series and sequences) belongs to MNHN unless otherwise mentioned. Detailed information on the tropical deep sea surveys run by MNHN, from which we obtained most of the new species described herein, can be found in Bouchet *et al.* (2008) and the BasExp database at <http://expeditions.mnhn.fr/>.

## Results

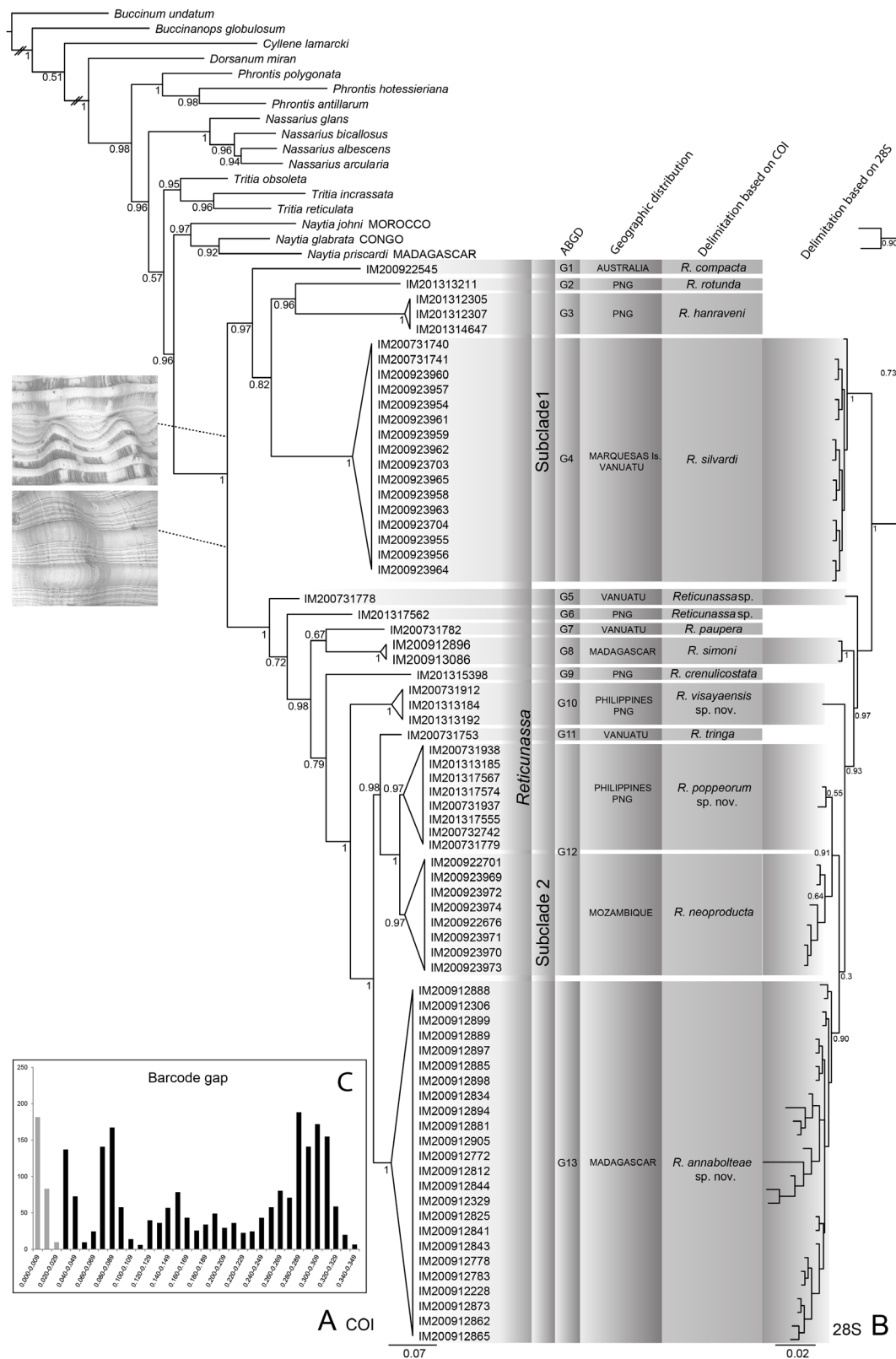
A comprehensive dataset on the *Nassarius pauperus* complex was gathered. For *COI*, 72 partial sequences were unambiguously aligned without gaps; 244 sites were variable positions, of which 204 were parsimony informative. For 28S, 51 sequences of the first subunit were successfully amplified. The 28S tree supported all the species hypotheses evidenced by *COI*.

The resulting trees, constructed after the analyses of *COI* and 28S markers separately (Fig. 1A–B), are in general characterized by strong support values (posterior probability, PP) of deep and terminal nodes. The *Nassarius pauperus* complex was recovered as a monophyletic group (PP=1). Branch lengths (sequence divergences), similar to those found for other major clades within Nassariinae (i.e., *Phrontis* Adams & Adams, 1853, *Nassarius*, *Tritia* Risso, 1826 and *Naytia* Adams & Adams, 1853), support our taxonomic decision to consider this clade as a separate genus. *Reticunassa* is the only available genus group name for this clade, because *Nassarius pauperus*, its type species, was included in it (see genus remarks for more details). The African clade *Naytia* is confirmed as the sister group (PP=0.96, 0.73) of the Indo-Pacific *Reticunassa*.

Within the *Reticunassa* clade, two subclades (SC) were recovered: SC1 is composed of species without spiral sculpture on the intercordal surface (e.g., *R. compacta* (Angas, 1865), *R. rotunda* (Melvill & Standen, 1896), *R. hanraveni* (Kool & Dekker, 2006) and *R. silvardi* (Kool & Dekker, 2006)); SC2 includes species with intercordal spiral sculpture (e.g., *R. paupera* (type species of *Reticunassa*), *R. simoni* (Kool & Dekker, 2007), *R. crenulicostata* (Shuto, 1969), *R. tringa* (Souverbie, 1864) and *R. neoproducta* (Kool & Dekker, 2007)). The *COI* and 28S taxonomic trees are completely congruent with the morphological hypotheses formulated by Kool & Dekker (2006, 2007). The tree for *COI* strongly supports the existence of several lineages, which constitute the primary species hypotheses to be delimited by an integrative approach.

The differences between the intra- and the interspecific genetic distances are shown in Fig. 1C. Among species of *Reticunassa*, the intraspecific genetic distances range between 0.000 and 0.029. However, no clear barcode gap (*sensu* Puillandre *et al.* 2012b) was found within this *Reticunassa* data set. Fig. 1C shows two main low frequency regions on the pairwise distance frequencies, one around 2% and a second near 5%.

ABGD was able to recover 13 groups (Fig. 1): seven correspond to species recognized as valid: G1 *R. compacta*, G2 *R. rotunda*, G3 *R. hanraveni*, G4 *R. silvardi*, G7 *R. paupera*, G8 *R. simoni* and G9 *R. crenulicostata*. G11 corresponds to a separate lineage represented by a single sequence for a specimen morphologically close to the original description of *Nassa tringa* Souverbie in Souverbie & Montrouzier, 1864, a species considered a synonym of *Nassarius pauperus* by Cernohorsky (1984).



**Fig. 1.** A. Bayesian tree based on *COI* sequences of species of *Reticunassa*. B. Bayesian tree based on 28S sequences of species of *Reticunassa*. C. Frequency of pairwise distance (K2P model) values among *COI* sequences. In gray, intra-specific variation. In black, inter-specific variation. PNG = Papua New Guinea.



Four lineages (G5, G6, G10 and G13) potentially correspond to new species. Two of these, G10 and G13, could be distinguished by shell features. However, it was not possible to find differences in shell morphology for the other two species (G5 and G6) and formal descriptions of these await the discovery of informative characters.

The ABGD approach grouped specimens from both Mozambique (originally identified as *R. neo-producta*), the Philippines and Papua New Guinea into G12. Those samples formed two separate (and sister) clades, well supported by reciprocal monophyly in the *COI* (PP= 1) and the 28S (PP=0.91) trees, and in accordance with the geographical distribution.

In this paper the genus *Reticunassa* is redefined, together with its type species. Additionally, six species are described as new to science.

Class Gastropoda Cuvier, 1797  
Subclass Caenogastropoda Cox, 1960  
Order Neogastropoda Wenz, 1938  
Superfamily Buccinoidea Rafinesque, 1815  
Family Nassariidae Iredale, 1916  
  
Genus *Reticunassa* Iredale, 1936

### Type species

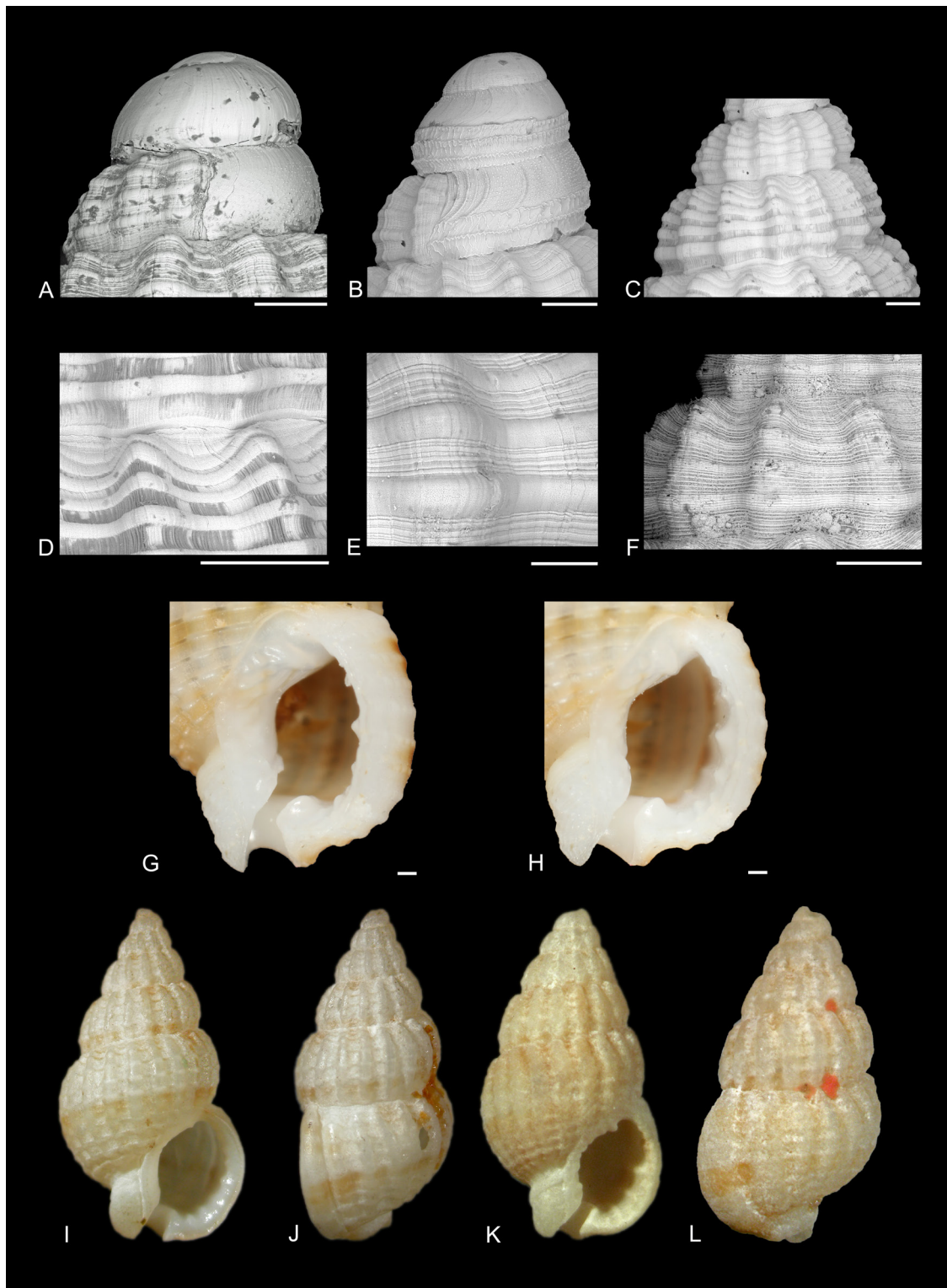
*Nassa paupera* Gould, 1850 by original designation (Iredale 1936: 322).

### Diagnosis

Morphological features of the protoconch are of great importance when recognizing species of *Reticunassa*. Several species have a multispiral protoconch, indicating a planktotrophic/planktonic larval development, resulting in a larger range of distribution. Others have a paucispiral protoconch, indicating a short, non-planktotrophic/direct larval development. All species of *Reticunassa* possess an unkeeled protoconch (Fig. 2A–B), as do other Nassariinae genera in the Atlantic Ocean (Galindo *et al.* 2016). However, *Reticunassa* lives in sympatry with the Indo-Pacific genus *Nassarius* s. str., characterized by a keeled protoconch. Protoconchs of *Reticunassa* can be rather broad and flattened; a few are pointed. They might possess microscopic sculpture, such as spiral ridges, axial striae and minute pustules (Fig. 2A–B), but frequently a much higher resolution is needed to see details of this sculpture. Due to the obvious importance of protoconch characters, the identification of specimens in this genus lacking a protoconch becomes more difficult.

Species of *Reticunassa* have strongly or weakly developed continuous spiral cords, from 10 to 15 on the body whorl (Fig. 2D–F), crossing over the axial ribs. The space between these spiral cords, the intercordal surface, can be smooth, axially striated or can display a number of (occasionally extremely) fine spiral striae (Fig. 2F). This makes the sculpture of the intercordal surface important for identification purposes within *Reticunassa*. Fig. 1A–B shows that differences on these intercordal surfaces are useful synapomorphies to separate SC1 from SC2.

Species within *Reticunassa* have an axially-ribbed teleoconch (Fig. 2C). These axial ribs may become weaker or absent on the body whorl towards the base and/or the outer lip. Ribs can be round or flat. The number of ribs differs among species. Most species develop a strong varix near the outer lip. The suture is usually deeply impressed.



**Fig. 2.** Characters of *Reticunassa* Iredale, 1936. **A–B.** Protoconchs. **A.** *R. paupera* (Gould, 1850), MNHN IM-2007-31782. **B.** *R. silvardi* (Kool & Dekker, 2006). **C.** Suture detail of *R. paupera*. **D.** Axial striae in *R. silvardi*. **E–F.** Intercordal spirals. **E.** *R. tringa* (Souverbie, 1864). **F.** *R. paupera*. **G–H.** Columellar details of *R. paupera*. **I–L.** Type series of *R. paupera*. **I–J.** Lectotype, USNM 5726, length 9.1 mm, width 4.8 mm. **K–L.** Paralectotype, MCZ 216602, length 7.2 mm, width 3.5 mm. All scale bars = 200  $\mu$ m.

The aperture is oval to sub-circular, the inside of the outer lip with a number of denticles or lirae (Fig. 2G–H). A columellar callus is present and varies in shape and sculpture. It can be limited to the columella or partly extend over the body whorl.

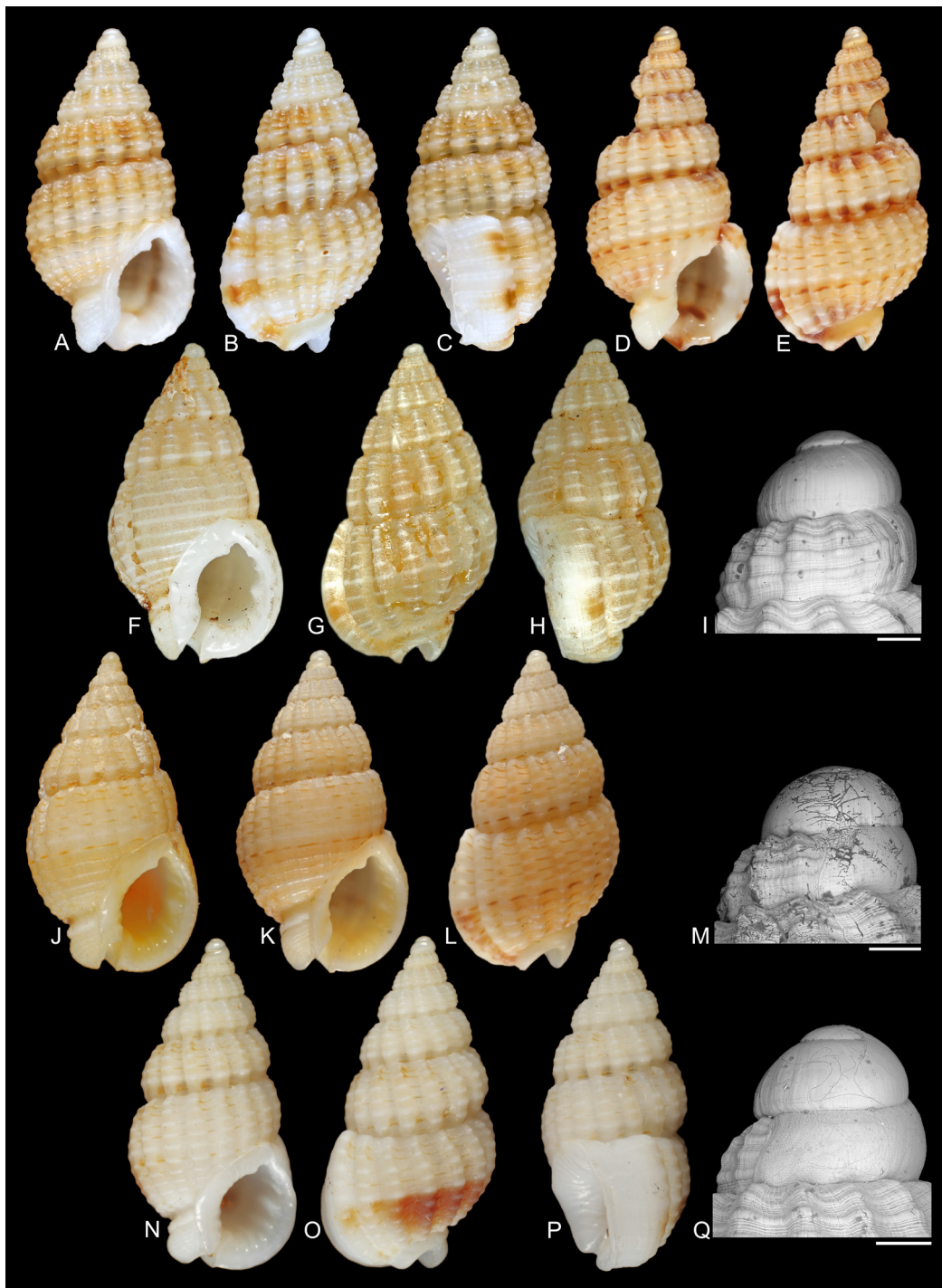
In some species, the color is variable; generally, it is cream-yellowish to orange, or white to dark brown. Banding with darker colors may also be present. Sometimes only some of the spiral cords are darker than the remaining part of the shell.

*Reticunassa* species are small, usually varying between 5 and 12 mm, but one is up to 16.5 mm (*R. goliath* sp. nov.). Most species live in littoral to sublittoral ecosystems, only empty shells having been found in waters deeper than 260 m. Their occurrence is in the Indo-Pacific Ocean, from the Miocene to the present.

### Remarks

The genus name *Reticunassa* was introduced to group together “species around *pauperus* Gould” by Iredale (1936: 322). Cernohorsky (1984: 175) regarded *Reticunassa* as a synonym of the subgenus “*Hima* Leach in Gray, 1852”, within the genus *Nassarius* Duméril, 1805. However, *Hima* is not an available name, but an incorrect subsequent spelling of *Hinia* Leach in Gray, 1847 (Gray 1847a: 269), since “*Hima*” included the same three species as in the original description of *Hinia* (during a period in which original descriptions only consisted of introducing new names). Nonetheless, “*Hima*” and not *Hinia* was listed by Adams & Adams (1853). Cossmann (1901) considered both *Hinia* and “*Hima*” as valid names, with “*Hima*” treated *sensu* Adams & Adams (1853), not Leach in Gray, 1852, and with “type species” *Nassa incrassata* “Müller”. Woodring (1928) noted the misspelling and this was reiterated by Lee (2013). Despite this, the error in the use of “*Hima*” has persisted. On the other hand, *Hinia* Leach in Gray, 1847 is a junior objective synonym of *Tritia* Risso, 1826 as they have the same type species, *Buccinum reticulatum* Linnaeus, 1758, designated for both genera by Gray (1847b: 139). Molecular results of Galindo *et al.* (2016) indicated that species considered part of the *Nassarius pauperus* complex, including “*Nassarius pauper*”, form a clade distant from *Buccinum reticulatum* (accepted as *Tritia reticulata*), the type species of *Tritia* (= *Hinia*), also shown in Fig. 1A. The only available genus group name for this *pauperus* clade is *Reticunassa* Iredale, 1936, which is herein reinstated with full generic status.

Other species might be confused as members of the genus *Reticunassa* because of their morphological similarities. As it is impossible to treat all the small and ridged species, we focus on the following characters: (1) *Reticunassa* is an Indo-Pacific group of molluscs, not occurring in Atlantic waters (Galindo *et al.* 2016); (2) species of *Reticunassa* lack keeled protoconchs (all species with this keel belong to the genus *Nassarius*); (3) fine spiral striae or axial striae on the intercardal surface (Fig. 2D–F) may be an indication of at least kinship with *Reticunassa*; (4) all species of *Reticunassa* have a distinct, elongate and slender shape (Figs 3, 8). These criteria exclude from *Reticunassa* any Mediterranean species, such as *Tritia incrassata* (Strøm, 1768) (previously *Nassarius incrassatus*), West African species, such as *Tritia senegalensis* (Von Maltzan, 1884) (previously *Nassarius senegalensis*) and Caribbean species, such as *Phrontis candidissima* (C.B. Adams, 1845) (previously *Nassarius candidissimus*) (Galindo *et al.* 2016). Most Indo-Pacific species, such as *Nassarius vanuatuensis* Kool & Galindo, 2014, can be distinguished from *Reticunassa* by the protoconch features. Additionally, Kool & Galindo (2014) demonstrated a 19% genetic distance between *Nassarius vanuatuensis* and *Reticunassa paupera*. *Naytia priscardi* (Bozzetti, 2006) from Madagascar is a member of the sister group of *Reticunassa* and exhibits great morphological similarity to some species of this genus. Molecular synapomorphies indicate that *N. priscardi* belongs to *Naytia*.



**Fig. 3.** Shells of *Reticunassa* Iredale, 1936. – A–C. Possible neotype of *R. paupera* (Gould, 1850), MNHN IM-2007-31782, length 6.9 mm, width 3.6 mm, Vanuatu, Aore I., 15°36.6' S, 167°10.1' E, 10–18 m. – D–I. *R. tringa* (Souverbie, 1864). D–E. Hologenophore, MNHN IM-2007-31753, length 9.5 mm, width 4.6 mm. F–H. Lectotype, MHNbx 2004.TY.89.1, length 9.0 mm, width 5.0 mm. I. Protoconch of the hologenophore. – J–M. *R. visayaensis* sp. nov. J–L. Holotype, MNHN IM-2007-31912, length 9.5 mm, width 4.6 mm, Philippines, Panglao I., 9°35.7' N, 123°44.7' E, 0–3 m. M. Protoconch. – N–Q. *R. poppeorum* sp. nov. N–P. Holotype, MNHN IM-2007-31779, length 9.0 mm, width 4.5 mm, Vanuatu, Aore I., 15°34.4' S, 167°12.6' E, 2–3 m. Q. Protoconch. Scale bars: I, M, Q = 200  $\mu$ m.

***Reticunassa paupera*** (Gould, 1850)  
Figs 2A, C, F–L, 3A–C, 4; Tables 1–2

*Nassa paupera* Gould, 1850: 155.

*Nassa paupera* – Gould 1852: 12, 262, pl. 19, fig. 330a–b; 1862: 70. — Johnson 1964: 124.

*Reticunassa paupera* – Iredale 1936: 322.

*Nassarius (Hima) pauperus* [in part] – Cernohorsky 1972: 186, figs 151–154; 1974: 54, fig. 7; 1984: 176, pl. 37, fig. 1.

*Nassarius pauperus* – Richard *et al.* 1984: 12, fig. 24.

**Type material**

**Lectotype** (ICZN Art. 74.5; Johnson 1964: 124)

PACIFIC OCEAN: length 9.1 mm, width 4.8 mm (USNM 5726, Fig. 2I–J, <http://n2t.net/ark:/65665/3flf5ebf5-d0d6-4c9a-bddd-3677d3efb7e2>).

**Paralectotype** (ICZN Art. 74.5; Johnson 1964: 124)

PACIFIC OCEAN: 1 spm, type locality, length 7.2 mm, width 3.5 mm (MCZ 216602, ex USNM, Fig. 2K–L).

**Neotype**

Both the lectotype and the paralectotype have been affected by Byne's disease (Kool & Dekker 2006). However, remnants of microscopic spiral sculpture on the intercardal surface of both specimens are vaguely visible. Gould (1850) did not mention this feature in his original description. The protoconch of the lectotype is badly damaged and that of the paralectotype is completely absent. The protoconch, figured by Cernohorsky (1984: 5, fig. 12) cannot be the protoconch of either of the types, but most likely belongs to *Reticunassa tringa*, which he considered a synonym of *Nassarius pauperus*. The poor condition of both existing types calls for the designation of a neotype for this species. Among the specimens in the MNHN collection, there is one sequenced individual that is very similar to the original types of the species. A proposal to designate a neotype is in the process of being submitted to the International Commission on Zoological Nomenclature (ICZN). If accepted, the neotype will be MNHN IM-2007-31782, length 6.9 mm, width 3.6 mm (Fig. 3A–C; <http://coldb.mnhn.fr/catalognumber/mnhn/im/2007-31782>).

**Type locality**

Pacific Ocean. If the designation of a neotype is accepted by the ICZN, the locality of MNHN IM-2007-31782 becomes the new type locality: SANTO 2006 Expedition, stn DB12, Vanuatu, South of Aore Island, 15°13.6' S, 167°10.1' E, 10–18 m.

**Other material examined**

INDONESIA: Bali, Benoa Port, in sand dumps, leg. T. de Boer (HK 995.06, 1 spm); Bali, Nusa Dua, Benoa Beach, leg. J. Post (HK 995.09, 1 spm); Flores Sea, Pulau Sabalana, Lamuruang, 10–20 m (HD 17295, 1 spm); Arafura Sea, near Pulau Kuringarankeke, W of Makassar, southern Sulawesi, 5°5'34" S, 119°17'09" E, leg. H. Morrison (GH, 1 spm); West-Papua, Manokwari, leg. D. Smits (HK 995.03, 5 spm; HD 38513, 6 spm); SNELLIUS 1929, Kera, near Timor (RMNH, 1 spm); Java, Bay of Jakarta, Pulau Dapur, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096216, 1 spm); Java, Bay of Jakarta, Pulau Ubi, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096218, 4 spm); Java, Bay of Jakarta, Pulau Kelor, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096219, 5 spm); Java, Bay of Jakarta, Pulau Untung Djawa, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096220, 3 spm); Java, Bay of Jakarta, Pulau Dapur, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096221, 9 spm); Java, Bay of Jakarta, Pulau Damar, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096222, 2 spm); Java, Bay of Jakarta, Pulau Sakit, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096223,

**Table 2.** Comparative table. Characters defining species of *Reticulassa*. DL = number of denticles on the lip; N°LW = number of axial ribs on the on last whorl; N°PW = number of axial ribs on the penultimate whorl; N°W = number of whorls on the protoconch; SC = sculpture of columella; TP = type of protoconch. [continued on next page]

Species name	Protoconch			Axial ribs			Spiral and axial structure			Aperture		Depth (m)			
	N°W	TP	Features	N°PW	N°LW	Features	primary cords	Intercordal striae	DL	SC	Color decoration		Length (mm)	Pustules	Clade
<i>R. annaboleae</i> sp. nov.	1.5–1.75	pauci	flattened, axially striated	15–16	12–14	weak, decreasing anteriorly	weak	spiral, very fine	7–9	plicate	yellowish-orange	7.5–12.6	no	SC2?	Madagascar
<i>R. cockburnensis</i>	1.33–1.5	pauci	tall	13–15	12–13	strong, round, straight	strong on rib	axial	7–9 liratae	wrinkled	creamy yellowish, faintly banded	6.9–9.7	?	SC1?	Western Australia
<i>R. compacta</i>	1.25	pauci	thick	13–14	12–14	broad	bell-shaped	axial	5–7	3–5	withish brown bands possible	5.4–8.7	?	SC1	Western Australia to Victoria
<i>R. crenulicostatus</i>	3.5	multi	glassy	14–15	13–14	strong, close set, rounded	Strong, rounded	spiral, fine	5–6	5–7 denticles	off white yellowish brown	4.5–6	?	SC2?	China Philippines Indonesia Vanuatu
<i>R. erythraea</i>	0.75–1	pauci	extruded	14–15	15–16	strong	strong	spiral	5–7	4–5	white, bands	4.5–7.4	?	SC2?	Egypt Red Sea Suez
<i>R. goliath</i> sp. nov.	1.75	pauci	pointed	11–13	11–12	strong, equidistant	weak	spiral, very fine	7	8 liratae	Off white-yellow, narrow brown band(s)	8.2–16.5	yes	?	Indonesia N Australia Vanuatu New Caledonia
<i>R. hanraveni</i>	1.75–2	multi	thick	13–15	13–15	fine	fine round	axial, very fine	4–5	lirate denticles	ligh yellow-brown, paler band	4.6–6.2	?	SC1	Malaysia (Borneo) West Java
<i>R. intrudens</i> sp. nov.	1.75	pauci	bulbous, flattened	13–14	12–13	strong, round	minute	spiral	5 liratae denticles	wrinkled	creamy yellowish	5.4–9.7	no	SC1?	New Caledonia
<i>R. jeanmartini</i>	2–2.5	multi	axial striae	15–16	16–17	strongly convex	well developed	axial, fine	6–9 weak	lirate throughout	light to dark brown	5.0–7.8	?	SC2?	Réunion Mauritius
<i>R. lateola</i>	1–1.25	pauci	smooth	12	19	not strongly developed	bell-shaped	fine axial striae	7 weak	smooth	ligh yellow-brown	7.2	?	?	Japan

Species name	Protoconch			Axial ribs			Spiral and axial structure			Aperture		Color decoration	Length (mm)	Pustules	Clade	Locality	Depth (m)
	N°W	TP	Features	N°PW	N°LW	Features	primary cords	Intercordal striae	DL	SC							
<i>R. neoproducta</i>	2-2.25	multi	smooth, shiny	14-15	15-17	strong	rounded	spiral, fine	10-12	lirate	White-yellowish bands	7.9-13	?	SC2	Red Sea Eastern Africa SW Sri Lanka	Subtidal-deep	
<i>R. paupera</i>	2-2.25	multi	pointy	12-14	14-16	strong, rounded	narrow, string-like	spiral, very fine	5-7 lirate denticles	6-9 fine denticles	White-yellowish brown, bands	6.8-10.3	yes	SC2	Indonesia Philippines Tonga Is	0-82	
<i>R. poppeorum</i> sp. nov.	2.5-2.75	multi	dome-shaped	14-15	12-15	evenly strong, rounded	weak	spiral, very fine	6 low denticles	lirate	Whitish-yellowish, broad bands	6.9-12	yes	SC2	Malaysia (Borneo) Indonesia Philippines Fiji Western Samoa	0-40	
<i>R. rotunda</i>	2	multi	glassy	13-14	11-12	crowded, strong, round	strong, squared, closely spaced	striae axial, very fine	6-7	5-7 lirae	yellowish-brown, 3 darker bands	6-7	?	SC1	Philippines New Guinea Vanuatu Loyalty I. Hawaii	1-30	
<i>R. silvardi</i>	2.33	multi	spiral ridges	7-8	10-12	strong	broad	axial, coarse	7	plicate	Creamy white-yellowish brown banded	4.3-7.4	yes	SC1	Indonesia New Guinea Marquesas Hawaii	1-68	
<i>R. simoni</i>	2.25	multi	smooth, shiny	14-15	14-16	strong, squared	strong	spiral, fine	6	4-9	whitish, bands	5.7-7.5	?	SC2	Madagascar Oman Sri Lanka Red Sea	4-45	
<i>R. thailandensis</i> sp. nov.	1.3	pauci	flattened	14-15	13-14	strong, rounded	narrow, thread-like	spiral, fine	8 unequal	lirae short	yellowish orange, banded	5.5-9.1	no	SC2??	Thailand - Indonesia Philippines	1-90	
<i>R. tringa</i>	1.5-1.75	pauci	nipple	13-17	12-17	strong, round, decreasing anteriorly	broad, low	spiral, fine	6-8 plicate denticles	lirate	white yellow-orange brown, bands	6.7-12.2	yes	SC2	New Caledonia, Vanuatu - Fiji	0-72	
<i>R. visayensis</i> sp. nov.	2.25-2.5	multi	smooth	14-16	13-15	strong, round, decreasing anteriorly	narrow, string-like	Spiral, very fine	9 lirate denticles	lirate	extremely variable	8.5-12.7	yes	SC2	Philippines Indonesia New Guinea	0-150	
<i>R. zanzibarensis</i>	1	pauci	smooth	14-15	14-16	strong	strong, broad	Spiral, fine	5-8	6-7	white, bands 2-3 spirals lighter	5.5-7.9	?	SC2??	East Africa Madagascar Seychelles	Intertidal	

3 spm); Java, Bay of Jakarta, Pulau Njamoek, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096224, 10 spm); Java, Bay of Jakarta, Pulau Noesi, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096225, 15 spm); Java, Bay of Jakarta, Pulau Ubi, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096226, 9 spm); Java, Bay of Jakarta, Pulau Ramboet, leg. J.D.F. Hardenberg, 1938 (ZMA.Moll.096227, 1 spm); KEPULAUAN SERIBU 2005, Java, Hantu Besar, 5°31.8' S, 106°32.3' E, 5–26 m (ZMA.Moll.175389, 1 spm); KEPULAUAN SERIBU 2005, stn SER05/33, Java, Pari East, 5°51.3' S, 106°38.3' E, 5–25 m (ZMA, 1 spm); KEPULAUAN SERIBU 2005, stn SER05/43, Java, Payung Besar, 5°40.3' S, 106°33.8' E, 5–25 m (ZMA.Moll.154531, 2 spm).

PHILIPPINES: all PANGLAO 2004: stn M10, Panglao I., Bingag/Tabalong, 9°37.8' N, 123°48.4' E, 0–3 m (1 spm); stn M26, Bohol I., Taloto, 9°40.9' N, 123°51.1' E, 0–2 m (1 spm); stn S25, Bohol I., Ubajan, 9°41.5' N, 123°51.0' E, 21 m (1 spm); stn B14, Panglao I., Sungcolan Bay, 9°38.5' N, 123°49.2' E, 2–4 m (3 spm).

AUSTRALIA: Queensland, Fitzroy I. (HK 995.08, 2 spm; HD 17298, 1 spm; PS, 1 spm); Queensland, Innisfail, leg. Pini (ZMA.Moll.096207, 1 spm).

GUAM: Neye I. Channel, leg. S.P. Kool (HK 995.04, 2 spm); Apra Harbor, by diving to 10 m, leg. H. Morrison (HK 995.05, 1 spm); Glass Breakwall, snorkeling, 1–2 m (HD 12297, 2 spm); Glass Breakwall, 6 m, in rubble (GH, 1 spm).

CAROLINE ISLANDS: Truk I., Moen I. (HK 995.10, 2 spm).

NEW CALEDONIA: CHALCAL 1: stn D17, Plateau Chesterfield-Bellona, 19°11' S, 158°55.8' E, 44 m (1 spm); stn D57, Plateau Chesterfield-Bellona, 21°29.5' S, 159°16.4' E, 62 m (1 spm). – LAGON: Ile Quen, Baie Prony, stn 64, 22°28' S, 166°25' E, 15 m (2 spm; NBC, 1 spm; HK 995.01, 1 spm); Ile Quen, Baie Prony, stn 78, 22°28' S, 166°31' E, 35 m (1 spm); Ile Quen, Baie Prony, stn 240, 22°23' S, 166°32' E, 42 m (1 spm); Nouméa, stn 290, 22°16' S, 166°32' E, 11 m (1 spm); Yaté, stn 620, 22°02' S, 166°56' E, 50–52 m (1 spm); Yaté, stn 625, 21°59' S, 166°54' E, 34–40 m (1 spm); Poindimié, stn 789, 21°03' S, 164°34' E, 29 m (1 spm); Poum, stn 1039, Balabio Section, 20°01' S, 164°02' E, 20–21 m (1 spm; HK 995.02, 1 spm); Belep, stn 1105, 19°40' S, 163°57' E, 25 m (1 spm); Belep, stn 1129, 19°29' S, 163°49' E, 40 m (1 spm); Belep, stn 1168, 19°16' S, 163°09' E, 50 m (2 spm); Nouméa, Pointe Magnin, stn 1355, 22°18.9' S, 166°26.6' E, 7–10 m (3 spm). – MONTROUZIER 1993: Touho, Lagon du grand Récif Mengalia, stn 1253, 20°46.6' S, 165°14.1' E, 2–3 m (1 spm); Touho, Lagon du grand Récif Mengalia, stn 1266, 20°39.6' S, 165°14.7' E, 10–15 m (1 spm); Touho, Lagon du grand Récif Mengalia, stn 1269, 20°35.1' S, 165°08.1' E, 15–20 m (2 spm); Koumac, stn 1298, 20°35.2' S, 164°16.6' E, 2–4 m (1 spm); Koumac, stn 1299, 20°34' S, 164°13.0' E, 12–14 m (11 spm; NBC, 1 spm; HD 24147, 1 spm); Koumac, stn 1308, 24°40' S, 164°15.2' E, 15–20 m (3 spm; ZMA, 1 spm); Koumac, stn 1312, 20°40' S, 164°14.9' E, 26–40 m (6 spm; HK 995.11, 1 spm); Koumac, stn 1314, 20°39.8' S, 164°15.3' E, 30–63 m (7 spm); Koumac, stn 1315, 20°40.7' S, 164°14.7' E, 66–87 m (3 spm); Koumac, stn 1318, 20°41.4' S, 164°14.8' E, 20–30 m (2 spm); Koumac, stn 1319, 20°44.7' S, 164°15.5' E, 15–20 m (2 spm); Koumac, stn 1322, 20°45.2' S, 164°15.2' E, 53–71 m (1 spm); Koumac, stn 1323, 20°40.9' S, 164°14.8' E, 82–120 m (1 spm). – CORAIL 2: stn DW32, Plateau de Chesterfield, 19°25' S, 158°49' E, 55 m (1 spm); stn DW34, Plateau de Chesterfield, 19°18' S, 158°47' E, 47 m (2 spm); stn DW 38, Plateau de Chesterfield, 19°22' S, 158°43' E, 61 m (1 spm); stn DW56, Plateau de Chesterfield, 19°18' S, 158°47' E, 66 m (1 spm); stn DW59, Plateau de Chesterfield, 19°19' S, 158°57' E, 50 m (1 spm); stn DW65, Plateau de Chesterfield, 19°15' S, 158°41' E, 62 m (1 spm); stn DW71, Plateau de Chesterfield, 19°15' S, 158°24' E, 55 m (HD 22467, 1 spm); stn DW72, Plateau de Chesterfield, 19°15' S, 158°21' E, 32 m (1 spm); stn DW156, Plateau de Chesterfield, 19°49' S, 158°21' E, 42 m (1 spm). – PALEO-SURPRISE, stn DW1382, 18°26.5' S, 163°05.9' E, 41–42 m (1 spm).



LOYALTY ISLANDS: both LIFOU 2000: Lifou, Santal Bay, stn 1423, 20°54.0' S, 167°07.1' E, 12 m (2 spm); Lifou, Santal Bay, stn 1444, 20°55.0' S, 167°05.2' E, 9–20 m (1 spm).

VANUATU: all SANTO 2006: stn FB56, NE of Tangisi I., 15°35.2' S, 167°02.1' E, 3–18 m (3 spm); stn DB08, E of Aore I., 15°34.6' S, 167°13.8' E, 12 m (1 spm); stn DB33, E of Aore I., 15°34.7' S, 167°13.8' E, 14–25 m (1 spm); stn ZB36, E of Aore I., 15°34.3' S, 167°12.4' E, intertidal (1 spm); stn ZS22, W of Aore I., 15°31.1' S, 167°09.6' E, 27–29 m (15 spm); stn ZB16, Aore I., 15°32.4' S, 167°12.1' E, 5m (2 spm); stn DB12, S of Aore I., 15°36.6' S, 167°10.1' E, on sand (9 spm); stn LD35, Aore I., 15°32.7/32.8' S, 167°11.5/11.6' E, 3–8 m (1 spm); stn DB48, W of Malo I., 16°38.7' S, 167°5.2' E, 10–17 m (1 spm); stn DB83, E of Malo I., 15°43.4' S, 167°15.0' E, on sand (2 spm); stn DS49, Malo I., 15°38.7' S, 167°05.2' E, 10–17 m (4 spm); stn ZM15, NW of Malo I., 15°38.1' S, 167°05.9' E, intertidal (1 spm); stn DB75, SE of Matewulu, 15°22.9' S, 167°11.9' E, 20 m (4 spm); Segond Channel, stn DB14, 15°39.9' S, 167°11.0' E, 10–14 m (3 spm); Segond Channel, stn DS04, 15°31.4' S, 167°14.1' E, 25 m (33 spm; HD 38512, 2 spm; HK 995.12, 3 spm); Segond Channel, stn DS06, 15°30.9' S, 167°11.1' E, 8–15 m (1 spm); Segond Channel, stn DS91, 15°33.7' S, 167°08.4' E, 7 m (20 spm); Segond Channel, stn FS54, 15°31.4' S, 167°14.1' E, 20–31 m (25 spm; HD35303, 2 spm); Segond Channel, stn FS77, 15°33.1' S, 167°09.6' E, 29 m (17 spm; HK 995.14, 2 spm); Segond Channel, stn FS79, 15°33.1' S, 167°09.6' E, 2 m (3 spm); Segond Channel, stn FS96, 15°33.1' S, 167°09.6' E, 35 m (6 spm); Segond Channel, stn FB80, 15°33.1' S, 167°09.6' E, 2 m (1 spm); Segond Channel, stn LS17, 15°31.1' S, 167°10.5' E, 7 m (2 spm); Segond Channel, stn ZS19, 15°31.4' S, 167°14.1' E, 15–30 m (20 spm); Segond Channel, stn NB12, 15°33.1' S, 167°09.6' E, 20 m (1 spm); Segond Channel, stn NS37, 15°31.4' S, 167°09.8' E, 2–3 m (4 spm); Palikulo Bay, stn DB53, 15°28.8' S, 167°15.2' E, 5 m (2 spm); Palikulo Bay, stn DB65, 15°25.8' S, 167°13.0' E, 13 m (2 spm); Palikulo Bay, stn DB77, 15°27.9' S, 167°14.7' E, 42–45 m (2 spm); Palikulo Bay, stn DS43, 15°27.9' S, 167°14.3' E, 22 m (5 spm); Palikulo Bay, stn DS54, 15°28.8' S, 167°15.2' E, 5 m (6 spm); Palikulo Bay, stn DS59, Aésé I., 15°24.6' S, 167°14.3' E, 6–43 m (1 spm); Palikulo Bay, stn DB16, Tutuba I., 15°35.5' S, 167°15.8' E, 32–40 m (4 spm); Palikulo Bay, stn DS103, West Tutuba I., 15°34.0' S, 167°16.0' E, 70–80 m (4 spm); Palikulo Bay, stn LD36, West Taluba I., 15°39.5' S, 167°16.8' E, 8–10 m (1 spm); Palikulo Bay, stn DS105, NW of Tutuba I., 15°33.0' S, 167°16.7' E, 92 m (3 spm); Palikulo Bay, stn DS110, Bruat Channel, 15°36.8' S, 167°08.8' E, 35 m (1 spm); Palikulo Bay, stn LD12, Bruat Channel, 15°36.6' S, 167°11.3' E, 2–4 m (1 spm); Palikulo Bay, stn ZB06, SW Urélapa I., 15°36.8' S, 167°01.3' E (1 spm); SE corner of SANTO 2006, shallow water (10 spm; NBC, 1 spm; HD 38511, 1 spm; HK 995.13, 2 spm).

FIJI: MUSORSTOM 10, stn DW1384, 18°18.5' S, 178°06' E, 260–305 m (1 spm).

TONGA: BORDAU 2, stn DW1581, 18°41' S, 174°02' E, 75–85 m (1 spm).

### Description

PROTOCONCH. Approximately 2.25 shiny whorls (Fig. 2A). SEM photography shows fine axial striae and minute pustules on last whorl.

SHELL. Teleoconch consists of approximately 5 convex whorls. Suture deep. Penultimate whorl with 12–14 and body whorl with 14–16 pronounced and rounded axial ribs. Outer lip with a strong varix.

SPIRAL CORDS. Penultimate whorl with 5–6 and body whorl with 10–11 continuous, narrow, string-like spiral cords, some more pronounced on axial ribs than in between them.

INTERCORDAL SCULPTURE. Between spiral cords, spiral striae faintly visible on well-preserved specimens (Fig. 2F).

**APERTURE.** Aperture oval-rounded, outer lip with 5–7 fairly prominent, lirate denticles, peripheral denticle most prominent. Columella (Fig. 2G–H) with 6–9 fine denticles, columellar callus sharply bordered and limited to columella. Parietal denticle strong, anal canal wide.

**OPERCULUM.** Whitish, serrated.

**SIPHONAL CANAL.** Fasciole strong, siphonal area with 5–7 weak cords, last one most prominent.

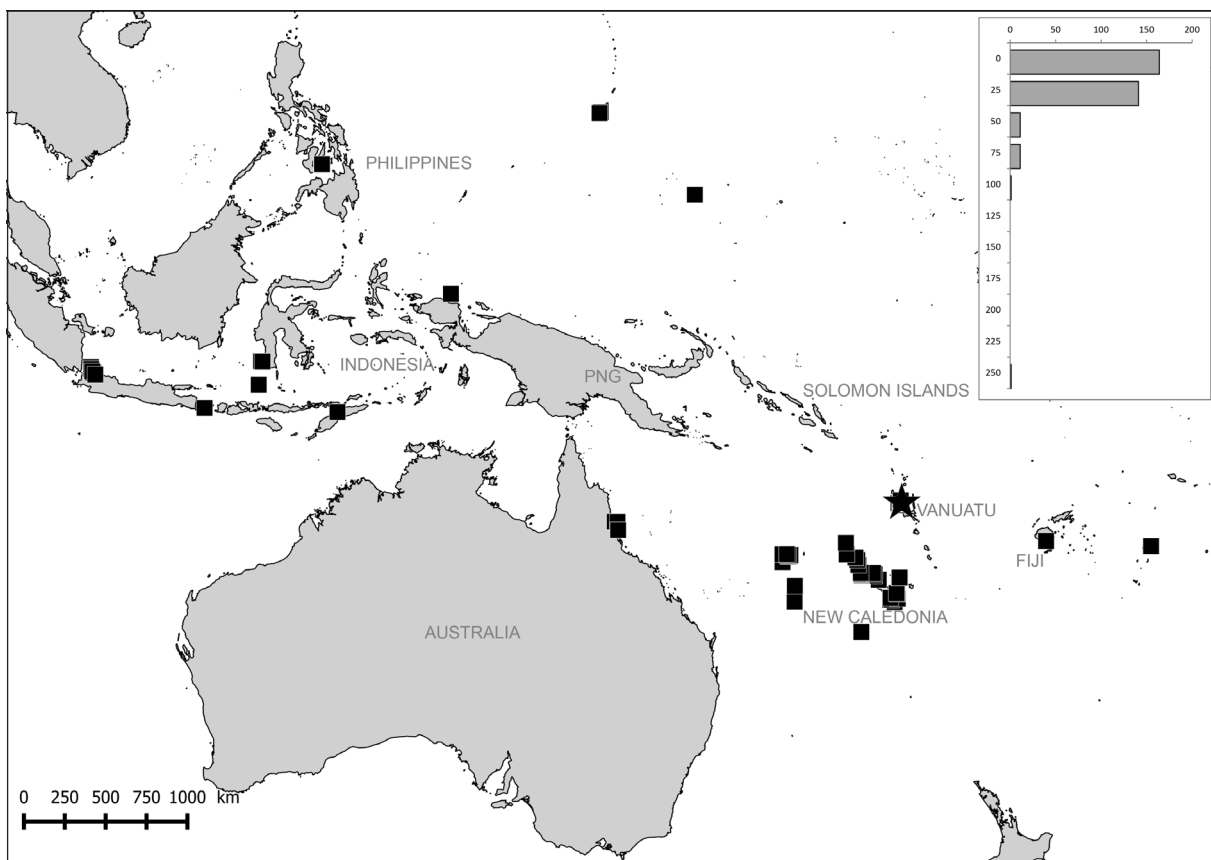
**COLOR.** Creamy-white to yellowish brown, occasionally with 1–3 darker spiral bands.

**ADULT SIZE.** 6.8–10.3 mm, usually 7.5–8.5 mm.

### Remarks

Several species, previously synonymized with *R. paupera* by Cernohorsky (1984), have been taken out of synonymy in the past few years. A series of published reviews (Kool & Dekker 2006, 2007), including the present article, demonstrate that the *Nassarius pauperus* complex is composed of several valid species. Therefore, the synonymy given for *Reticunassa paupera* s. str. has become very short and caution is advised with citations of this species name in the literature.

The combination of the multispiral protoconch, the many pronounced, round ribs, the deep suture, the broad varix, the very fine spirals, the sharply-bordered columella and the columellar denticles not lirae characterize this species, one of the smaller within the genus.



**Fig. 4.** Geographical and bathymetrical distribution of *Reticunassa paupera* (Gould, 1850). Star indicates type locality. Each bar represents all lv or dd specimens.

The differences between *R. paupera* and the other species of *Reticunassa*, described below, will be discussed in the remarks section in each case.

In the taxonomic history of *Nassa paupera*, several declensions on the specific epithet have been used. In Latin, there are two different adjectives with the same meaning: the classical *pauper* (3<sup>rd</sup> declension, nominative unchanged) and the post-classical (medieval, generally clerical) *pauperus* (1<sup>st</sup> declension, *paupera* feminine, *pauperum* neuter), both meaning “poor.” The second adjective is obviously a derivation of the first. The fact that Gould (1850) used *paupera* in his original description indicates that he was referring to the second meaning. Combined with *Reticunassa*, the new combination is *R. paupera* (Gould, 1850).

### Habitat

Specimens were collected from the intertidal to a depth of 82 m, mostly from 0 to 25 m; one empty shell was obtained at 260 m (Fiji Islands). The proposed neotype was collected on sand with dead corals. Specimens from Guam (HD 12797) were found in rubble.

### Distribution

Widely distributed in the western Pacific Ocean, from Indonesia and the Philippines to the Tonga Islands (Fig. 4).

### *Reticunassa tringa* (Souverbie, 1864)

Figs 2E, 3D–I, 5; Tables 1–2

*Nassa tringa* Souverbie in Souverbie & Montrouzier, 1864: 272, pl. 10, fig. 7.

*Nassa mamillata* Preston, 1907: 267, textfig. 1.

*Nassarius (Hima) pauperus* [in part] – Cernohorsky 1972: 186, fig. 152 only; 1984: 176, pl. 37, figs 5–6 (syntypes of *Nassa tringa*), fig. 7 (holotype of *N. mamillata*).

### Type material

NEW CALEDONIA: 6 syntypes of *Nassa tringa* (MHNbX 2014.TY.89.0, 2 spm; MNHN IM-2000-28389, 4 spm, <http://coldb.mnhn.fr/catalognumber/mnhn/im/2000-28389>). We designate MHNbX 2004.TY.89.1 (from the former MHNbX 2004.TY.89.0) as the lectotype (Fig. 3F–H), length 9.0 mm, width 5.0 mm.

NEW CALEDONIA: holotype of *N. mamillata* (NHMUK 1923.2.20.8).

### Other material examined

NEW CALEDONIA: MONTROUZIER 1993: Touho, stn 1237, 20°46.9' S, 165°13.8' E, 0–1 m (15 spm; HD, 2 spm; HK 994.02, 3 spm); Touho, stn 1240, 20°46.5' S, 165°14.0' E, 0–2 m (19 spm; HK 994.01, 3 spm; HD 24146, 1 spm); Touho, stn 1241, 20°48.0' S, 165°15.7' E, 0–2 m (2 spm; NBC, 1 spm); Touho, stn 1242, 20°46.2' S, 165°14.5' E (29 spm); Touho, stn 1244, 20°49.3' S, 165°15.2' E (1 spm); Touho, stn 1245, 20°45.2' S, 165°16.3' E (3 spm); Touho, stn 1246, 20°42.8' S, 165°08.7' E (4 spm); Touho, stn 1253, 20°46.6' S, 165°14.1' E, 2–3 m (15 spm); Touho, stn 1259, 20°44.6' S, 165°13.7' E, 15–35 m (2 spm); Touho, stn 1261, 20°46'–20°47' S, 165°15'–165°16.5' E, 45–56 m (2 spm); Koumac, stn 1277, 20°34' S, 164°16' E, 0–2 m (4 spm); Koumac, stn 1278, 20°34' S, 164°16' E, 0–2 m (2 spm); Koumac, stn 1279, 20°35' S, 164°15.5' E (3 spm); Koumac, stn 1282, 20°33.5' S, 164°13' E (10 spm); Koumac, stn 1283, 20°33.5' S, 164°12.2' E (1 spm); Koumac, stn 1284, 20°33.7' S, 164°19' E (19 spm); Koumac, stn 1286, 20°38'–20°39' S, 164°16'–164°17' E (2 spm); Koumac, stn 1288, 20°40' S, 164°19' E (1 spm); Koumac, stn 1289, 20°29.2' S, 164°10.2' E (6 spm); Koumac, stn 1290, 20°29.2' S, 164°10.2' E (1 spm); Koumac, stn 1291, 20°22.4' S, 164°06.8' E (1 spm); Koumac,

stn 1292, 20°22.4' S, 164°06.8' E (4 spm); Koumac, stn 1298, 20°35.2' S, 164°16.6' E, 2–4 m (1 spm). – LAGON: stn 77, Ile Ouen-Baie du Prony, 22°26' S, 166°32' E, 22 m (1 spm); stn 384bis, Grand Récif Sud, 22°34' S, 167°11' E, 72 m (1 spm); stn 441, Atoll de Huon, 18°04' S, 162°56' E, 37 m (1 spm). – New Caledonia, leg. Rossiter, ex coll. Dautzenberg (ZMA.Moll.098635, 5 spm); beach S of Noumea, leg. Mrs Wijsman-Best, 1968 (ZMA Moll. 096210, 2 spm); Ile des Pins (PS, 2 spm); Nouméa, leg. A.P. Greeven-Lels, 1965 (HD 21379, 9 spm).

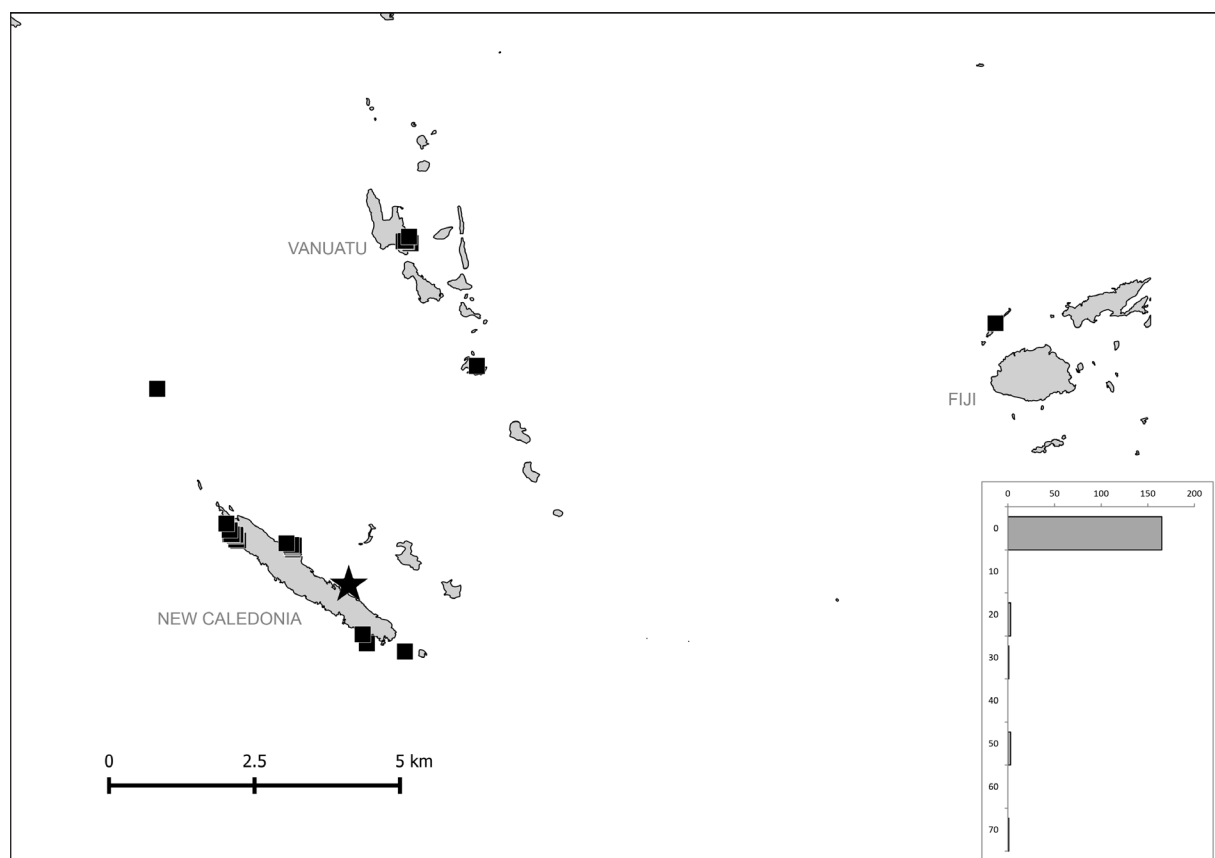
VANUATU: SANTO 2006: stn AT52, Segond Channel, 15°31.5' S, 167°12.7' E, 52–62 m (MNHN IM-2007-31753, 1 lv, 19.5 mm, w 4.6 mm, Fig. 3D–E, I); stn LM23, Segond Channel, 15°31.5' S, 167°09.6' E, intertidal (1 spm); stn VM53, Segond Channel, 15°31.0' S, 167°11.9' E, intertidal (6 spm); stn VM69, Tutuba I., 15°33.4' S, 167°16.7' E, intertidal (MNHN IM-2007-31758, 1 lv); stn FB92, Tutuba I., 15°33.6' S, 167°16.6' E, 2–4 m (1 spm); stn VM32, W of Aésé I., 15°26.6' S, 167°15.2' E, intertidal (2 spm). – Efate, snorkeling, 2–3 m, leg. T. McCleery, 2002 (HD 17091, 4 spm; HK 994.20, 3 spm).

FIJI: Yasawa I., leg. S.P. Kool (coll. S.P. Kool, 3 spm; HK 994.26, 1 spm).

### Description

PROTOCONCH. Whitish, paucispiral, consisting of 1.5–1.75 whorls (Fig. 3I). SEM photograph shows very fine growth lines, and in addition minute pustules on part of last whorl.

SHELL. Elongate-ovate, teleocoel with 5–6 whorls, suture impressed. On penultimate whorl 13–17 and on body whorl 12–17 pronounced, round axial ribs, on ventral side of body whorl often decreasing in height towards base.



**Fig. 5.** Geographical and bathymetrical distribution of *Reticunassa tringa* (Souverbie, 1864). Star indicates type locality. Each bar represents all lv or dd specimens.

**SPIRAL CORDS.** Continuous, moderately broad, rounded primary cords, approximately 4–5 on penultimate and approximately 10–12 on body whorl.

**INTERCORDAL SCULPTURE.** Fine, evenly-spaced, continuous striae (Fig. 2E), 7–9 on body whorl, sometimes visible between, as well as on spiral cords.

**APERTURE.** Roundish; outer lip thick, plicate inside, with strong varix; peripheral denticle and more pronounced pleat near siphonal canal. Columella callused, callus sharply bordered, posteriorly slightly extending over body whorl. Columellar lip liriate throughout. Parietal denticle moderately strong.

**OPERCULUM.** Yellowish, serrated.

**SIPHONAL CANAL.** Narrow, with strong fasciole. Siphonal area with weak cords and in some specimens faint axial striae between cords.

**COLOR.** Off white, yellowish to orange or brown. Banding very variable: some specimens with chestnut to dark brown, or nearly black bands; on penultimate whorl a sub- and/or a supra-sutural band; on body whorl occasionally one band directly below periphery and one at base. Occasionally, some or most spiral cords darker, especially between axial ribs. Aperture yellowish, showing outside banding, if present.

**ADULT SIZE.** 6.7–12.2 mm, usually 8–9.5 mm.

### Remarks

Characteristics of this species are a paucispiral protoconch, low spiral cords, in combination with numerous, evenly-spaced intercordal spiral striae (Fig. 2E), axial ribs decreasing in height anteriorly on the ventral side of the body whorl, and the presence of lirae on the columellar callus. In well-preserved specimens, spiral striae are also visible on top of the spiral cords. The intercordal spiral striae were not mentioned in the original description by Sowerbie (in Sowerbie & Montrouzier, 1864). However, Preston (1907) mentioned this sculpture in the description of *Nassa mamillata*. We agree with Cernohorsky (1984), that the latter is a synonym of *Reticunassa tringa*.

*R. tringa* can easily be distinguished from *R. paupera* by its paucispiral protoconch, probably figured by Cernohorsky (1984: 5, fig. 12). Cernohorsky did not discuss protoconch morphology or other conchological features shared by species within the *Nassarius pauperus* complex, resulting in numerous synonyms of *R. paupera*, followed by many authors.

*R. tringa* closely resembles *R. visayaensis* sp. nov. and *R. poppeorum* sp. nov. For the differences between *R. tringa* and these species, see respective Remarks sections.

### Habitat

Intertidal to 72 m, more frequently within the first 10 m of depth.

### Distribution

New Caledonia, Vanuatu and Fiji (Fig. 5).

*Reticunassa visayaensis* sp. nov.

[urn:lsid:zoobank.org:act:742DB3E4-4D0F-40DD-985C-948F113C4C65](https://doi.org/10.3896/urn:lsid:zoobank.org:act:742DB3E4-4D0F-40DD-985C-948F113C4C65)

Fig. 3J–M, 6; Tables 1–2

*Nassarius mamillatus* – Martin 2008: 122, pl. 356, fig. 3 (non Preston).

*Nassarius pauperus* – Martin 2008: 126, pl. 358, figs 1–4 (non Gould).

*Nassarius fuscolineatus* – Martin 2008: 126, pl. 358, fig. 6 (non Smith).

### Etymology

The name refers to the Visayas, a group of central Philippine Islands where this species is common.

### Type material

#### Holotype

PHILIPPINES: Iv, Panglao Island, 9°35.7' N, 123°44.7' E, 0–3 m, seagrass and hard bottom, length 9.5 mm, width 4.6 mm, sequenced (MNHN IM-2007-31912).

#### Paratypes

PHILIPPINES: Panglao Island, Momo Beach, 9°36.1' N, 123°45.2' E, 0–3 m (MNHN IM-2000-28395, 9.2 mm; MNHN IM-2000 28405; MNHN IM-2000-28404, 3 spm); Panglao I. area (HD 24336, 60 spm; HK 184.13, 2 spm).

### Other material examined

PHILIPPINES: PANGLAO 2004: Panglao I., stn B8, Napaling, 9°37.1' N, 123°46.1' E, 3 m (2 spm); Panglao I., stn M1, Alona Beach, 9°32.9' N, 123°50.5' E, 5m (2 spm); Panglao I., stn M5, Doljo Point, 9°35.5' N, 123°43.3'/123°44.3' E, 0–2 m (1 spm); Panglao I., stn M7, Momo Beach, 9°36.1' N, 123°45.2' E, 0–3 m (2 spm); Panglao I., stn M9, near Doljo Point, 9°35.1' N, 123°43.6' E, 0.5 m (1 spm); Panglao I., stn M10, Bingag/Tabalong, 9°37.8' N, 123°48.4' E, 0–3 m (1 spm); Panglao I., stn M22, Napaling, 9°37.2' N, 123°46.4' E, 0–3 m (1 spm); Panglao I., stn M40, Looc, 9°35.7' N, 123°44.7' E, 0–3 m (1 spm); Panglao I., stn R19, Napaling, 9°37.1' N, 123°46.1' E, 2–54 m (2 spm); Panglao I., stn S24, Momo Beach, 9°36.1' N, 123°45.0' E, 2–4 m (1 spm); Pamilacan I., stn S42, 9°30.1' N, 123°55.5' E, 15–20 m (1 spm). – Cebu, leg. R. Martin (ZMA.Moll.175495, 10 spm); Cebu (HK 184.09, 1 spm; ZMA Moll. 080981, 1 spm); Cebu, Liloan, 50–150 m, 2013 (HD 35803, 1 spm); Mactan I., Maribago, Buyon, in sandy tide pools, leg. O.K. McCausland (HK 184.07, 1 spm); Punta Engaño, in tangle nets, 150 m (HK 184.05, 3 spm); Punta Engaño, in coral rubble, 20 m (HK 184.14, 3 spm); Punta Engaño (HD 11610, 8 spm); Punta Engaño, 80–100 m (HD 17300, 3 spm); Mactan I., Punta Engaño, 25–50 m (HD 33879, 1 spm); Punta Engaño, leg. S.P. Kool, 2005 (HK 184.11, 1 spm); Punta Engaño, 1–2 m, live (HK 184.12, 2 spm); Punta Engaño, 25–30 m, 2009 (AMD, 2 spm); Punta Engaño, 100–150 m, 2009 (AMD, 2 spm); Balicasag I. (HD 15930, 2 spm); Olango I., night dive, 20–25 m (HD 17292, 3 spm); Olango I., 2014 (HD 35872, 4 spm); Olango I., 20–25 m, 2009 (AMD, 2 spm); Cuyo I., 15–20 m (HD 35488); Calituban I., 10 m (HK 184.01, 6 spm); SW side of Catanduanes, San Rafael, leg. S.P. Kool, 2005 (HK 184.10, 1 spm); Aliguay I., tangle nets, 150–180 m (HK 184.08, 2 spm); Palawan, 10–25 m, 2009 (AMD, 2 spm).

INDONESIA: SNELLIUS 1929: Ternate I., 1–2 Apr. 1930 (RMNH, 1 spm); Tidore I., 24–29 Nov. 1929 (RMNH, 1 spm). – RUMPHIUS 1990: Ambon, stn 05 Leitimur, Ambon Bay, outer bay, Tg. Benteng (RMNH, 2 spm); Ambon, stn 17, SE side of Pombo I. (RMNH, 2 spm); Ambon, stn 20 Hitu, N coast, Hitulama (RMNH, 1 spm); Ambon, stn 21 Hitu, N coast, Mamala (RMNH, 2 spm); Ambon, stn 23 Hitu, Kaitetu (near Hila), 22–23 Nov. 1990 (RMNH, 1 spm); Ambon, stn 26 Hitu, 4 km W of Kaitetu, 23 Nov. 1990 (RMNH, 3 spm); Ambon, stn 27 Leitimur, S coast, Hutumuri (RMNH, 1 spm); Ambon, stn 34 Hitu, Ruhmatiga 3–5 Dec. 1990 (RMNH, 4 spm; HK 184.03, 1 spm). – LAGON, stn Seith, Karubar, Amboine, low tide (1 spm); South Moluccas, leg. Rijkschroeff (ZMA.Moll.096203, ex coll. Butot 12403, 7 spm); South Moluccas, leg. Rijkschroeff (ZMA.Moll.096204, ex coll. Butot 12404, 5 spm); Ceram, N coast, Seleman Bay, leg. H. Strack (HK 184.04, 1 spm); Sulawesi, Lintido, leg. Semmelink (ZMA.Moll.096205, ex coll. Schepman, 1 spm); Bali, Sanur, leg. K. van Duin, 1989 (ZMA. Moll.099329, 1 spm); Bali, Kaliyasem, Lovina area, 8°09.7' S, 115°01.7' E, 1–2 m (HK 184.16, 3 spm);

Flores, Labuan Bajo, Binongko Beach, leg. J.N.J. Post (HK 184.15, 1 spm); West Papua, Manokwari, near Uriami River, leg. D. Smits 1958/1961 (HK 184. 02, 11 spm; HD 38514, 11 spm).

PAPUA NEW GUINEA: PAPUA NIUGINI: stn PM22, Sek I., 05°04.7' S, 145°48.9' E, 0–1 m (MNHN IM-2013-13184; MNHN IM-2013-13192, 2 lv); stn PM19, Islet SE of Megas Islet, 05°05.4' S, 145°48.6' E, 0–1 m (2 spm); stn PB23, Lauhamug I., outer slope, 04°59.5' S, 145°47.7' E, 13 m (1 spm); stn DP31, Alexishafen, 05°05.3' S, 145°48.1' E, 1–6 m (4 spm); stn PM38, Biliau I., 05°11.8' S, 145°48.2' E (1 spm); stn PD78, Tabad I., 05°08.2' S, 145°48.7' E, 5 m (1 spm); stn PR202, S of Tab I., 05°10.3' S, 145°50.3' E, 2–4 m (2 spm).

## Description

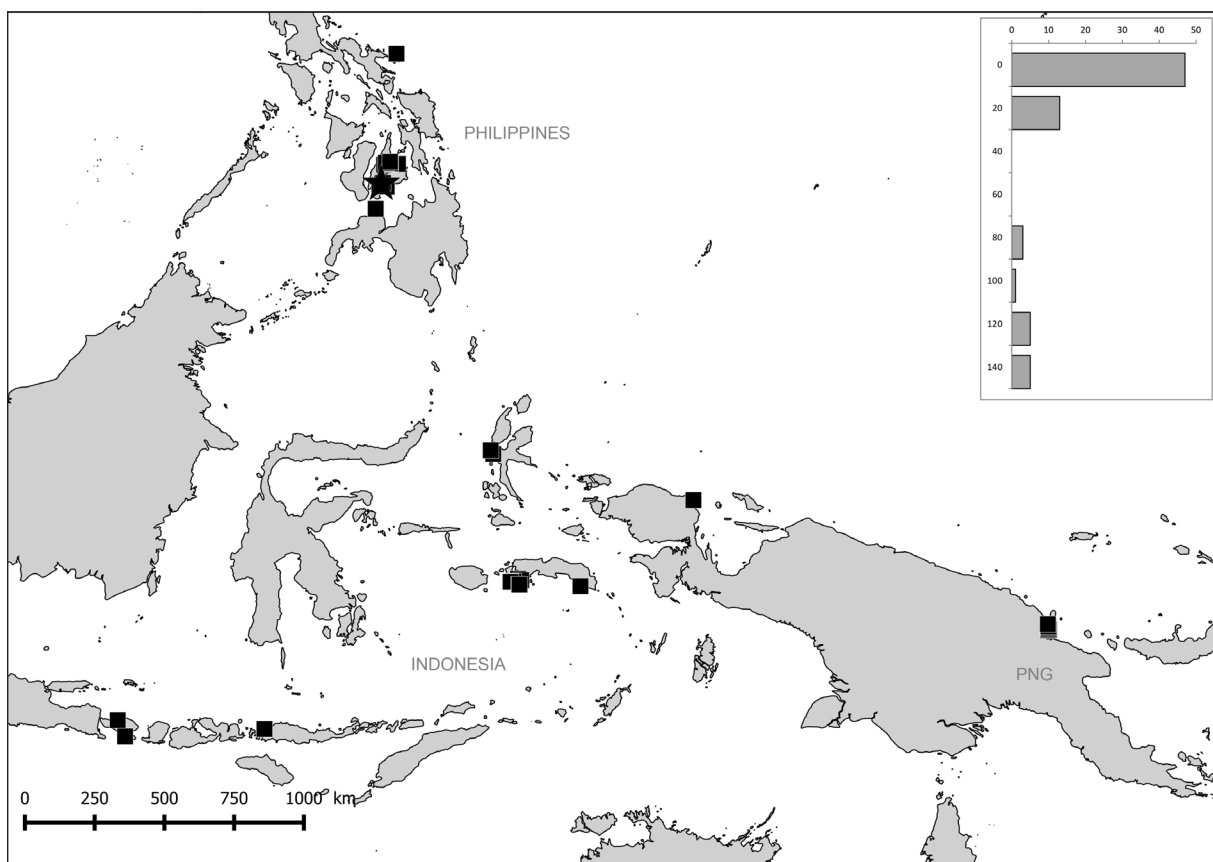
### Holotype

PROTOCONCH. Smooth, multispiral, whitish-yellowish, consisting of 2.5 whorls. Beset with rows of minute pustules (Fig. 3M).

SHELL. Elongate-ovate, 5.5 postnuclear whorls, suture impressed. Penultimate whorl with 15 nearly equally pronounced, round ribs; body whorl with 14 ribs, decreasing in height or disappearing on ventral side. Varix broad and strong.

SPIRAL CORDS. Continuous, flat and narrow, 7 cords on penultimate, and 11 on body whorl, peripheral one somewhat darker.

INTERCORDAL SCULPTURE. Approximately 6 very fine, evenly spaced striae between spiral cords.



**Fig. 6.** Geographical and bathymetrical distribution of *Reticunassa visayaensis* sp. nov. Star indicates type locality. Each bar represents all lv or dd specimens.

**APERTURE.** Oval, inside outer lip with 9 lirate denticles, peripheral denticle slightly more pronounced. Parietal denticle moderate, anal canal wide. Columellar callus wide, anteriorly somewhat elevated, posteriorly partly extending over whorl; well delineated border. Fine lirae over entire surface.

**OPERCULUM.** Yellowish, serrated.

**SIPHONAL CANAL.** Fasciole strong, siphonal area with 1 strong and 5 weak cords.

**COLOR.** Yellowish, most spiral cords reddish between ribs.

**ADULT SIZE.** 8.5–12.7 mm, usually 8.5–10.5 mm.

### Remarks

The intraspecific variability is considerable. The number of ribs and spiral cords may vary, and the color is extremely variable, white to yellow and orange to brown, unicolor or with narrow or broad yellow, brown, dark brown, or grey bands on all whorls or only on the body whorl.

*Reticunassa visayaensis* sp. nov. has a broader, less pointed protoconch than *R. paupera* (Gould, 1850). *R. visayaensis* sp. nov. also differs from *R. paupera* by its larger size, its more bulbous shape and its lower ribs, especially on the body whorl, and by usually displaying dark bands.

*R. visayaensis* sp. nov. is very similar to *R. tringa*. When the protoconch is missing, a positive identification is almost impossible. The protoconch of *R. tringa* is paucispiral with 1.5–1.75 whorls, whereas *R. visayaensis* sp. nov. has a protoconch of 2.25–2.5 whorls. The protoconch of *R. tringa* is nipple-shaped, hence the name “*mamillata*” (Preston 1907); the protoconch of *R. visayaensis* sp. nov. is dome-shaped. Preston’s description is accompanied by a drawing of the paucispiral protoconch.

*R. visayaensis* sp. nov. is the *Reticunassa* species most commonly offered in the shell trade from the central Philippines, as well as *R. crenulicostata* (Shuto, 1969). The latter is smaller (5–7 mm) and has a large multispiral protoconch of 3.5 whorls (Cernohorsky 1984: pl. 38, figs 1–2; Martin 2008: pl. 354, figs 4–5). These features are the most distinguishing differences between *R. crenulicostata* and *R. visayaensis* sp. nov. *Reticunassa tringa* has a paucispiral protoconch. Identification based on geographical distribution alone (Fig. 6) may be possible in specimens lacking a protoconch or well-defined teleoconch sculpture.

### Habitat

Intertidal to 150 m, commonly from 0 to 20 m.

### Distribution

Philippines, Indonesia and New Guinea (Fig. 6).

*Reticunassa poppeorum* sp. nov.

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Fig. 3N–Q, 7; Tables 1–2

### Etymology

The name is given to honor Guido T. and Philippe Poppe for their many valuable contributions to the knowledge of and myriad publications on molluscs, including four volumes on Philippine marine molluscs and the magazine “Visaya.”



**Type material****Holotype**

VANUATU: SANTO 2006, stn FB61, Aore Island, Port Benier, 15°34.4' S, 167°12.6' E, 2–3 m, in fine coral sand (MNHN IM-2007-31779, 1v, length 9.0 mm, width 4.5 mm).

**Paratypes**

VANUATU: SANTO 2006, stn DR03, Segond Channel, 15°31.0' S, 167°15.8' E, 2–30 m, reef slope, fine rubble with *Halimeda* (MNHN IM-2007-32742, 1 lv); Éfate, snorkeling, 2–3 m, leg. T. McCleery, 2002 (HD 35802, 1 spm); Tutuba I., 15°32.3' S, 167°16.9' E, 13 m (HK 137.23, 1 spm).

PHILIPPINES: PANGLAO 2004, stn S2, Bohol I., Baclayon, 9°37.4' N, 123°54.5' E, 4–5 m (MNHN IM-2007-31938, MNHN IM-2007-31937, 2 lv; HK 137.21, 2 spm); stn S15, Cortes Takot, 9°41.3' N, 123°49.5' E, 4–6 m (MNHN IM-2000-22721, 1 lv; HK 137.01, 3 spm; HD 24148, 2 spm).

**Other material examined**

MALAYSIA: Sarawak, South China Sea, Muri I., off NW coast, 01°54'13" N, 108°38'49.4" E, 10–30 m, leg. H. Morrison (GH, 1 spm); Sarawak, Miri, outer reef off Tanjung Lobang (JGMR, 1 spm); Sabah, Kota Kinabalu, Tanjung Aru (JGMR, 1 spm).

PHILIPPINES: PANGLAO 2004, stn S2, Bohol I., Baclayon, 9°37.4' N, 123°54.5' E, 4–5 m (41 spm); stn S15, Bohol I., Cortes Takot, 9°41.3' N, 123°49.5' E, 4–6 m (15 spm; ZMA.Moll.4.09.449, 1 spm); stn S1, Panglao I., Biking, 9°35.6' N, 123°50.5' E, 5m (2 spm); stn B5, Panglao I., Biking, 9°35.2' N, 123°50.4' E, 4 m (2 spm); stn B8, Panglao I., Napaling, 9°37.1' N, 123°46.1' E, 3 m (3 spm); stn S5, Panglao I., Napaling, 9°37.1' N, 123°46.1' E, 2–4 m (10 spm); stn S7, Panglao I., Sungcolan Bay, 9°38.5' N, 123°49.9' E, 1–4 m (2 spm); stn S17, Panglao I., San Isidro, 9°34.6' N, 123°49.9' E, 6 m (1 spm); stn S24, Panglao I., Momo Beach, 9°36.1' N, 123°45.0' E, 2–4 m (1 spm); stn S32, Panglao I., Looc, 9°35.8' N, 123°44.6' E, 2–3 m (12 spm); Pamilacan I., stn B11, 9°29.4' N, 123°56.0' E, 2–4 m (1 spm); Pamilacan I., stn B24, 9°29.4' N, 123°56.0' E, 38 m (2 spm); Pamilacan I., stn S10, 9°29.4' N, 123°56.0' E, 6–14 m (2 spm); Pamilacan I., stn S14, 9°29.3' N, 123°55.1' E, 5–12m (1 spm). – Cebu, leg. R. Martin (ZMA.Moll.175495, 2 spm); Cebu, by lumen lumen, 50–150 m (HK 137.19, 2 spm); Panglao I. area (HD 14809, 15 spm; HK 137.14, 1 spm); Siquijor I., tangle nets, 100 m (HD 17294, 1 spm); Balicasag I. (MUZEE, 2 spm); Mactan I., 10–30 m, 2012 (HD 28994, 7 spm); Mactan I., 20 m, 2014 (HD 35816, 1 spm); Olango I., 2014 (HD 35873, 1 spm); Camotes I., Santiago, 15 m, 2007 (HD 21366, 1 spm); Palawan I., 10–15 m, 2009 (HD 33880, 2 spm).

INDONESIA: Kalimantan, Berau Is, 02°12'16.3" N, 118°35'18.9" E, 10–25 m (ZMA.Moll.175383, 1 spm); RUMPHIUS 1990, Ambon, stn 39 Hitu, W coast, S side of Larike (RMNH, 1 spm); Nusa Tenggara, Alor Strait, SE bay of Pantar I., 9–25 m, leg. H. Morrison (GH, 1 spm); Banda Sea, Wakatobi Group, E side of Moromaho I., 06°08'59" S, 124°35'11" E, leg. H. Morrison (GH, 6 spm); Flores Sea, S of Buton, 7–40 m, leg. H. Morrison (HK 137.08, 2 spm); N coast of Nusa Penida, leg. H. Morrison (GH, 1 spm); NW side of Sulawesi, Makassar Strait, Tambu Bay, sand and rubble slope, 10–40 m, among gorgonian corals, 00°01'07" S, 119°43'77" E (GH, 6 spm); Karang Kapota Atoll, SE of Buton I., 5°27'73" S, 123°24'10" E, on ledges of wall, 10–40 m, leg. H. Morrison (GH, 1 spm); Berau I., W side of Maratua I., 02°12'16.3" N, 118°35'18.9" E, 10–25 m (ZMA.Moll.175383, 1 spm); near Kalimantan, Pejantan I., 0°30'48.8" N, 107°13'24" E, 10–20 m, leg. H. Morrison (GH, 1 spm); sand, near wreck of Japanese fighter, 0°45'16" N, 105°36'11" E, 45 m, leg. H. Morrison (GH, 2 spm); near wreck, Acasta Rock, 01°39'12" N, 106°18'26" E, 9–50 m (GH, 1 spm); sand, near wreck, 0°45'15" N, 105°36'11" E, leg. H. Morrison (GH, 2 spm); Badas I. Group, 0°33'8.9" N, 106°58'47.4" E, 8–30 m, leg. H. Morrison (GH, 1 spm); 01°38'7" N, 106°21'23" E, on reef, 10–25 m, leg. H. Morrison (GH, 1 spm); Sebangmawang I., S of Bunguran I., 03°33.92' N, 108°02.08' E, 10–15 m, leg. H. Morrison

(GH, 4 spm); Sumatra, Kelulekabung I. (HK 137.07, 1 spm); West Papua, Manokwari, mouth of Uriami River, leg. D. Smits (HK 137.06, 2 spm); Bay of Hollandia, leg. Mrs H. Grootens-Boerefijn (HK 137.11, 6 spm); off NW coast, Waigeo I., Sorong, leg. H. Morrison (HK 137.04, 2 spm); off Sorong, Kri I., 10–15 m, leg. H. Morrison (HK 137.05, 2 spm).

PAPUA NEW GUINEA: PAPUA NIUGINI: stn PB18, Sek I., outer slope, 05°06.3' S, 145°49.1' E, 26 m (1 spm); stn PB28, E of Kranket I., 05°11.9' S, 145°49.6' E, 10 m (2 spm); stn PB45, Sinub I., 05°07.9' S, 145°48.9' E, 8 m (4 spm); stn PB47, N of Kranket I., 05°11.3' S, 145°49.6' E, 5 m (MNHN IM-2013-17574, 1 lv); stn PB47, N of Kranket I., 05°11.3' S, 145°49.6' E, 5 m (3 spm); stn PB48, N of Riwo, 05°08.7' S, 145°48.2' E, 2 m (MNHN IM-2013-17567, 1 lv); stn PB51, N of Bilbil I., 05°17.7' S, 145°46.9' E, 5 m (3 spm); stn PD31, Alexishafen, 05°05.3' S, 145°48.1' E, 1–6 m (1 spm); stn PD32, N of Sek I., Ottilien Passage, 05°04.4' S, 145°48.7' E, 1–8 m (1 spm); stn PD36, Rempi Area, W of Barag I., 05°01.2' S, 145°47.9' E, 5–10 m (1 spm); stn PM19, Alexishafen, islet SE of Megas Islet, 05°05.4' S, 145°48.6' E, 0–1 m (1 spm); stn PM22, Sek I., 05°04.7' S, 145°48.9' E, 0–1 m (MNHN IM-2013-13185, 1 lv); stn PM25, Rempi Area, Barag I., 05°01.1' S, 145°47.9' E (1 spm); stn PR202, S of Tab I., 05°10.3' S, 145°50.3' E, 2–4 m (MNHN IM-2013-17555, IM-2013-17556, IM-2013-17557, IM-2013-17558, IM-2013-17559, IM-2013-17560, 6 lv); stn PS04, Tab I., 05°10.0' S, 145°50.1' E, 12 m (1 spm); stn PS27, Bilbil I., 05°17.9' S, 145°46.7' E, 14 m (1 spm); stn PS41, S of Urembo I., outer slope, 05°15.9' S, 145°47.1' E, 10 m (HK 137.20, 3 spm); stn PS45, W Yabob I., 05°15.4' S, 145°47.0' E, 6 m (MNHN IM-2013-17562, 1 lv); stn PS47, N of Sek I., inner slope, 05°04.7' S, 145°48.9' E, 8 m (1 spm). – Bismarck Archipelago, New Ireland, Kavieng, Baudisson Bay, 15–35 m, leg. H. Morrison (HK 137.03, 2 spm).

SOLOMON ISLANDS: SALOMON 2, stn DW2234, Choiseul I., 6°51' S, 156°24' E, 182–277 m (1 spm); SALOMONBOA 3, stn DW2827, N of San Cristobal, 10°26' S, 161°51' E, 134–272 m (2 spm).

FIJI: Suva Point, leg. S.P. Kool (HK 137.15, 1 spm); Yasawa Group, Wayasewa I., 17°21' S, 177°08' E, intertidal (HK 137.17, 1 spm).

SAMOA: Savaii I., Asau Bay (PS, 4 spm; HK 137.10, 2 spm).

## Description

### Holotype

PROTOCONCH. Multispiral consisting of 2.5 whitish whorls, body whorl with rows of microscopic pustules, otherwise smooth (Fig. 3Q).

SHELL. Teleoconch consisting of 5.5 whorls; penultimate whorl with 15 and body whorl with 12 rounded ribs of equal size; broad varix.

SPIRAL CORDS. Body whorl with approximately 10 continuous, weak spiral cords.

INTERCORDAL SCULPTURE. Very fine, evenly spaced spiral striae, occasionally not only between, but also on spiral cords.

APERTURE. Six low denticles on outer lip, that at periphery more pronounced. Columellar callus elevated anteriorly, backside of elevation with microscopic growth lines. Callus partly extending posteriorly over body whorl onto anal canal. Columellar lip liriate onto moderately strong parietal denticle; anal canal deep.

OPERCULUM. Cream colored, serrated.

SIPHONAL CANAL. Narrow. A strong fasciole; siphonal area with several fine, one dominating, cords.

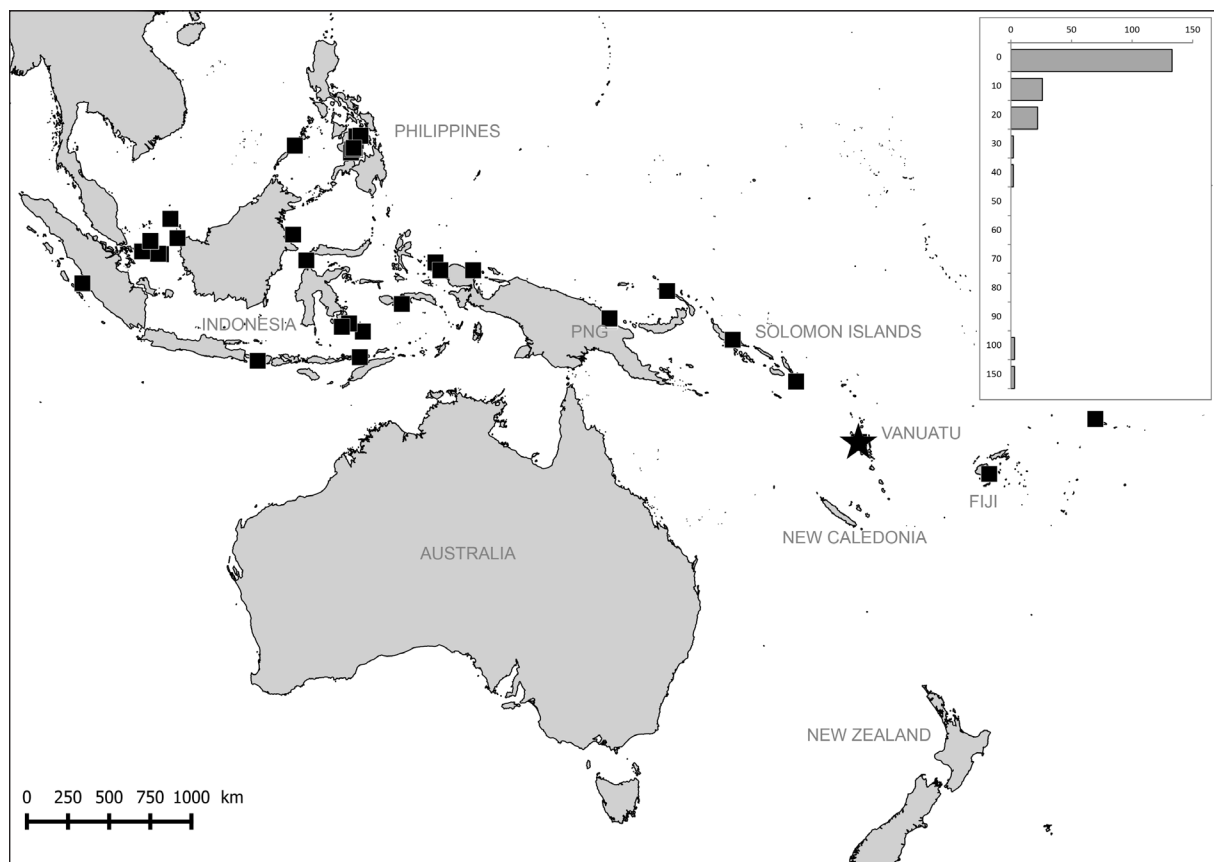
COLOR. Whitish to yellowish; some spiral cords light brown between ribs. Lower half of dorsal side of body whorl frequently with broad, orange-brown band (Fig. 30).

ADULT SIZE. 6.9–12.0 mm.

### Remarks

The color varies from white to yellow and orange; the spiral cords occasionally brown, sometimes only locally between the axial ribs. Some specimens have 2 brown bands on the body whorl, occasionally only visible on the varix. Some specimens, including the holotype, display a broad orange-brown band on the lower part of the body whorl. *R. poppeorum* sp. nov. is often recognizable by a broad, dark orange-brown band on the last half or the last third of the ultimate whorl, and is characterized by its more slender shape compared to other species in this genus.

*Reticunassa poppeorum* sp. nov. shows resemblance to *R. tringa* and *R. visayaensis* sp. nov. The greatest difference among the three species is the morphology of the protoconch. *R. tringa* has a paucispiral protoconch with 1.5–1.75 whorls, *R. visayaensis* sp. nov. has a multispiral protoconch of 2.25–2.5 whorls, whereas the protoconch of *R. poppeorum* sp. nov. has 2.5–2.75 whorls. The axial ribs of *R. poppeorum* sp. nov. are more pronounced and are present on the entire body whorl, whereas they decrease in height on the ventral side of the body whorl in *R. tringa* and *R. visayaensis* sp. nov.



**Fig. 7.** Geographical and bathymetrical distribution of *Reticunassa poppeorum* sp. nov. Star indicates type locality. Each bar represents all lv or dd specimens.

The most noticeable difference between *R. paupera* on the one hand and *R. tringa*, *R. visayaensis* sp. nov. and *R. poppeorum* sp. nov. on the other, is the presence of lirae in the latter three species over the entire surface of the extended columella. Besides this sculptural feature, the shape of the columellar callus differentiates *R. paupera* from the other three species; the callus of *R. paupera* is practically limited to the columella, whereas the callus of the other three partly extends over the body whorl.

There are no morphological differences between *R. neoproducta* Kool & Dekker, 2007 and the closely related *R. poppeorum* sp. nov. (Fig. 3N–Q). However, we decided to consider these two lineages as different species based on the reciprocal monophyly indicated by the taxonomic trees (*COI* and *28S* separately). Furthermore, *R. neoproducta* is found in the western Indian Ocean and *R. poppeorum* occurs in the western Pacific Ocean. To date, no specimens of these two species have been found east of Sri Lanka or west of Sumatra, respectively. It seems very unlikely that these two allopatric lineages still share any gene flux.

### Habitat

In sand and coral rubble, 0–40 m, mainly between 1 to 20 m. Some freshly dead specimens with operculum were collected on a hard bottom with small pockets of sediment and in coral sand at a depth of 4–6 m. Some specimens were collected in mangrove areas and in seagrass.

### Distribution

Malaysia, Indonesia, the Philippines, Fiji, and Western Samoa (Fig. 7).

### *Reticunassa annabolteae* sp. nov.

[urn:lsid:zoobank.org:act:781F25AD-B216-47A1-8084-FC46ED4C8029](https://doi.org/10.21203/rs.3.rs-1811111/v1)

Fig. 8A–D, 9; Tables 1–2

### Etymology

The species is dedicated to Mrs Anna Bolte, the second author's partner and travel companion for more than 20 years.

### Type material

#### Holotype

MADAGASCAR: ATIMO VATAE, stn BM06, South Madagascar, Ambatobe, Bavarama, 25°27.9' S, 44°57.6' E, 0–1 m, in rolling stones (MNHN IM-2009-12843, 1 lv, sequenced, length 11.5 mm, width 5.3 mm).

#### Paratypes

MADAGASCAR: same collection data as holotype (MNHN IM-2009-12812, MNHN IM-2009-12849, MNHN IM-2009-12862, MNHN IM-2009-12868, 4 lv; HK 302.01, 3 spm; HD 37306, 2 spm); S coast, Lavanono (HK 302.05, 5 spm; HK 302.06, 2 spm).

### Other material examined

MADAGASCAR: ATIMO VATAE, South Madagascar: stn BB03, Lavanono, 25°26.4' S, 44°56.1' E, 14–18 m (MNHN IM-2009-12865, 1 lv); stn BM02, Ambatobe, Soamanitse, 25°27.4' S, 44°57.4' E, 0–1 m (MNHN IM-2009-12772, 1 lv); stn BM06, Ambatobe, Bavarama, 25°27.9' S, 44°57.6' E, 0–1 m (MNHN IM-2009-12778, MNHN IM-2009-12783, MNHN IM-2009-12825, MNHN IM-2009-12841, MNHN IM-2009-12844, 5 lv); stn BM09, Saririaka, 25°29.0' S, 44°59.6' E, 0–1 m (MNHN IM-2009-12228, 1 lv); stn BM10, Andramara, 25°28.8' S, 44°58.3' E, 0–1 m (MNHN IM-2009-12873, 1 lv); stn

BS14, Cap Sainte Marie, 25°36.0' S, 45°08.7' E, 16 m (MNHN IM-2009-12329, 1 lv); stn CP3547, Cap Andavaka, 25°18.0' S, 46°40.3' E, 69–70 m (MNHN IM-2009-12893, 1 lv); stn TM01, Monseigneur Bay, 25°02.1-2' S, 46°59.9' E, 0–1 m (MNHN IM-2009-12793, 1 lv); stn TM05, Lokaro I., 24°56.5' S, 47°07.1' E, 0–1 m (MNHN IM-2009-12306, MNHN IM-2009-12888, MNHN IM-2009-12889, MNHN IM-2009-12897, MNHN IM-2009-12899, MNHN IM-2009-12905, MNHN IM-2009-13087, 7 lv); stn TM08, NE of Evatra lighthouse, 24°58.7' S, 47°05.9' E, 0–1 m (MNHN IM-2009-12894, 1 lv); stn TS09, Lokaro Bay, Fort Dauphin, 24°57.0' S, 47°06.4' E, 5–6 m (MNHN IM-2009-12834, MNHN IM-2009-12881, 2 lv); stn TS10, Lokaro Bay, Fort Dauphin, 24°56.8' S, 47°06.6' E, 7 m (HK 302.02, 2 spm); stn TS21, Phare Flacourt, 25°01.5' S, 47°00.0' E, 2–4 m (HK 302.03, 2 spm); stn TV07, Phare Flacourt, Amparihy, 25°01.3' S, 47°00.2' E, 12–16 m (MNHN IM-2009-12885, MNHN IM-2009-12898, 2 lv). – South Madagascar (HK 302.04, 1 spm); Lavanono (HD 21156, 2 spm); Lavanono (HD 36646, 21 spm); Soamanitse (HD 20287, 3 spm).

## Description

### Holotype

PROTOCONCH. Paucispiral consisting of 1.5–1.75 broad, flattened, axially-striated whorls. Separation between protoconch and teleoconch indistinct (Fig. 8D).

SHELL. Elongate-ovate, consisting of 5.5 convex whorls, suture deep; axial ribs poorly developed, decreasing in height on body whorl; 16 ribs on penultimate whorl and 14 on body whorl; broad varix.

SPIRAL CORDS. Fine, weak compared to other species in genus, more pronounced where they cross axial ribs. Two anterior spiral cords more developed, resulting in two deep spiral grooves.

INTERCORDAL SCULPTURE. Very fine spiral striae between spiral cords.

APERTURE. Oval, inside outer lip 8 lirate denticles; columellar callus plicate throughout, somewhat elevated anteriorly, posteriorly slightly extended over body whorl; parietal denticle weak, anal canal wide; siphonal area with 4–5 low cords.

OPERCULUM. Yellowish, serrated.

SIPHONAL CANAL. Deep and narrow. Fasciole deep.

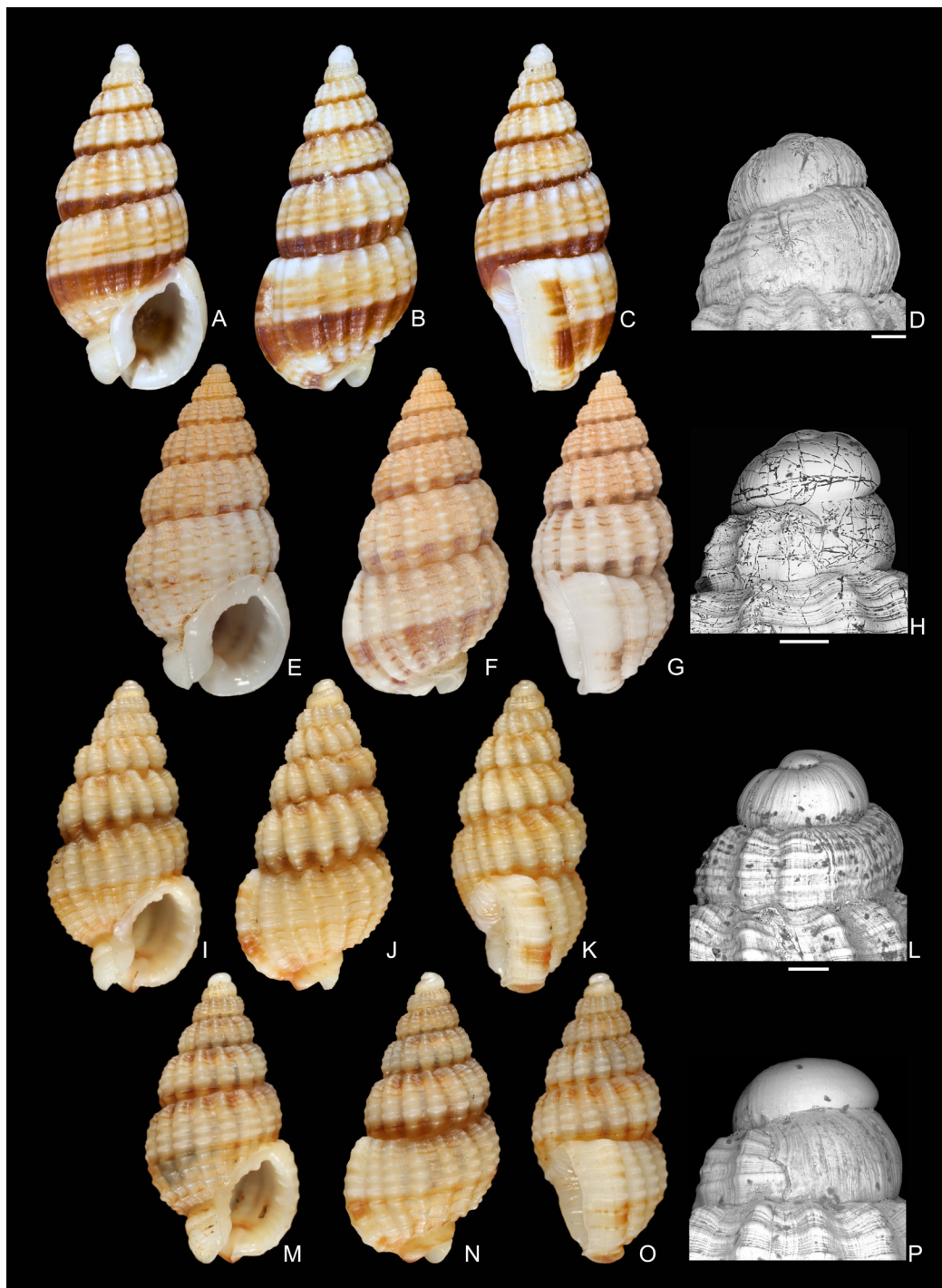
COLOR. Yellow-orange, narrow brown band above suture and broad brown band below periphery. Most spiral cords darker.

ADULT SIZE. 7.5–12.6 mm, usually 9–11 mm.

## Remarks

Besides the variability in color, from off-white to yellowish-orange, the difference in size of adult specimens is remarkable. Some specimens have somewhat more developed spiral cords.

Comparison with some other *Reticunassa* species with a paucispiral protoconch: *R. tringa* is a smaller, more bulbous species with a pointed protoconch; *R. goliath* sp. nov. also has fine spiral cords as found in *R. annabolteae* sp. nov., but differs in its pointed protoconch; *R. intrudens* sp. nov. has a protoconch intruded by the teleoconch spiral cords; *R. zanzibarensis* (Kool & Dekker, 2007) has a smooth protoconch contrasting the axially-striated protoconch in *R. annabolteae* sp. nov.



**Fig. 8.** Shells of *Reticunassa* Iredale, 1936. – **A–D.** *Reticunassa annabolteae* sp. nov. **A–C.** Holotype, MNHN IM-2009-12843, length 11.5 mm, width 5.3 mm, S Madagascar, Ambatobe, Bavarama, 25°27.9' S, 44°57.6' E, 0–1 m. **D.** Protoconch. – **E–H.** *R. goliath* sp. nov. **E–G.** Holotype, MNHN IM-2000-22724, length 15.5 mm, width 7.9 mm, New Caledonia, Nouméa, leg. D. Massemin, ex coll. H. Kool. **H.** Protoconch of paratype, MNHN IM-2000-28394. – **I–L.** *R. intrudens* sp. nov. Holotype, MNHN IM-2000-22726, length 7.9 mm, width 4.3 mm, New Caledonia, Touho, 20°44' S, 165°14' E, 49–59 m. **L.** Protoconch. – **M–P.** *R. thailandensis* sp. nov. **M–O.** Holotype, ZMA Moll.4.09.047, length 7.35 mm, width 3.8 mm, Thailand, Gulf of Thailand, 6°40.313' N, 101°43.852' E, 3–15 m. **P.** Protoconch. Scale bars: D, H, L, P = 200  $\mu$ m.

### Habitat

Intertidal to 70 m, frequently between 0 and 10 m. Some specimens were found living on rocky platforms with algae, associated to eunicid tubes, coarse sand, and rolling stones.

### Distribution

Only known from southern Madagascar (Fig 9).

### *Reticunassa goliath* sp. nov.

[urn:lsid:zoobank.org:act:5C34E90F-3AD2-42ED-B7A6-582525AD11DB](https://doi.org/10.3896/BI.2022.5C34E90F-3AD2-42ED-B7A6-582525AD11DB)

Fig. 8E–H, 10; Table 2

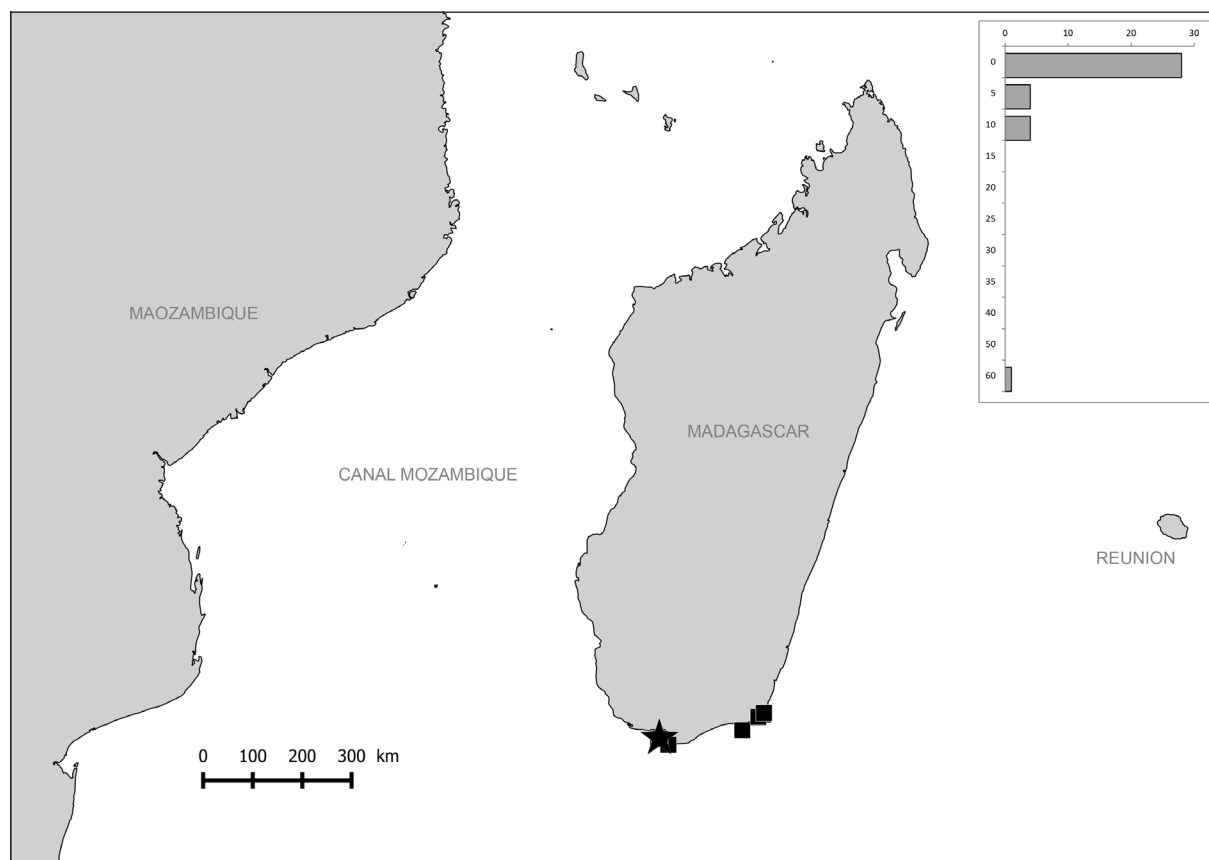
### Etymology

This species is named after the biblical Goliath, the giant who fought against David. This name is chosen because *Reticunassa goliath* sp. nov. is to date the largest known species in the genus *Reticunassa*.

### Type material

#### Holotype

NEW CALEDONIA: Nouméa, in sandy areas within coral reef, snorkeling at night, leg. D. Massemin (MNHN IM-2000-22724, ex coll. H. Kool, length 15.4 mm, width 7.9 mm).



**Fig. 9.** Geographical and bathymetrical distribution of *Reticunassa annabolteae* sp. nov. Star indicates type locality. Each bar represents all lv or dd specimens.

### **Paratypes**

NEW CALEDONIA: PLOUVEAL, stn 1221, Lagon d'Ouvéa, 20°29' S, 166°31' E, 10 m (MNHN IM-2000-22725, MNHN IM-2000-22723, MNHN IM-2000-28394, 3 spm; ZMA.Moll.4.09.050, 1 spm; GH, 1 spm; HD 24143, 2 spm; HK 997.01, 3 spm; HUI, 1 spm); PLOUVEAL, stn 1227, 12°37' S, 166°25' E, 12 m (HD 35304, 2 spm; HK 997.05, 2 spm); Nouméa, sand between coral reefs, snorkeled at night (HK 997.07, 1 spm); Nouméa, Nouville Beach, brown sand, 10 m (HK 997.08, 1 spm); New Caledonia, 5–10 m (HD 26939, 1 spm).

### **Other material examined**

INDONESIA: West Papua, Manokwari, leg. D. Smits (HK 997.03, 2 spm).

AUSTRALIA: North Queensland, Bowen, Grey's Bay, ex coll. Hessel (ZMA, 4 spm; HK 997.06, 1 spm).

VANUATA: SANTO 2006, stn FB52, Malokilikili, 15°42.7' S, 167°15.1' E, 7 m (1 spm).

NEW CALEDONIA: LAGON: stn 161, Ile Ouen-Baie du Prony, 22°34' S, 166°38' E, 20 m (1 spm); stn 943, Koumac, 20°37' S, 164°11' E, 15 m (1 spm). – PLOUVEAL, Lagon d'Ouvéa: stn 1218, 20°36' S, 166°30' E, 13 m (8 spm); stn 1219, 20°30' S, 166°28' E, 15 m (26 spm); stn 1220, 20°29' S, 166°29' E, 14 m (4 spm); stn 1221, 20°29' S, 166°31' E, 10 m (69 spm); stn 1222, 20°28' S, 166°30' E, 15 m (13 spm); stn 1223, 20°28' S, 166°28' E, 19 m (1 spm); stn 1224, 20°32' S, 166°28' E, 18 m (25 spm); stn 1225, 20°36' S, 166°28' E, 18 m (6 spm); stn 1226, 20°32' S, 166°24' E, 21 m (5 spm); stn 1227, 12°37' S, 166°25' E, 12 m (29 spm); stn 1228, 20°36' S, 166°24' E, 18 m (8 spm); stn 1229, 20°37' S, 166°23' E, 16 m (19 spm); stn 1230, 20°35' S, 166°23' E, 18 m (22 spm); stn 1231, 20°31' S, 166°23' E, 23 m, 6 spm); stn 1232, 20°32' S, 166°24' E, 31 m (7 spm); stn 1233, 20°29.1' S, 166°29.0' E, 15 m (1 spm). – MONTROUZIER 1993: Koumac, stn 1271, 20°52.7' S, 165°19.5' E, 5–25 m (3 spm); Koumac, stn 1286, Plateau Karembé, 20°38'–20°39' S, 164°16'–164°17' E (3 spm); Koumac, stn 1287, Récif de l'Infernet, 20°37' S, 164°14' E (2 spm); Koumac, stn 1301, Récif de l'Infernet, 20°37.1'–20°37.5' S, 164°14.7'–164°15' E, 1–5 m (3 spm); Koumac, stn 1303, Lagon, parages du Plateau Karembé, 20°37.7'–20°38.8' S, 164°15.9'–164°17.1' E, 0–8 m (2 spm); Koumac, stn 1304, Chenal de l'Infernet, 20°38.6' S, 164°13.2' E, 12–15 m (2 spm); Koumac, stn 1306, Chenal de l'Infernet, 20°39.1' S, 164°12.4' E, 11–13 m (1 spm); Koumac, stn 1312, 20°40' S, 164°14.9' E, 26–40 m (1 spm); Touho, stn 1245, Grand Récif Mengalia, 20°45.2' S, 165°16.3' E (4 spm); Touho, stn 1273, Touho region, outer reef, 20°50.4' S, 165°22.8' E, 20 m (2 spm). – PALEO-SURPRISE 1999, stn CP1388, 18°23.8' S, 163°06.9' E, 40 m (2 spm).

LOYALTY ISLANDS: LIFOU 2000, stn 1419, Lifou, Santal Bay, Bay of Gaatcha, 20°55.6' S, 167°04.5' E, 5 m (8 spm; HK 997.02, 1 spm); LIFOU 2000, stn 1426, Lifou, Santal Bay, 20°45.9' S, 167°06.2' E, 4–7 m (2 spm); Lifou, leg. J.R. le B. Tomlin (ZMA.Moll.096228, ex coll. Schepman, 6 spm); Lifou, leg. R.P. Goubin (ZMA.Moll.089599, ex coll. Dautzenberg, 3 spm); Lifou (HUI 9055, ex coll. Dautzenberg, ex coll. Coen 7553, 3 spm).

### **Description**

#### **Holotype**

PROTOCONCH. Paucispiral, pointed, 1.75 milky whorls, beset with rows of microscopic pustules. Protoconch missing in holotype, seen in paratype (Fig. 8H).

SHELL. Rather heavy, conical, acuminate, teleoconch consisting of 7 whorls, suture impressed. On penultimate 13 and on body whorl 12 well pronounced, equidistant axial ribs and strong varix. Ribs equally strong on dorsal and ventral side of body whorl.



**SPIRAL CORDS.** Continuous, moderately broad on top of axial ribs, but between ribs narrower and weak, approximately 6 cords on penultimate and 10 on body whorl.

**INTERCORDAL SCULPTURE.** Numerous very fine, evenly spaced spiral striae, occasionally also on top of spiral cords.

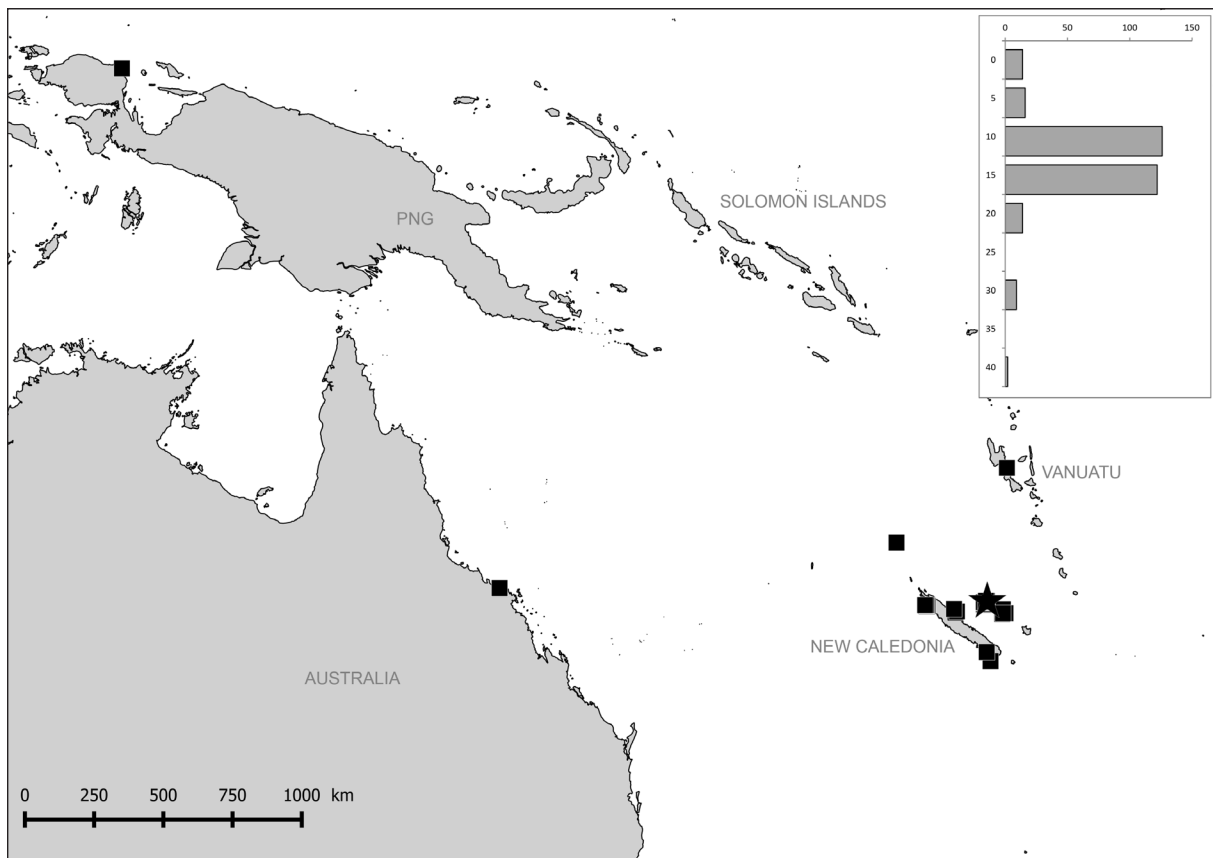
**APERTURE.** Round, proportionally small, approximately  $\frac{1}{5}$  of shell length. Outer lip with 7 unequal denticles. Columella callused, somewhat elevated anteriorly and with evenly spaced lirae throughout. Callus sharply bordered, bending over part of fasciole and somewhat extending over body whorl posteriorly. Inside outer lip with 8 lirae and pronounced tooth at siphonal canal. Elevated part of callus with fine growth lines on left (out)side. Parietal denticle strong, anal canal deep.

**OPERCULUM.** Yellowish, serrated.

**SIPHONAL CANAL.** Narrow, fasciole strong. Siphonal area with one strong and some weak cords.

**COLOR.** Off white to yellow, narrow band just above suture and broader band below periphery; columella and outer lip white, aperture yellowish.

**ADULT SIZE.** 8.2–16.5 mm, usually 13–15 mm.



**Fig. 10.** Geographical and bathymetrical distribution of *Reticunassa goliath* sp. nov. Star indicates type locality. Each bar represents all lv or dd specimens.

### Remarks

Color and banding pattern variable; some specimens have light to dark brown bands and others lack banding. In banded specimens, one band occurs on the body whorl, with an additional band on the sutural area. In some specimens, the spiral cords may be colored orange/brown, but only between the axial ribs. Aperture white, inside faintly showing the outside bands if present.

*Reticunassa visayaensis* sp. nov. and *R. poppeorum* sp. nov. have a multispiral protoconch, whereas the protoconch of *R. goliath* sp. nov. is paucispiral.

The strong columellar callus, together with the thickening of the inside of the outer lip and the strong varix, gives the aperture a round, “open mouth” appearance, whereas the other species in this group have a more oval-shaped aperture.

*R. goliath* sp. nov. and *R. tringa* both have a paucispiral protoconch, but the former has a considerably heavier and larger shell. It is similar to *R. tringa*, *R. visayaensis* sp. nov. and *R. poppeorum* sp. nov. in having weak spiral cords. *R. goliath* sp. nov. differs from *R. paupera* in weight, in its larger size, in the number of whorls, and in the size of the aperture relative to the total shell length.

### Habitat

Sublittoral to 0–40 m, frequently between 10 and 20 m.

### Distribution

Western Pacific; Indonesia (Papua), Australia (Queensland), Vanuatu, New Caledonia, and Loyalty Islands (Fig. 10).

### *Reticunassa intrudens* sp. nov.

[urn:lsid:zoobank.org:act:C79E7864-DE80-4A17-94BC-54932F8532CA](https://doi.org/10.21203/rs.3.rs-1711111/v1)

Fig. 8I–L, 11; Table 2

### Etymology

The name of this species refers to the spiral cords that seemingly intrude and continue over part of the body whorl of the protoconch.

### Type material

#### Holotype

NEW CALEDONIA: MONTROUZIER 1993, stn 1260, Touho, Banc de Touho, 20°44' S, 165°14' E, 49–59 m, Sep. 1993 (MNHN IM-2000-22726, length 7.9 mm, width 4.3 mm).

#### Paratypes

NEW CALEDONIA: same collection data as holotype (MNHN IM-2000-22722, MNHN IM-2000-28406, MNHN IM-2000-28407, 3 spm; ZMA.Moll.4.09.051, 1 spm; HD 35302, 3 spm; HK 196.01, 4 spm).

### Other material examined

NEW CALEDONIA: LAGON: stn 146, Ile Ouen-Baie du Prony, 22°24' S, 166°55' E, 40–52 m (1 spm); stn 357, Grand Récif Sud, 22°30' S, 167°07' E, 77 m (1 spm); stn 603, Yaté, 22°16' S, 167°05' E, 78–80 m (1 spm). – MUSORSTOM 4, stn DW 203, 22°36' S, 167°05' E, 105–110 m (1 spm); SMIB 5, stn DW 81, S New Caledonia, 22°38' S, 167°35' E, 110 m (5 spm); BATHUS 1, stn DW 678, W coast, 20°49' S, 165°19' E, 94–100 m (7 spm). – MONTROUZIER 1993, Touho, stn 1237, Touho Bay, 20°46.9' S, 165°13.8' E, 0–1 m (5 spm); Touho, stn 1249, Passe de Touho, 20°49' S, 165°19' E, 80–140 m (3 spm); Touho, stn 1250, 20°46.7' S, 165°13.7' E, 3–6 m (7 spm); Touho, stn 1251, 20°46.0'–20°46.5' S,

165°13.0' E, 15 m (4 spm); Touho, stn 1253, 20°46.6' S, 165°14.1' E, 2–3 m (1 spm); Touho, stn 1257, lagoon in front of Vieux-Touho, 20°44' S, 165°11' E, 25–28 m (3 spm); Touho, stn 1260, 20°44' S, 165°14' E, 49–59 m (70 spm); Touho, stn 1261, 20°46'–20°47' S, 165°15'–165°16.5' E, 45–56 m (33 spm); Touho, stn 1268, 20°45.2' S, 165°08.0' E, 9–11 m (1 spm); Touho, stn 1275, 20°49' S, 165°17' E, 50–62 m (1 spm).

## Description

### Holotype

**PROTOCONCH.** Bulbous, flattened, paucispiral, 1.75 whorls, yellowish, axially striate; separation between protoconch and teleoconch indistinct, last half whorl appears to have been “intruded” by the 5 spiral cords on first whorl of teleoconch.

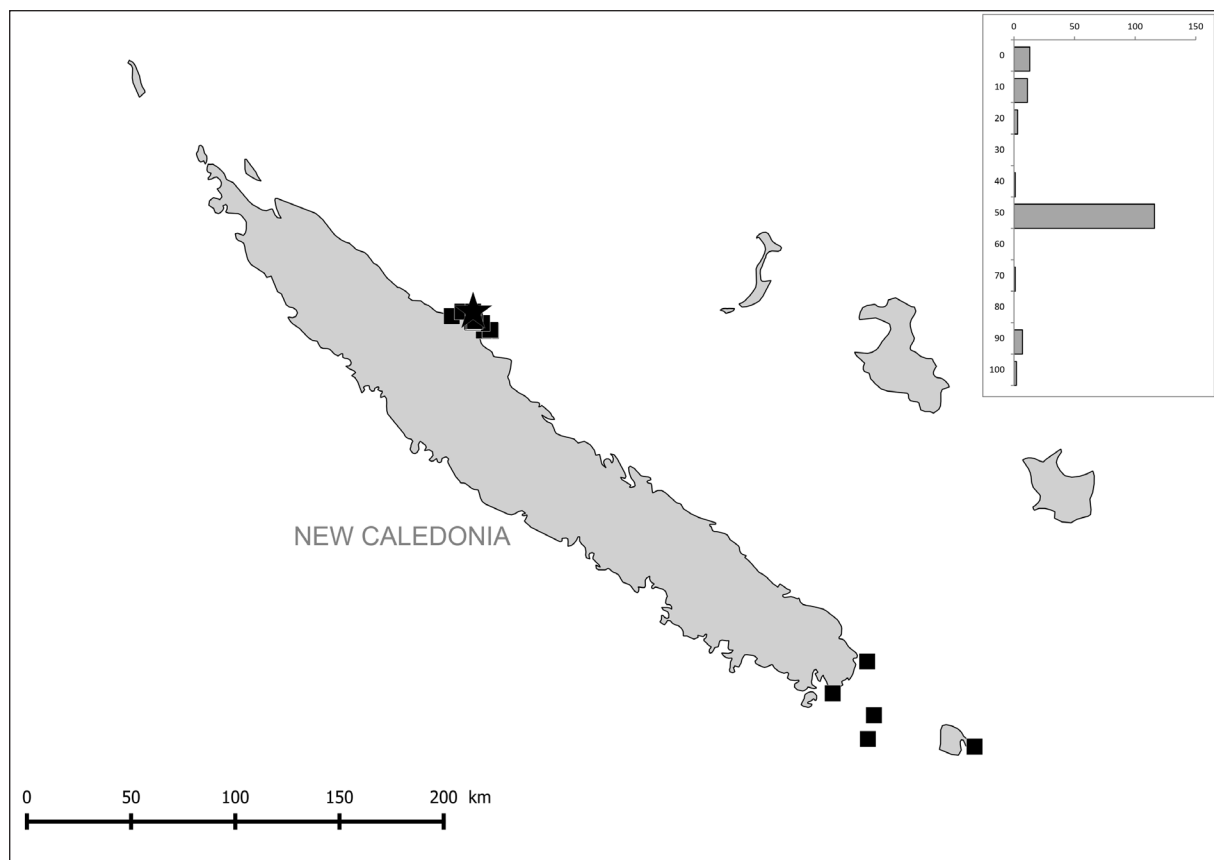
**SHELL.** Teleoconch consisting of 5 strongly impressed whorls. Penultimate whorl and body whorl with 13 pronounced strong, round axial ribs, varix strong.

**SPIRAL CORDS.** Penultimate whorl with 7 and body whorl with 10 narrow, fine, equally wide spiral cords.

**INTERCORDAL SCULPTURE.** Minute spiral striae, occasionally also located on spiral cords.

**APERTURE.** Outer lip with 5 short and low lirate denticles. Columella wrinkled, columellar callus margined, elevated anteriorly and somewhat curved towards fasciole, posteriorly slightly extending onto body whorl. Parietal denticle prominent, anal canal rather wide.

**OPERCULUM.** Unknown.



**Fig. 11.** Geographical and bathymetrical distribution of *Reticunassa intrudens* sp. nov. Star indicates type locality. Each bar represents all lv or dd specimens.

SIPHONAL CANAL. Siphonal area with 1 stronger and 4 weak cords. Fasciole strong.

COLOR. Creamy-yellowish, some spiral cords darker. Whorls with light subsutural band, body whorl with 3 bands, darkest on the thick varix and at base of shell.

ADULT SIZE. 5.4–9.7 mm, usually 7.5–8.5 mm.

### Remarks

The most characteristic feature of this species is the broad, flattened, paucispiral and axially striated protoconch with, on the last part of it, 1–5 spiral cords that intrude from the teleoconch (Fig. 8L). This character was also mentioned by Cernohorsky (1984) in his description of *Nassarius (Hima) pauperus* (Gould, 1850) and was treated as intraspecific variation. These features, the broad, flat paucispiral protoconch and the extremely fine intercordal spiral striae of *Reticunassa intrudens* sp. nov., make it easy to distinguish it from *R. paupera* and the other species described in this paper. Moreover, *R. intrudens* sp. nov. lacks the minute pustules present in some other species described herein and most of the others also have a wider distribution; *R. intrudens* sp. nov. is only known from New Caledonia. It is one of the smallest species within this group.

### Habitat

0–110 m in muddy sand, with the largest concentration of specimens collected at 45–60 m.

### Distribution

Only known from New Caledonia (Fig. 11).

*Reticunassa thailandensis* sp. nov.

[urn:lsid:zoobank.org:act:E0731396-9A77-4C1C-99F7-24B72E5B55DD](https://doi.org/10.21203/rs.3.rs-1396-9A77-4C1C-99F7-24B72E5B55DD)

Fig. 8M–P, 12; Table 2

### Etymology

This species is named after Thailand, the type locality.

### Type material

#### Holotype

THAILAND: SE coast, Gulf of Thailand, Pattani Province, Ko Lopi, 06°40.313' N, 101°43.852' E, scuba diving, 3–15 m, leg. R.G. Moolenbeek and H. Dekker, 2003 (ZMA.Moll.4.09.047, length 7.35 mm, width 3.8 mm).

#### Paratypes

THAILAND: same collection data as for holotype (ZMA.Moll.4.09.048, 222 spm; 5 spm; MNHN IM-2000-32481, 10 spm; GH, 2 spm; HD 24145, 6 spm; HK 139.01, 6 spm); Gulf of Thailand, Rayong Province, Talengam, near Suan Son, E of Ban Phe beach, leg. O.K. McCausland (HK 139.03, 1 spm).

### Other material examined

THAILAND: Gulf of Thailand: type locality (4 spm); Ban Pak Nam Sakom, local fishery, 06°57' N, 100°49.36' E (ZMA.Moll.4.09.062, 3 spm; HD 1789, 6 spm); Ban Pak Nam Sakom, near Leela Resort, 06°57.4' N, 100°51.6' E, muddy pools (ZMA, 3 spm; HD 1190, 6 spm); Ban Talokapo, 06°54.0' N, 101°22.4' E, local fishery (HD 2146, 3 spm); Trat Province, Ko Chang, beach (HD 2793, 1 spm); Ko Samui, NE side of Chaweng Beach, 09°32.6' N, 100°05.7' E, in seagrass (HD 9572, 5 spm); Ko Samui, Ban Bangkao, 09°25.2' N, 99°59.7' E, sand flat (HD 9574, 1 spm); Ko Kham, 06°58.4' N, 100°51.6' E,

scuba diving, 3–5 m (ZMA.Moll.093866, 14 spm); Pattani, in shell grit (ZMA.Moll.098947, 2 spm); off Pattaya, Ko Lan, scuba diving, reef, 3–6 m, leg. R.G. Moolenbeek (ZMA.Moll.4.09.063, 12 spm).

SINGAPORE: Bedok River area of East Coast Park, beached, leg. Chan Sow Yan (HK 139.04, 6 spm).

MALAYSIA: E coast, South China Sea, 02°38'11" N, 105°13'30" E, 30–35 m, leg. H. Morrison (GH, 2 spm; HK 139.02, 3 spm); South China Sea, on sand near wreck, 0°45'15" N, 105°36'11" E, leg. H. Morrison (GH, 1 spm).

INDONESIA: Laboratorium Onderzoek der Zee, 1938, stn Bat38/07a, Bay of Jakarta (ZMA.Moll.096217, 2 spm). – KEPULAUAN SERIBU 2005, stn Ser05/03, Java, Bay of Jakarta, Damar Kecil, 5°59'00" S, 106°50'43" E, scuba diving, 5–15 m (ZMA.Moll.175169, 7 spm); stn ser05/07, Java, Bidadari, scuba diving, 6°01'55" S, 106°44'47" E (ZMA.Moll.175470, 12 spm); stn ser05/08, Java, Ayer Besar, 6°00'06" S, 106°46'48" E (ZMA.Moll.154506, 1 spm); stn ser05/09, Java, Ubi Besar, scuba diving, 5°59'55" S, 106°44'23" E (ZMA.Moll.175172, 8 spm); stn ser05/10, Java, Kelor, scuba diving, 5°51'00" S, 106°35'05" E, 5–35 m (ZMA.Moll.175173, 3 spm). – Java, W coast, Tjilintjing (ZMA.Moll.096215, ex coll. Butot 12405, 1 spm); Flores, E coast, near Larantuka, between Weri and Waibalun, leg. Fr.M. Vianney (ZMA.Moll.096211, 1 spm); Kalimantan, South China Sea, Pejantan I., 0°30'48.8" N, 107°13'24" E, 10–20 m, leg. H. Morrison (GH, 5 spm); NETHERLANDS BERAU 2003, stn ber03/38, Berau Is, Maratua, 10–25 m (ZMA.Moll.175049, 1 spm).

PHILIPPINES: Palawan, Balabac I. (RMNH, 5 spm; 5 spm; HD 24144, 20 spm; GH, 6 spm; HK 139.05, 140 spm; coll. L. van Gemert, Zeist, the Netherlands, 20 spm; AMD, >300 spm); Olango I., Ziczac Point, 10–20 m, 2010 (HD 33413, 1 spm); Mindanao, Surigao del Norte, Basul I., 80–90 m, 2013 (HD 33414, 1 spm).

## Description

### Holotype

PROTOCONCH. Bulbous, flattened, paucispiral, 1.3 whorls, whitish, part of body whorl with growth lines.

SHELL. Teleoconch consisting of 4.5 impressed whorls. Axial ribs pronounced, rounded, 14 on penultimate and 13 on body whorl. Varix strong and broad.

SPIRAL CORDS. Continuous, narrow, thread-like spiral cords, increasing in height where they cross over axial ribs; 6 on penultimate and approximately 9 on body whorl. Spiral cord on periphery, the two above it, and the three at the base of body whorl more distinct; intercordal distances unequal.

INTERCORDAL SCULPTURE. Fine, distinct spiral striae, number depending on distance between spiral cords.

APERTURE. Oval, outer lip with 8 unequal denticles, one near periphery strongest. Columellar callus well bordered, slightly extending over body whorl; entire lip with short lirae. Parietal denticle strong.

OPERCULUM. Yellowish, finely serrated.

SIPHONAL CANAL. Narrow; fasciole strong. Siphonal area with approximately 4 cords; parietal denticle strong, anal canal wide.

COLOR. Yellowish-orange, penultimate whorl with two, body whorl with three orange-brown bands.

ADULT SIZE. 5.5–9.1 mm, usually 7–8 mm. One of the smaller species of the group.

## Remarks

The color is variable. Well-preserved specimens are cream or orange to light brown, either unicolor or with several darker-colored spiral cords. Occasionally remnants of bands are only present on the varix and on the fasciole.

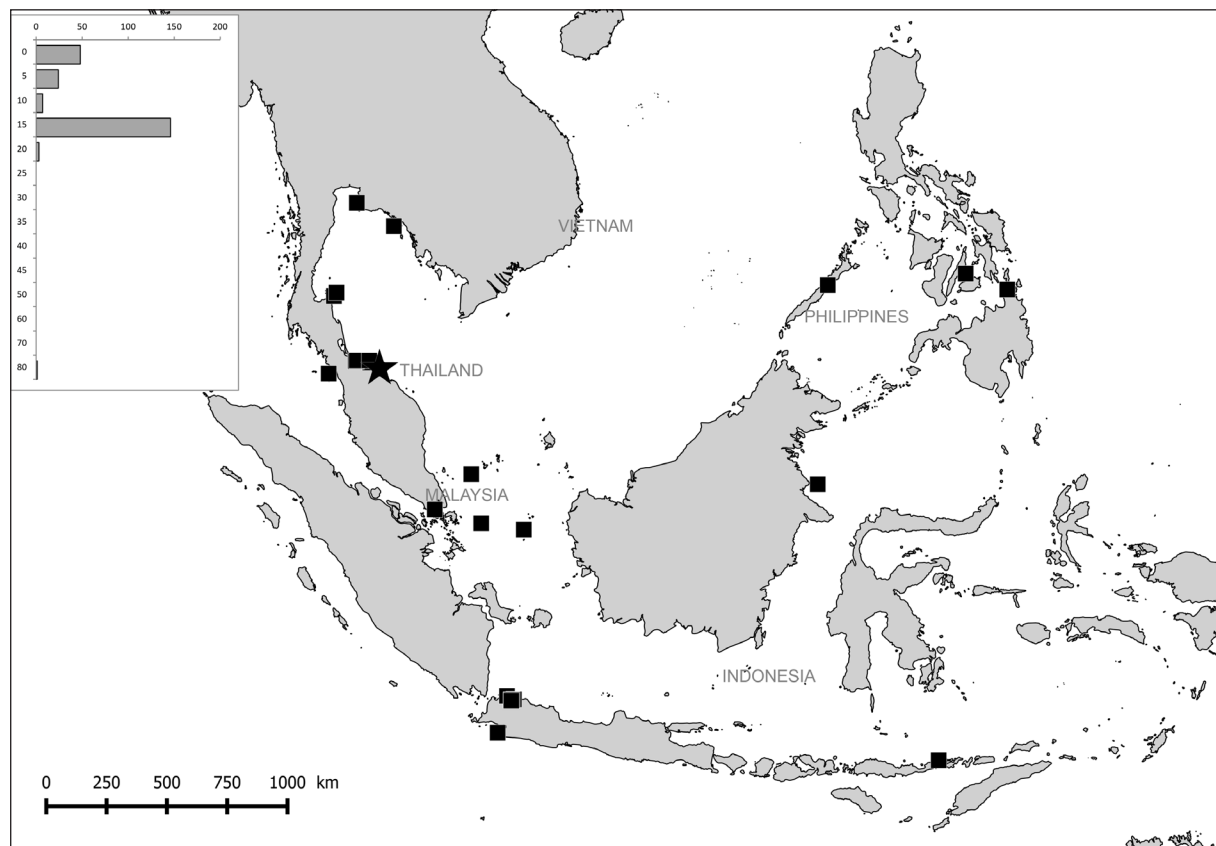
The main difference between *Reticunassa intrudens* sp. nov. and *R. thailandensis* sp. nov. is to be found in the protoconch morphology: the former has a protoconch with axial striae, in the latter it is partly smooth. Both are paucispiral and bulbous, and lack the microscopic pustules found in the other species described in this paper. *R. paupera* (Gould, 1850), *R. visayaensis* sp. nov. and *R. poppeorum* sp. nov. have a multispiral protoconch. *R. thailandensis* sp. nov. has more well developed spiral cords than the other species described here. Furthermore, in some specimens the 2–3 most anterior spiral cords are more strongly developed. In general, the distribution of the species, as shown on Fig. 12, might help with the identification.

## Habitat

This species lives in sand and between dead corals, in depths of 1–90 m, usually found between 15 and 20 m.

## Distribution

Thailand, Singapore, Malaysia, Indonesia, and the Philippines, where it is common at Balabac I., but apparently rare in the central Visayas (Fig. 12).



**Fig. 12.** Geographical and bathymetrical distribution of *Reticunassa thailandensis* sp. nov. Star indicates type locality. Each bar represents all lv or dd specimens.

## Discussion

This paper presents the first review on the diversification of genus *Reticunassa* from a molecular perspective. An integrative approach permitted the match between DNA sequences and morphological features to define the taxa discussed here. Previous references to “*Nassarius pauperus*” must be treated with caution because other species of *Reticunassa* might remain masked under that concept. This problem is particularly challenging when working with collections where specimens are kept dry and protoconchs have been lost, considering the small morphological interspecific differences among the species of *Reticunassa*.

So far, the only available morphological characters to distinguish species of the genus are the features of the protoconch, the spiral cords, the intercordal surface and the columella. Table 2 is a comparison of all available characters to facilitate species identification. However, in this paper we provide *COI* sequences that could help future identification of molecular samples. Reliably identified hologenophores for previously described species are becoming accessible, with their *COI* sequences available in online public libraries. For our new species we have prioritized the choice of name-bearing types such that they are also hologenophores, whenever possible, in order to avoid the perpetuation of a molluscan taxonomy in which many type specimens do not fulfill their function as name bearers (Bouchet & Strong 2010).

As can be seen in Fig. 1A–B, the trees are congruent with our taxonomic hypotheses concerning the status of *Reticunassa* and the new species described in this paper, initially based on morphological observations. Our results are also consistent with what has been observed in other nassariids: the intraspecific variability is about 1.9% among species of *Nassarius* (Kool & Galindo 2014) and ranges from 1.1% to 2.5% within species of *Tritia* (Couceiro *et al.* 2012; Couceiro *et al.* 2007; Simon-Bouhet *et al.* 2006). In general, K2P genetic distances between gastropod species span from 4.2% to 5.9% (Li *et al.* 2010; Kantor *et al.* 2012; Fedosov *et al.* 2014; Lorenz & Puillandre 2015).

The absence of a discrete barcode gap in a dataset can be explained many ways. In this case, it can be related to poor intraspecific replication within some species, i.e., there is only one sequence each representing *R. paupera* and *R. tringa*.

The trees (Fig. 1A–B) reveal the existence of several lineages, with, so far, no morphologically recognizable characters (i.e., MNHN IM-2007-31778 and MNHN IM-2013-17562), preventing their description. Further studies on *Reticunassa* might disclose patterns to help assign names to those taxonomic units.

In this paper, no particular taxonomic ranking has been given to the two subclades found within *Reticunassa*. However, there are clear differences among them. SC1 is formed by species that lack spiral striae; instead, they have either axial striae (*R. hanraveni* and *R. silvardi*) or relatively smooth intercordal surfaces (*R. compacta*, *R. rotunda*). Species of SC1 are distributed from the western Pacific Ocean to the Marquesas Islands. On the contrary, species of SC2 show the presence of spiral striae on the intercordal surface, and they occur in the Indian Ocean and the western Pacific Ocean. This result supports Galindo *et al.*'s (2016) hypothesis that geographical distribution patterns play an important role in the diversification of Nassariidae.

Kool & Dekker (2006) placed *Nassarius gregarius* (Grabau & King, 1928) in the *N. pauperus* complex, because it is similar in size and shape and had been treated as a synonym of *N. pauperus* by Cernohorsky (1984). However, because this species has a keeled protoconch, it should not be included in *Reticunassa*, but should continue to be included in the genus *Nassarius*.

An integrative approach to taxonomy with all available data permits us to test the monophyly and the relationships of the species within the *Nassarius pauperus* complex, to reconstruct its taxonomic history and to present a comprehensive discussion of morphological features that are informative in species discrimination. Our results allow us to confer full generic status to the clade *Reticunassa*, which now includes 20 Recent species from the Indo-Pacific region.

## Acknowledgements

As sources of material used in this paper, we want to highlight in particular the following expeditions: MONTRouZIER 1993 to New Caledonia; PANGLAO 2004 to the Philippines; SANTO 2006 to Vanuatu; and PAPUA NIUGINI to the Madang District of Papua New Guinea. They were sponsored by the Total Foundation, the Stavros Niarchos Foundation, the Prince Albert II of Monaco Foundation, Entrepouse Contracting and Fondation EDF. In the field, Y. Kantor, N. Puillandre, E.E. Strong and M.C. Boisselier specifically preserved mollusk samples for molecular sequencing. Another source of sample material is the series of cruises to New Caledonia, Fiji, Tonga and the Solomon Island as part of the *Tropical Deep-Sea Benthos* programme (Bouchet *et al.* 2008), and also Bertrand Richer de Forges' *Programme Lagon* (material collected by Richer de Forges in 1995). We are grateful to P. Bouchet for placing the nassariid material from these sources at our disposal. Thanks to V. Héros, P. Maestrati and B. Buge for their highly appreciated support and comments. We are much indebted to the following persons for the loan of material, providing information, supplying literature and allowing us access to the collections in their care: J. Goud and R.G. Moolenbeek, both NBC, G.M. Hansen, D. Massemin and P. Stahlschmidt. Special thanks to L. Charles (Musée d'Histoire Naturelle de Bordeaux) for providing the *R. tringa* type series. R.H. Cowei, R.G. Moolenbeek and S.P. Kool reviewed the text and gave very valuable remarks. P. Bouchet guided us through many taxonomic and nomenclatural decisions. M.A. Alonso Zarazaga (International Commission on Zoological Nomenclature) helped us with the Latin declensions. G. Marani built and has managed the Geographic Information System for the biodiversity of Nassariidae. M. Caballer is thanked for photographing the holotypes as part of the E-RECOLNAT ANR-11-INBS-0004, MNHN program and S. Pont (SEM-EDS) for securing the electronic microscopic images. This project was supported by the "Bibliothèque du Vivant" network, funded by the CNRS-MNHN-INRA-CEA (Genoscope), the 'Service de Systématique Moléculaire' (UMS 2700 CNRS-MNHN), and the deep-sea studies developed in the French-Taiwanese TF-DeepEvo ANR-NSC project (ANR 12-ISV7-0005-01). Thanks to B.A. Marshall and an anonymous reviewer for their comments, which helped to improve the manuscript.

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*Manuscript received: 1 February 2016*

*Manuscript accepted: 1 August 2016*

*Published on: 10 February 2017*

*Guest editors: Line Le Gall, Frédéric Delsuc, Stéphane Hourdez, Guillaume Lecointre and Jean-Yves Rasplus*

*Desk editor: Danny Eibye-Jacobsen*

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