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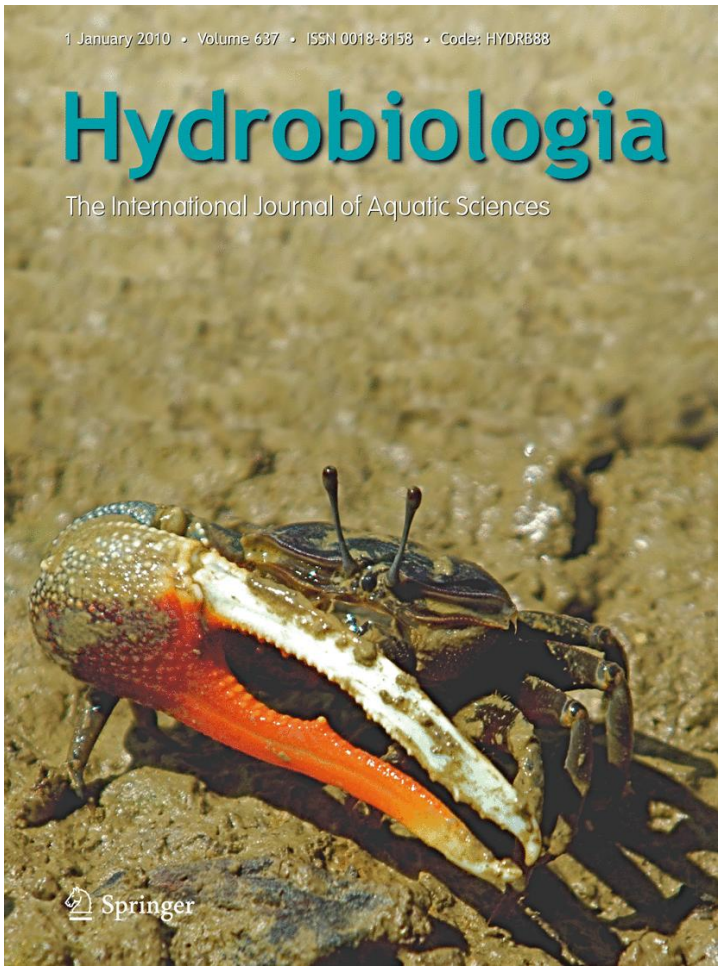

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PRIMARY RESEARCH PAPER

Rissooidean freshwater gastropods from the Vanuatu archipelago

Martin Haase · Benoit Fontaine · Olivier Gargominy

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Abstract During expeditions to Santo and the Torres islands belonging to the Vanuatu archipelago in 2006 and 2007, ten new species of tateid gastropods confined to springs, the upper most, slowly flowing regions of streams or the groundwater had been discovered. These species were now described based on shell morphology and anatomy. In accordance with geography, these characters placed the species from Vanuatu between those from New Caledonia and Fiji, suggesting a stepping stone-like dispersal across the Pacific with an origin in New Zealand and the far end on the Austral islands. We also assessed the threat status of the new species according to the IUCN Red List criteria and concluded that they should be amended by explicit incorporation of the scale of potential human impact or stochastic natural events relative to the size of the habitat of organisms.

Keywords Crenobiontic · Dispersal · IUCN Red List categories · Pacific islands · Santo · Tateidae · Torres islands

Handling editor: K. Martens

M. Haase (✉)
Vogelwarte, Zoological Institute, University of Greifswald, Soldmannstraße 23, 17489 Greifswald, Germany
e-mail: martin.haase@uni-greifswald.de

B. Fontaine · O. Gargominy
Muséum National d'Histoire Naturelle, 55 Rue Buffon, 75231 Paris Cedex 05, France

B. Fontaine
e-mail: fontaine@mnhn.fr

O. Gargominy
e-mail: gargo@mnhn.fr

Introduction

Rissooidean freshwater gastropods of the family Tateidae have a remarkable distribution across the South Pacific. Apart from mainland Australia, Tasmania and New Guinea, they occur in New Zealand (Haase, 2008), on Lord Howe Island (Ponder, 1982), New Caledonia (Haase & Bouchet, 1998), and on the islands of the archipelagos of Vanuatu (Ancey, 1905; Solem, 1959; Starmühlner, 1976), Fiji (Haase et al. 2006), and the Australs (Haase et al., 2005). A species from Norfolk Island probably got extinct in historical times (Ponder, 1981). Except for Lord Howe and Norfolk Islands, these islands and archipelagos have at least parts that are older than 10 Mio years (Kroenke, 1996; Bonneville et al., 2002). Eua, which detached from New Caledonia 41 Mya and today is situated in the Tonga archipelago, and Mangaia belonging to the Cook Islands (Kroenke, 1996) are the only older elements where tateids do not occur. All other island groups in the Pacific are younger than 10 Mio years and do not harbour tateids

despite being close to and partly interspersed between the above listed islands. Anatomical investigations suggested that the species occurring in New Zealand, on New Caledonia, Fiji and on the Austral islands form a monophyletic group, which may have originated in New Zealand (Haase et al., 2006). Among these islands, brackish-water species exist only in New Zealand, where freshwater has been invaded three times independently (Haase, 2005). Therefore, Haase et al. (2005, 2006) hypothesized that rissooidean freshwater gastropods dispersed from New Zealand to the other islands, probably transported by migratory birds.

Prior to this article, only a single species of tateids was known from Vanuatu, viz. *Fluviopupa brevior* (Ancey, 1905) originally described from the island of Éfaté. Later findings from the same island as well as from Gaua and Espiritu Santo (short: Santo) were attributed to the same species (Solem, 1959; Starmühlner, 1976). In 2006, a large scale expedition aiming at inventorying biodiversity on the whole of the island of Espiritu Santo was organized by the Muséum National d'Histoire Naturelle, the Institut de Recherche pour le Développement and the NGO Pronatura International. Sampling covered most of the habitats of the island, from degraded forests around the capital city Luganville to the highest summits of the island. As spin-offs of 'SANTO 2006', several smaller missions were made to Vanuatu in 2007, including one in November 2007 targeting the northernmost group of islands of the Vanuatu archipelago, namely the Torres islands. This expedition yielded 10 species of tateid gastropods. The whereabouts of Ancey's single, only vaguely described specimen are unknown (Harriet Wood, pers. comm.). Therefore, it is impossible to redescribe and define his species according to modern standards. However, since none of the species from Fiji or the Austral Islands occurs on more than one island, and in accordance with the general pattern of narrow distributions of freshwater rissooids, it is safe to assume that islands as distant as Éfaté and Espiritu Santo (ca. 250 km) or the Torres islands (ca. 500 km) do not share tateid species. Therefore, we introduce new names for all 10 recently discovered species. In addition, we assessed the role of Vanuatu as potential stepping stone for the dispersal of tateid gastropods across the Pacific.

Materials and methods

The material was collected in November 2006, July 2007, December 2007 (Santo) and November 2007 (Torres islands) (Fig. 1). Snails were picked or washed from their substrates and fixed immediately in 95% ethanol. Alternatively, sediment samples including the benthic fauna were preserved in ethanol and sorted in the lab. Five shell dimensions were measured (parallel and perpendicular to the coiling axis) under a dissecting microscope equipped with an ocular micrometre. Whorls were counted to the nearest eighth of a whorl following Verduin (1982). Based on the shell measurements, nine populations were submitted to a multivariate analysis of variance (MANOVA) including a canonical variates analysis (CVA), thus a multigroup discriminant analysis, followed by Hotelling's pairwise comparisons using the programme PAST 1.81 (Hammer et al., 2001) to corroborate the taxonomic assessment statistically (e.g. Haase et al., 2006). Snails were dissected and anatomies drawn with a camera lucida after dissolving the shells in about 5% HCl. Shells, opercula and radulae were cleaned in a ca. 2.5% sodium hypochlorite solution for scanning electron microscopy (SEM). Hexamethyldisilazane was used to dry cephalopodia of males (Nation, 1983). These and the hard-parts were investigated in a JEOL JSM 840A Scanning Microscope after sputter coating with gold. Ideally, for each population, 20 adult shells—these species have determinate growth and adulthood is indicated by a thickened and continuous aperture—were measured, each three females and males dissected, and four–six radulae and three cephalopodia prepared for SEM. The number of specimens investigated is only stated where it deviates from these numbers. Morphometric data and sex ratios are given in Table 1. This reference is not repeated under each species description.

As proposed by Haase & Bouchet (2006), we discriminated species in case shell and anatomical character states suggested that differences were fixed and that they had a more complex genetic basis than being simply alternative alleles at a single locus so that genetic isolation can be inferred.

Acronyms of collectors: BF, Benoit Fontaine; OG, Olivier Gargominy; PB, Philippe Bouchet; RP, Rufino Pineda; VP, Vincent Prié.

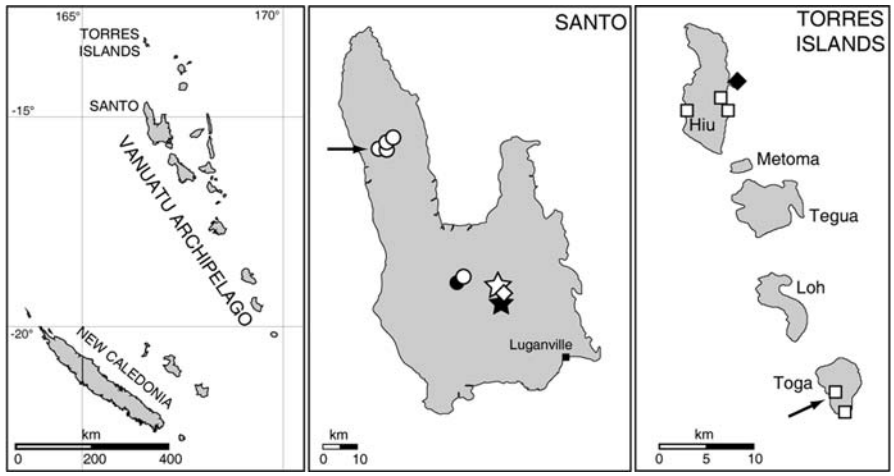

Fig. 1 Localities. *Open circle*, *F. espiritusantoana* sp. nov.; *solid circle*, *F. espiritusantoana* sp. nov., *F. melissae* sp. nov.; *open star*, *F. priei* sp. nov.; *solid star*, *F. pascali*; *open diamond*, *F. walterlinii* sp. nov., *F. narii* sp. nov., *F. snel* sp. nov.; *solid diamond*, *F. titusi* sp. nov., *F. smolwan* sp. nov.; *open square*, *F. torresiana* sp. nov. *Arrows* indicate type localities of species occurring in more than one place

Results

Systematic descriptions

Fluviopupa Ponder & Haase, 2005
Type species: *Fluviopupa pupoidea* Pilsbry, 1911 (original designation, by monotypy).
Synonymy: *Fluviopupa* Pilsbry, 1911: 549.

Description

Shell (Figs. 2, 3): Light brown or without colour, clear or semitransparent; turriform, conical or pupiform; protoconch well differentiated from teleoconch, surface with wrinkles gradually becoming finer towards the teleoconch (Fig. 4); teleoconch smooth apart from growth lines; umbilicus narrow; aperture simple, occasionally with varix behind outer lip, without posterior channel.
Operculum (Fig. 5): Corneous, yellow, elongate-ellipsoidal, paucispiral, nucleus submarginal, muscle attachment area either with peg, or white, non-calcareous smear, or without such features.
External features: Epidermis usually black, but reductions of pigmentation frequent; eyes only rarely without pigment; tentacles without conspicuous pattern of ciliation.
Mantle cavity: Ctenidium well developed with broadly triangular filaments, abutting directly on pericardium or connected by short vessel; osphradium ovate-elongate, usually behind middle of ctenidium; kidney may or may not protrude into roof of mantle cavity, renal gland orientated longitudinally; hypobranchial gland only occasionally apparent in dissections.
Digestive system: Radula (Fig. 6) taenioglossate, central tooth with lateral edges at about 45°, U-shaped basal tongue and 2–5 pairs of basal cusps, innermost largest; lateral tooth with long, parallel sided face and well-developed basal tongue, transition into outer wing ventrally thick but narrow, above this stalk membranous; marginal teeth with numerous pointed denticles, longer on the inner marginal teeth; stomach with fan-shaped caecum (Fig. 7); intestine bending backwards around style sac and again forward in front of anterior chamber of stomach; rectum either running 'straight' along pallial genital glands or making angulation in pallial roof (Fig. 8).
Female genitalia: Oviparous; ovary lobate or sac-shaped, only occasionally extending to stomach; renal oviduct coiling first 180° clockwise and then 270° counter-clockwise, the proximal loop often bent anteriorly or towards albumen gland; one distal receptaculum seminis globular with moderately wide, short duct, lying against left side of middle part of bursa copulatrix; bursa copulatrix behind albumen gland, pyriform to elongate or large, globular sac; pallial oviduct with ovate cross section; albumen gland to at least two-thirds in pallial roof; capsule gland with two distinct glandular areas; genital opening terminal to subterminal (Fig. 9).
Male genitalia: Testis lobate, usually covering proximal chamber of stomach; vas deferens leaving testis ca 0.25 whorls proximal to anterior end

Table 1 Shell morphometry and sex ratio

Species/Loc/Sex rat	sh	sw	ah	aw	bww	sh/sw	sw/bww	w
F. espiritusantoana/SA32/7 f/13 m								
Holotype	2.4	1.34	0.95	0.9	1.18	1.79	1.14	4.25
Median	2.30	1.28	0.92	0.86	1.11	1.80	1.17	4.50
Mean	2.33	1.29	0.93	0.86	1.11	1.80	1.17	4.44
Max	2.58	1.46	1.08	0.94	1.20	1.89	1.25	4.88
Min	2.04	1.18	0.85	0.78	1.02	1.70	1.09	4.13
Sd	0.14	0.08	0.06	0.05	0.06	0.07	0.04	0.23
Cv	6.29	6.08	6.53	5.57	5.04	3.77	3.45	5.27
F. espiritusantoana/SAPB1								
Median	2.37	1.34	0.96	0.89	1.17	1.76	1.15	4.50
Mean	2.37	1.35	0.95	0.88	1.17	1.76	1.15	4.42
Max	2.94	1.54	1.07	0.98	1.34	1.96	1.20	4.75
Min	2.00	1.24	0.86	0.80	1.06	1.61	1.11	4.00
Sd	0.24	0.09	0.06	0.06	0.08	0.09	0.03	0.23
Cv	10.22	6.68	6.59	6.40	6.72	5.06	2.44	5.20
F. pascali/SA110/6 f/14 m								
Holotype	2.41	1.44	1.02	0.9	1.21	1.67	1.19	4.50
Median	2.18	1.33	0.95	0.88	1.18	1.66	1.12	4.38
Mean	2.18	1.33	0.94	0.88	1.17	1.65	1.13	4.34
Max	2.50	1.50	1.10	0.96	1.28	1.77	1.24	4.75
Min	1.92	1.20	0.86	0.80	1.09	1.44	1.08	4.00
Sd	0.16	0.07	0.06	0.05	0.05	0.07	0.04	0.23
Cv	7.49	5.42	6.33	5.48	4.46	4.42	3.23	5.42
F. melissae/SAPB1/14 f/4 m								
Holotype	2.06	1.02	0.72	0.7	0.95	2.02	1.07	4.125
Median	1.95	1.03	0.74	0.66	0.91	1.87	1.12	4.38
Mean	1.93	1.04	0.73	0.66	0.92	1.86	1.13	4.28
Max	2.23	1.12	0.85	0.71	1.01	2.06	1.24	4.50
Min	1.56	0.94	0.64	0.58	0.83	1.59	1.08	3.88
Sd	0.15	0.05	0.05	0.04	0.05	0.10	0.04	0.19
Cv	7.75	5.10	7.17	6.08	5.39	5.35	3.72	4.57
F. walterlinii/SAPB3/15 f/5 m								
Holotype	1.99	1.2	0.87	0.78	1.08	1.66	1.11	4.25
Median	2.11	1.28	0.95	0.82	1.09	1.65	1.17	4.38
Mean	2.11	1.28	0.94	0.81	1.09	1.64	1.18	4.43
Max	2.38	1.42	1.06	0.91	1.18	1.69	1.32	4.75
Min	1.80	1.14	0.80	0.72	0.98	1.55	1.15	4.25
Sd	0.14	0.08	0.06	0.05	0.06	0.04	0.04	0.16
Cv	6.64	6.01	6.37	6.70	5.28	2.38	3.28	3.76
F. narii/SAPB3/4 f/15 m								
Holotype	2.94	1.58	1.11	1.01	1.38	1.86	1.15	5.00
Median	2.51	1.44	1.04	0.94	1.26	1.75	1.15	4.75
Mean	2.55	1.46	1.06	0.94	1.28	1.75	1.14	4.73
Max	2.93	1.63	1.18	1.01	1.40	1.85	1.18	5.00
Min	2.32	1.34	0.98	0.86	1.18	1.63	1.08	4.38

Table 1 continued

Species/Loc/Sex rat	sh	sw	ah	aw	bww	sh/sw	sw/bww	w
Sd	0.17	0.09	0.07	0.04	0.06	0.06	0.03	0.19
Cv	6.74	6.44	6.23	4.80	4.87	3.48	3.09	4.00
F. snel/SAPB3								
Holotype	1.24	0.72	0.51	0.46	0.66	1.72	1.09	3.25
F. priei/SAVP13								
Holotype	2.02	1.06	–	–	–	1.91	–	4.25
Median	1.92	1.02	–	–	–	1.83	–	4.25
Mean	1.88	1.02	–	–	–	1.84	–	4.16
Max	2.28	1.20	–	–	–	2.16	–	4.38
Min	1.34	0.83	–	–		1.58		3.63
Sd	0.23	0.09	–	–	–	0.14	–	0.17
Cv	12.49	9.11	–	–	–	7.78	–	4.06
F. torresiana/To28/7 f/13 m								
Holotype	2.28	1.24	0.95	0.78	1.06	1.84	1.17	4.50
Median	1.87	1.04	0.75	0.70	0.95	1.78	1.09	4.06
Mean	1.92	1.07	0.77	0.71	0.98	1.79	1.09	4.11
Max	2.32	1.24	0.92	0.84	1.14	1.93	1.13	4.63
Min	1.56	0.92	0.66	0.62	0.86	1.70	1.05	3.75
Sd	0.22	0.10	0.08	0.06	0.09	0.07	0.02	0.23
Cv	11.58	9.06	10.29	8.87	9.00	3.71	2.00	5.55
F. torresiana/To2/8 f/11 m								
Median	1.99	1.03	0.76	0.70	0.97	1.87	1.08	4.19
Mean	2.00	1.06	0.78	0.72	0.98	1.89	1.09	4.17
Max	2.36	1.22	0.90	0.84	1.11	2.15	1.15	4.63
Min	1.62	0.92	0.67	0.61	0.84	1.75	1.02	3.75
Sd	0.24	0.09	0.07	0.06	0.08	0.11	0.03	0.25
Cv	12.04	8.97	9.41	8.74	8.29	5.74	2.58	6.01
F. titusi/To5/$N = 10$								
Holotype	1.13	0.68	0.49	0.46	0.65	1.66	1.05	3.375
Median	1.14	0.68	0.47	0.46	0.63	1.67	1.09	3.56
Mean	1.15	0.68	0.47	0.45	0.62	1.67	1.10	3.53
Max	1.33	0.77	0.50	0.50	0.66	1.80	1.20	3.75
Min	1.00	0.63	0.42	0.42	0.58	1.56	1.03	3.25
Sd	0.09	0.04	0.03	0.03	0.02	0.07	0.06	0.21
Cv	8.33	6.60	5.88	5.85	4.11	4.33	5.21	6.13
F. smolwan/To5								
Holotype	1.28	0.68	0.49	0.45	0.63	1.88	1.08	3.625

If not otherwise stated, 20 individuals were measured, but not necessarily also sexed. In case of *F. priei* sp. nov., not all the variables could be meaningfully measured because of its detached whorls. *ah* Aperture height; *aw* aperture width; *bww* width of body whorl (=penultimate whorl); *cv* coefficient of variation adjusted for sample size; *f* females; *Loc* locality; *m* males; *max* maximum; *min* minimum; *N* number of specimens; *sd* standard deviation; *Sex rat* sex ratio; *sh* shell height; *sw* shell width; *w* number of whorls; measurements in mm

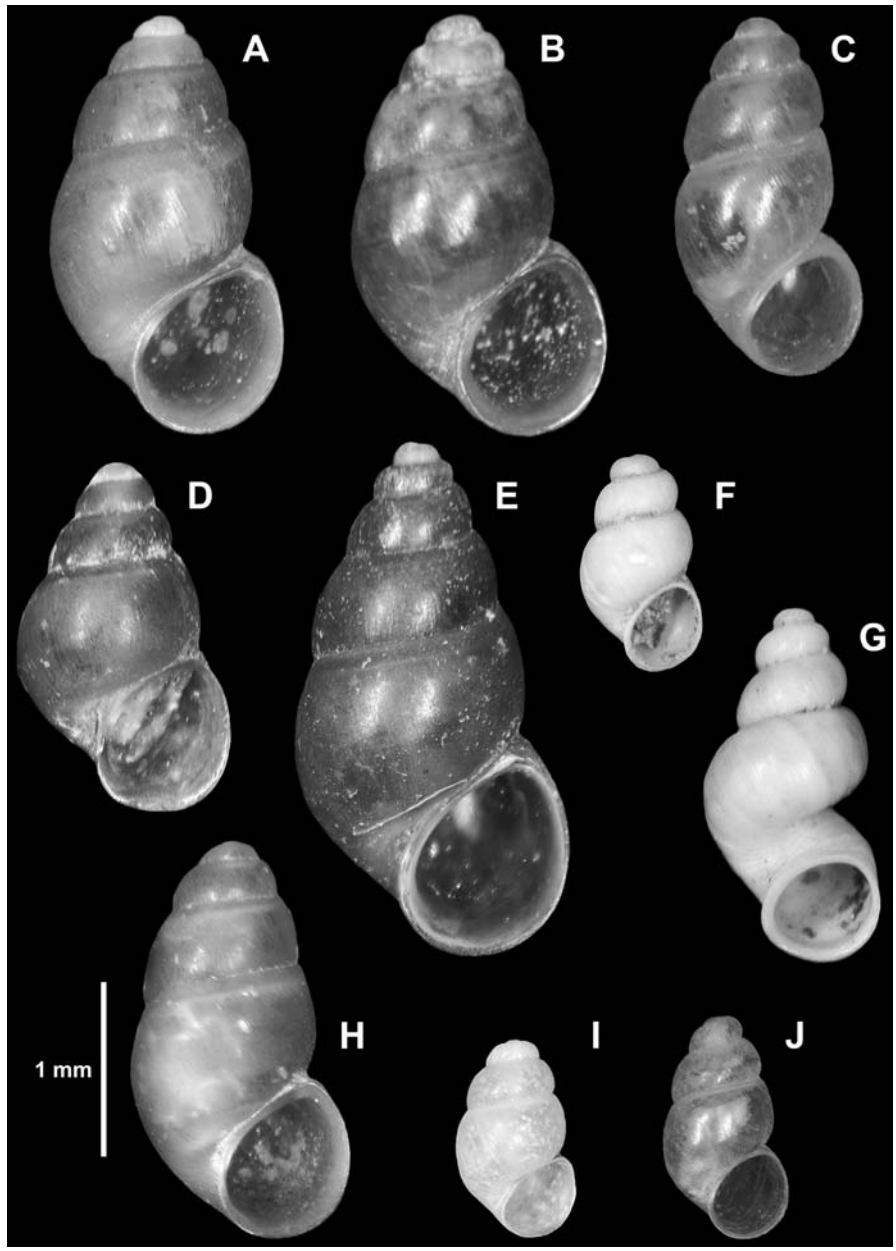

Fig. 2 Holotypes. **A** *F. espiritusantoana* sp. nov.; **B** *F. pascali* sp. nov.; **C** *F. melissae* sp. nov.; **D** *F. walterlinii* sp. nov.; **E** *F. narii* sp. nov.; **F** *F. snel* sp. nov.; **G** *F. priei* sp. nov.; **H** *F. torresiana* sp. nov.; **I** *F. titusi* sp. nov.; **J** *F. smolwan* sp. nov.

initially coiling as vesicula seminalis; vas deferens entering prostate in posterior third; pallial vas deferens leaving prostate in anterior third, becoming a muscular ejaculatory duct when entering the neck; prostate with ovate cross section; penis simple, usually tapering more or less continuously from broad base, central chondroid tissue in middle section occasionally bulging out to form a flange on right side, penial tip pointed or with blunt appearance due to a terminal lappet on the right side, in this case genital opening through left lappet (Fig. 10).

Remarks: The species from Vanuatu are morphologically between the *Hemistomia*-clade from New Caledonia and *Fluviopupa* from Fiji and the Austral Islands as outlined in more detail in "Discussion" section (see Haase & Bouchet, 1998; Haase et al., 2005, 2006). We tentatively ascribe the new species to

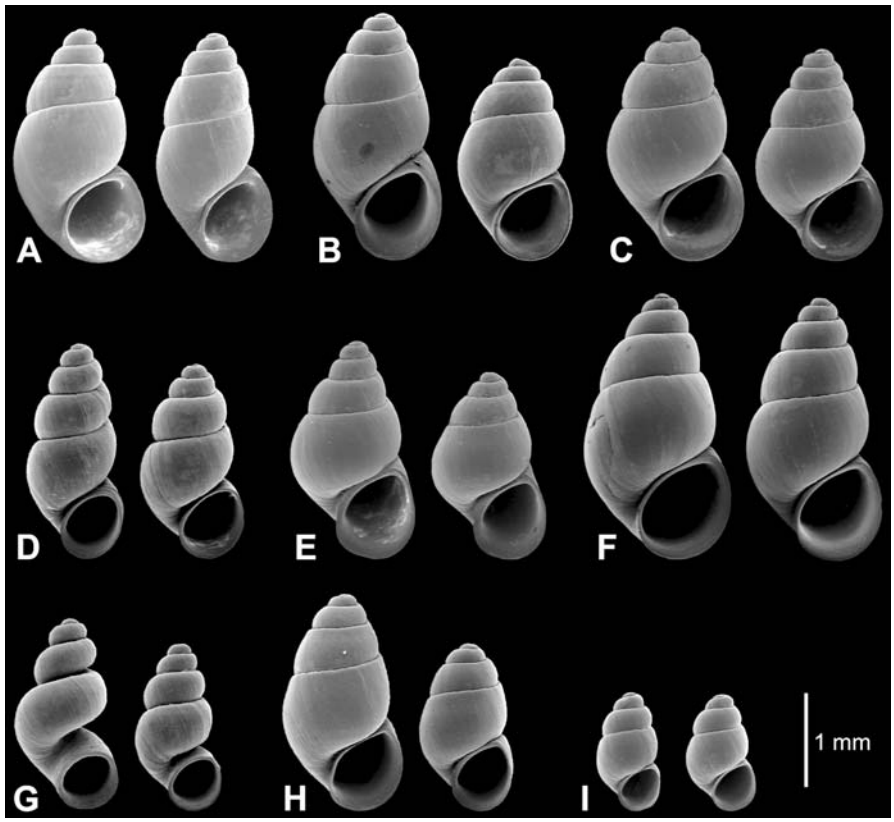

Fig. 3 Shells (SEM micrographs). **A** *F. espiritusantoana* sp. nov. type locality; **B** *F. espiritusantoana* sp. nov., SAPB1; **C** *F. pascali* sp. nov.; **D** *F. melissae* sp. nov.; **E** *F. walterlinii* sp. nov.; **F** *F. narii* sp. nov.; **G** *F. priei* sp. nov.; **H** *F. torresiana* sp. nov., type locality; **I** *F. titusi* sp. nov. All shells are paratypes except (**B**)

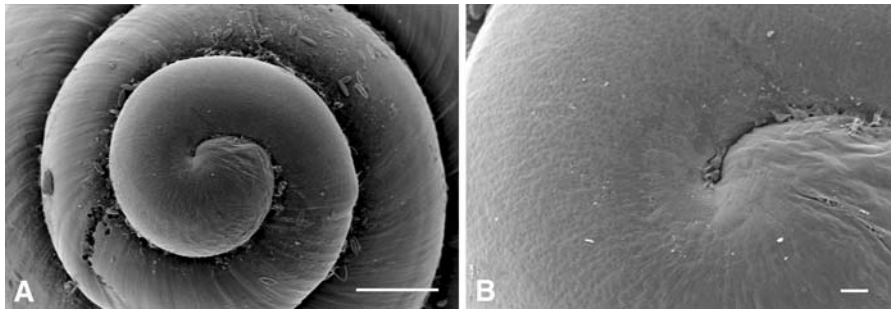

Fig. 4 Protoconch. *F. walterlinii* sp. nov. Scale bars = 100 μm in (**A**) and 10 μm in (**B**)

the genus *Fluviopupa* pending comprehensive genetic investigations, because of the lack of the autapomorphies characterizing the New Caledonian species such as the well-developed, often complex, opercular pegs or the palatal tooth behind the outer lip. A simple opercular peg may be present in species from Vanuatu, but it has a distinct shape not observed in New Caledonia. Its reduction to a white, non-calcareous smear, which may be entirely absent in small species, links the species from Vanuatu to those from the islands further East. The above description of the genus is thus an extension of those given by Haase et al. (2005, 2006).

General remarks to species descriptions

Measurements and whorl counts are given in Table 1. This reference is not repeated in the descriptions. All species share the following character states, which are therefore not repeated in the descriptions, either: Shell: Protoconch, teleoconch and umbilicus (where present) as for the genus; aperture simple.

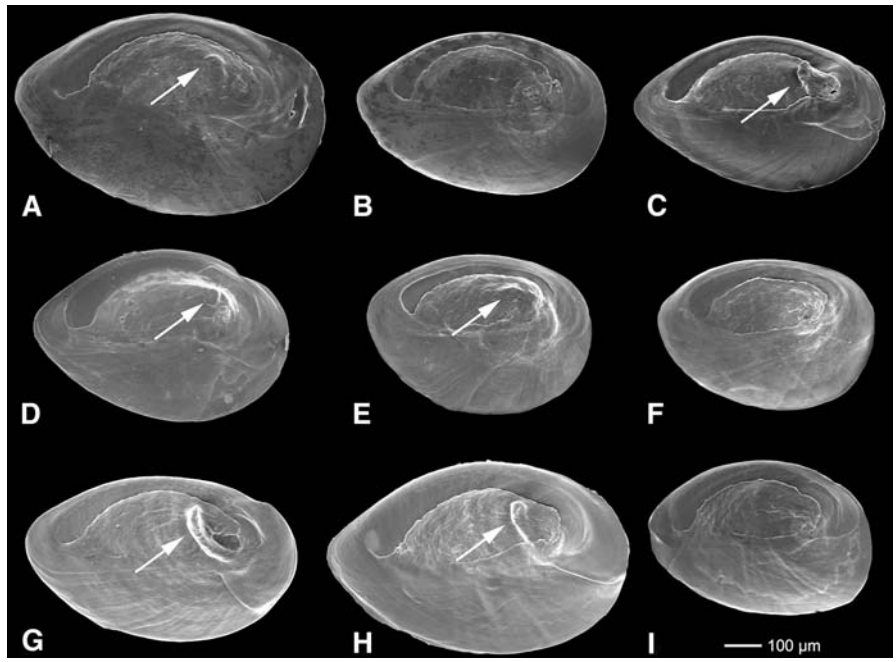

Fig. 5 Operculum. **A**, **B** *F. espiritusantoana* sp. nov., SAPB1; **C**, **D** *F. pascali* sp. nov.; **E**, **F** *F. melissae* sp. nov.; **G** *F. walterlinii* sp. nov.; **H** *F. narii* sp. nov.; **I** *F. titusi* sp. nov. *Arrows* indicate peg or rudiment of peg

Operculum (Fig. 5): Corneous, yellow, elongate-ellipsoidal, paucispiral, nucleus submarginal.
External features: Tentacles without conspicuous pattern of ciliation.
Mantle cavity: Kidney not protruding into pallial roof; hypobranchial gland not recognized in dissections.
Digestive system: Radula as for the genus (Fig. 6).
Female genitalia: As for the genus. Specific differences only in extent of ovary and shape of bursa copulatrix (Fig. 9).
Male genitalia: Testis, vas deferens and prostate as for the genus; penis with terminal lappet on right side of tip resulting in blunt appearance (Fig. 10). Specific differences only in extent of testis.

Fluviopupa espiritusantoana sp. nov.

Type material: holotype MNHN; paratypes MNHN (>100).
Type locality: Penaoru, Sousteo, Cumberland, Espiritu Santo, Vanuatu. SA32. Stream in shaded gulley in the forest. 255 m a.s.l. 14.96448°S, 166.63662°E. Coll. OG BF, 14.XI.2006.
Additional material: Penaorou, Saratsi, Cumberland, Santo. SA39. Stream in wet forest. 900 m a.s.l. 14.96709°S, 166.65843°E. Coll. OG BF, 17.XI.2006; Béésel valley, right bank, below Mt. Pao, Cumberland, Espiritu Santo, Vanuatu. SA43. Slow stream. 725 m a.s.l. 14.94528°S, 166.66569°E. Coll. OG BF, 18.XI. 2006; Béésel valley, right bank, below Mt Pao, Cumberland, Espiritu Santo, Vanuatu. SA48. Small encrusting stream. 710 m a.s.l. 14.9434°S, 166.66668°E. Coll. OG BF, 20.XI.2006; Right bank of river Ora, 500 m upstream of ford, Espiritu Santo, Vanuatu. SAPB2. Seepage in marl limestone. 43 m a.s.l. 15.3053°S, 166.8683°E. Coll PB RP, 05.VII.2007; Right bank of river Ora, 1000 m upstream of ford, Espiritu Santo, Vanuatu. SAPB1. Seepage in marl limestone, below waterfall. 151 m a.s.l. 15.3076°S, 166.8598°E. Coll PB RP, 05.VII.2007.
Habitat and distribution: Streams with slow current in forested areas. Limestone and volcanic substrate. Widely distributed throughout the western mountain range of Espiritu Santo, from 40 to 900 m a.s.l.
Etymology: The new species is named after the island of Espiritu Santo, where it has the widest distribution of all tateids known so far.

Description

Shell (Figs. 2A, 3A, B): Light brown, conical, 1.76–1.80 times higher than wide, males significantly smaller than females (Mann–Whitney *U*-test, $P = 0.043$ and $P = 0.019$ for SA32 and the Ora-population,

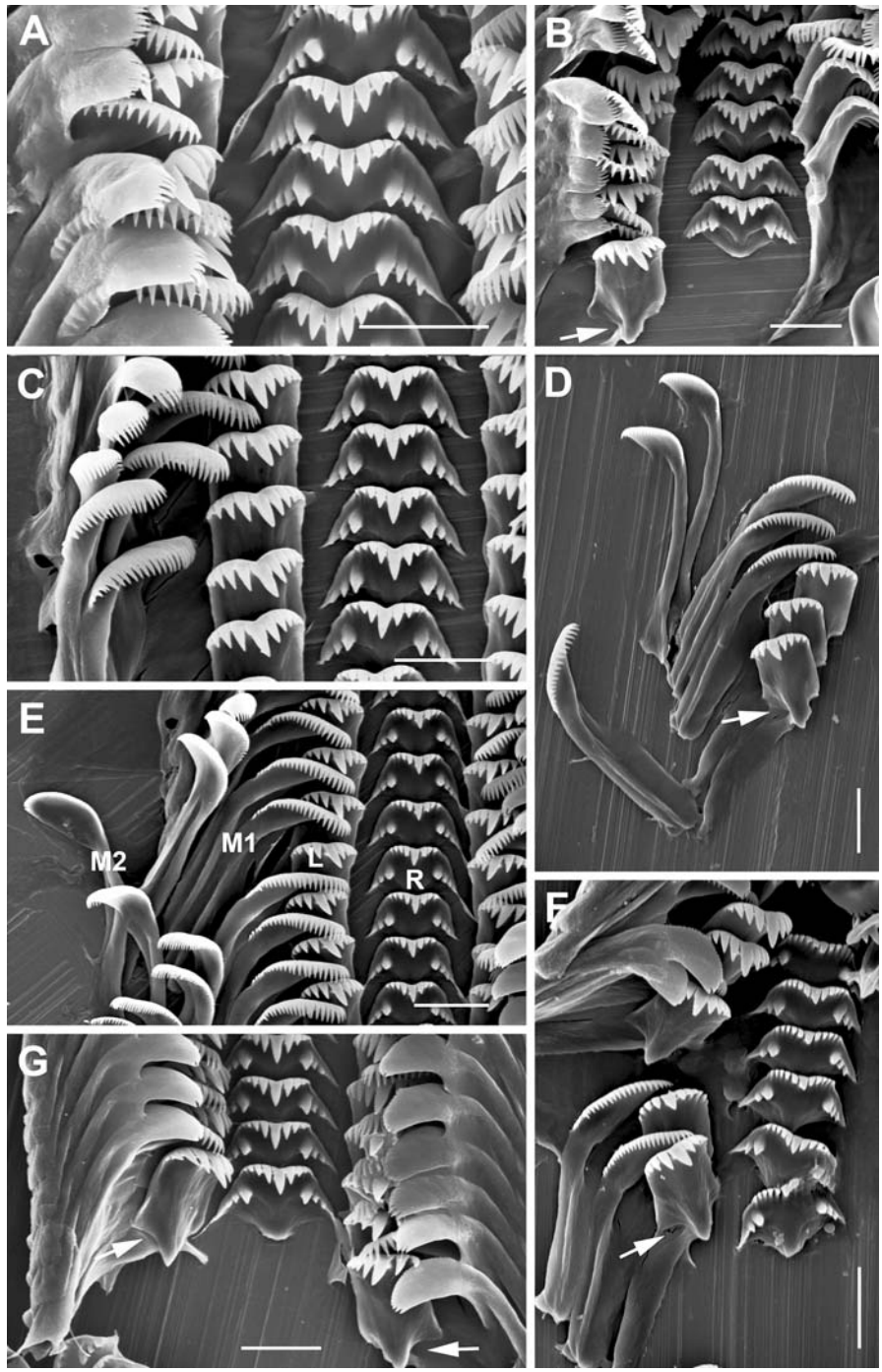

Fig. 6 Radula. **A**, **B** *F. espiritusantoana* sp. nov., type locality; **C**, **D** *F. pascali* sp. nov.; **E**, **F** *F. melissae* sp. nov.; **G** *F. walterlinii* sp. nov.; **L** lateral teeth; *M1* inner marginal teeth; *M2* outer marginal teeth; *R* central teeth. *Arrows* indicate membranous neck region of lateral teeth. Scale bars = 10 μm

respectively), whorls moderately convex; protoconch with 0.9–1.0 whorls; aperture almost round, only slightly higher than wide.

Operculum: The extent of a white smear is very variable; in the type population, a small part of the attachment area close to the nucleus may be white, whereas in the river Ora, this white smear can cover the entire upper half (orientation as in Fig. 5) of the attachment area bearing even a tiny remnant of a simple peg (Fig. 5A); in both populations, however,

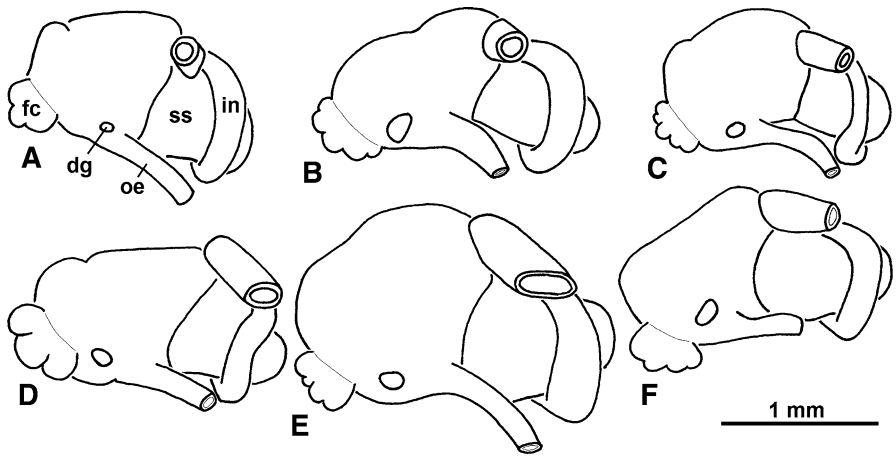

Fig. 7 Stomach. **A** *F. espiritusantoana* sp. nov., type locality; **B** *F. pascali* sp. nov.; **C** *F. melissae* sp. nov.; **D** *F. walterlinii* sp. nov.; **E** *F. narii* sp. nov.; **F** *F. torresiana* sp. nov., type locality. *dg* Opening into digestive gland; *fc* fan-shaped caecum; *in* intestine; *oe* oesophagus; *ss* style sac

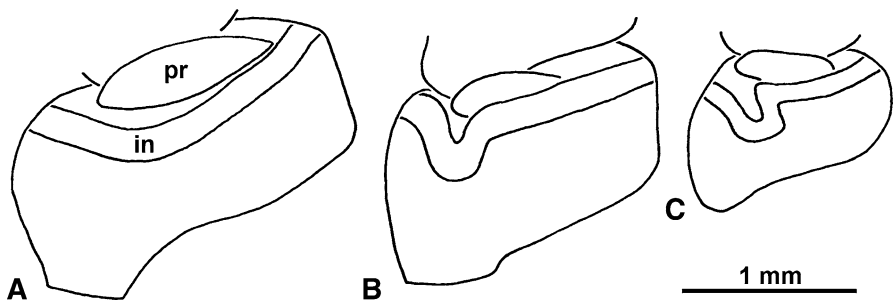

Fig. 8 Rectum. **A** *F. pascali* sp. nov.; **B** *F. melissae* sp. nov.; **C** *F. titusi* sp. nov.; *pr* prostate; *re* rectum

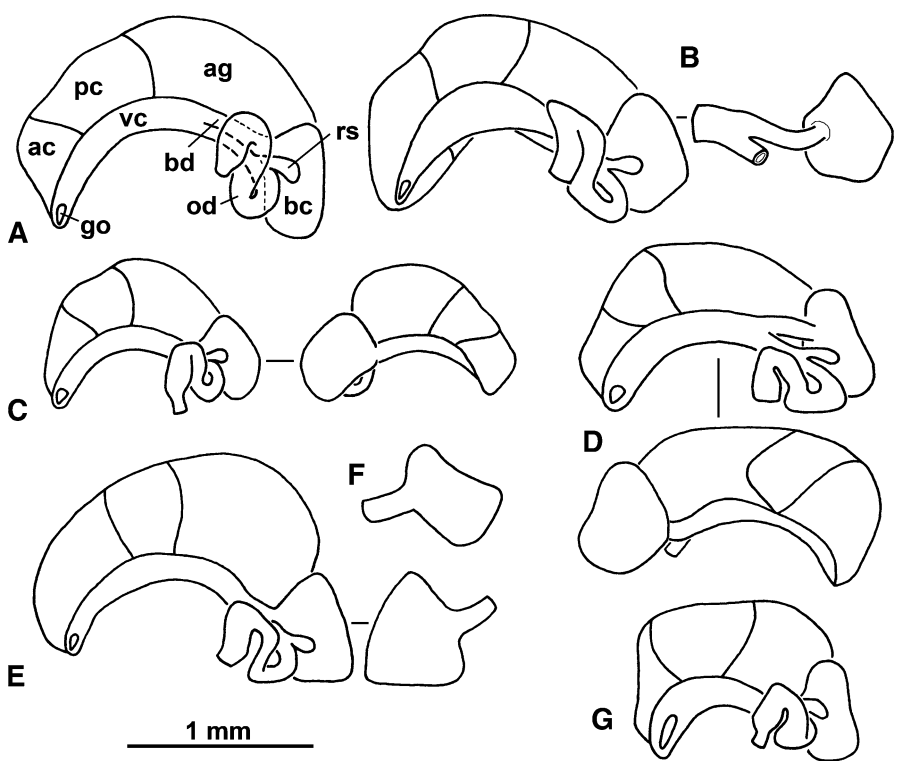

Fig. 9 Distal female genitalia. **A** *F. espiritusantoana* sp. nov., type locality; **B** *F. pascali* sp. nov.; **C** *F. melissae* sp. nov.; **D** *F. walterlinii* sp. nov.; **E**, **F** *F. narii* sp. nov., **F** bursa copulatrix of a second specimen; **G** *F. torresiana* sp. nov., type locality. *ac* Anterior capsule gland; *ag* albumen gland; *bc* bursa copulatrix; *bd* bursal duct; *go* genital opening; *od* oviduct; *rs* receptaculum seminis; *vc* ventral channel

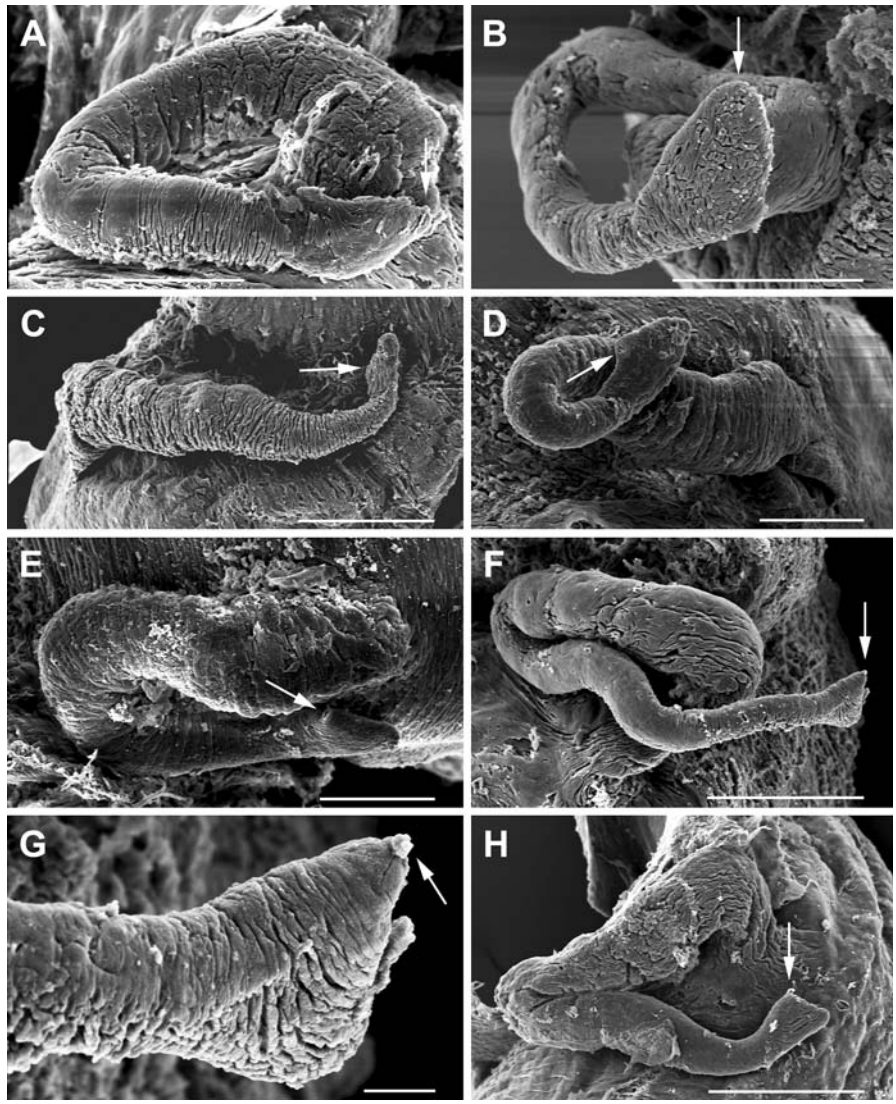

Fig. 10 Penis. **A** *F. espiritusantoana* sp. nov., type locality; **B** *F. pascali* sp. nov.; **C** *F. melissae* sp. nov.; **D** *F. walterlinii* sp. nov.; **E** *F. narii* sp. nov.; **F**, **G** *F. torresiana* sp. nov., type locality; **H** *F. titusi* sp. nov. *Arrows* indicate genital openings. Scale bars = 100 μm in (**A**)–(**F**), (**H**), 10 μm in (**G**)

opercula entirely lacking a smear were found (Fig. 5B).

External features: Mantle largely black except rim, area covering pallial glands and parts facing the columella; epidermis around and behind eyes as well as on snout black, tentacles may bear a black, longitudinal stripe.

Mantle cavity: Ctenidium with 21–25 filaments; osphradium ovate-elongate, behind middle of ctenidium, reaching almost half length of ctenidium.

Digestive system: Radular formula (Fig. 6A, B): R: 4-5 1 4-5/3-5 3-5, L: 4-5 1 5, M1: 22–24, M2: 32–36; fan-shaped caecum relatively small (Fig. 7A); rectum close to pallial genital glands in both sexes.

Female genitalia: Ovary lobate, starting 1.0–2.0 whorls below apex, comprising 0.75 whorls, not reaching stomach; bursa copulatrix elongate with relatively long bursal duct entering antero-ventrally.

Male genitalia: Testis starting 1.0–1.5 whorls below apex, comprising 1.0–1.75 whorls; penis may be pigmented on proximal half.

Remarks: *F. espiritusantoana* sp. nov. has the highest number of denticles on M2 among all species from Vanuatu. It is more slender than *F. pascali* sp. nov. and has a less pronounced size dimorphism than *F. torresiana* sp. nov., which, in addition, has a more central origin of the bursal duct. Other conical species differ in having a defined opercular peg. There is

some variation in terms of shell and opercular morphology among the populations from the North of Espiritu Santo and those from the river Ora. Whether they are indeed conspecific has to be confirmed by means of molecular methods.

Fluviopupa pascali sp. nov.

Type material: holotype MNHN; paratypes MNHN (>100).
Type locality: Butmas, Espiritu Santo, Vanuatu. SA110. Spring on the edge of a taro plantation. 565 m a.s.l. 15.3741°S, 166.97449°E. Coll. OG, 03.XII. 2007.
Habitat and distribution: Spring on limestone. Only known from the type locality, i.e. endemic on the Butmas plateau (Mont Tankara).
Etymology: This species is dedicated to Olivier Pascal, coordinator of the terrestrial field work in the frame of the expedition 'Santo 2006' and the most pleasant friend in the field, who joined two of us (OG and BF) during one of the highlights of the expedition—the crossing of the Cumberland range during which *Fluviopupa* were sampled.

Description

Shell (Figs. 2B, 3C): Light brown, broadly conical, on average only 1.65 times higher than wide, males significantly smaller than females (Mann–Whitney *U*-test, $P = 0.013$), whorls convex; protoconch with 0.9–1.0 whorls; aperture ovate-pyriform, much higher than wide.
Operculum: Attachment area almost entirely covered by white smear, opercular peg small and distinct or rudimental (Fig. 5C, D).
External features: Mantle largely black except rim, area covering pallial glands and parts facing the columella; head black as well.
Mantle cavity: Ctenidium with 21–24 filaments; osphradium ovate-elongate, under middle of ctenidium, 1/3 to almost half length of ctenidium.
Digestive system: Radular formula (Fig. 6C, D): R: 3-4 1 3-4/3-4 3-4, L: 4-6 1 4-5, M1: 20–23, M2: 28–30; fan-shaped caecum well developed (Fig. 7B); rectum close to pallial genital glands in both sexes (Fig. 8A).
Female genitalia: Ovary lobate, starting 1.125–1.5 whorls below apex, comprising 0.5–1.0 whorls, eventually reaching stomach; bursa copulatrix a large sac of undefined shape, bursal duct entering antero-centrally.
Male genitalia: Testis starting 1.0–1.5 whorls below apex, comprising 1.0–1.125 whorls; penis with central, black blotch.
Remarks: *F. pascali* sp. nov. is much broader than *F. espiritusantoana* sp. nov. and *F. torresiana* sp. nov., and is clearly defined by the operculum with large, white smear and small peg.

Fluviopupa melissae sp. nov.

Type material: holotype MNHN; paratypes MNHN (>50).
Type locality: Right bank of river Ora, 1000 m upstream of ford, Espiritu Santo, Vanuatu. SAPB1. Seepage in marl limestone, below waterfall. 151 m a.s.l.. 15.3076°S, 166.8598°E. Coll PB RP, 05.VII.2007.
Habitat and distribution: Seepage in marl limestone. Only known from the type locality, on the lower eastern slope of the western mountain range of Espiritu Santo.
Etymology: This species is dedicated to Grace Melissa, whose exceptional political and social commitment has helped paving the way for Vanuatu's independence.

Description

Shell (Figs. 2C, 3D): Colourless, very slender-conical, on average 1.86 times higher than wide, no size dimorphism detected, whorls convex; protoconch with 0.9–1.0 whorls; aperture almost ovate, much higher than wide.
Operculum: Attachment area with elongate white smear, eventually with rudimental peg (Fig. 5E, F).
External features: Mantle rarely with faint, black blotches, usually only eyes pigmented.
Mantle cavity: Ctenidium with 16–18 filaments; osphradium ovate, behind middle of ctenidium, 1/4–1/3 length of ctenidium.
Digestive system: Radular formula (Fig. 6E, F): R: 3-5 1 3-5/2-4 2-4, L: 4-5 1 4-5, M1: 23–26, M2: 27–32; fan-shaped caecum well developed (Fig. 7C); rectum bending in pallial roof, more pronounced in males than in females (Fig. 8B).
Female genitalia: Ovary lobate, starting 1.25–2.0 whorls below apex, comprising 0.3–0.75 whorls,

eventually reaching stomach; bursa copulatrix cuboidal, bursal duct entering antero-ventrally.
Male genitalia: Testis starting 0.5–1.0 whorls below apex, comprising 0.75–1.0 whorls.
Remarks: The slender-conical shape with the small, ovate aperture combined with the almost entire lack of pigment distinguish *F. melissae* sp. nov. from its congeners. In addition, this species has the highest number of denticles on the inner marginal teeth despite its relatively small size.

Fluviopupa walterlinii sp. nov.

Type material: holotype MNHN; paratypes MNHN (>100).
Type locality: Fapon, Butmas, Espiritu Santo, Vanuatu. SAPB3. Stream. 420 m a.s.l. 15.3393°S, 166.9721°E. Coll. PB RP, 05.IV.2007.
Habitat and distribution: Stream on limestone. Only known from the type locality, i.e. endemic from the Butmas plateau (Mont Tankara).
Etymology: This species is dedicated to Walter Lini, father of Vanuatu's independence.

Description

Shell (Figs. 2D, 3E): Light brown, broadly conical, on average only 1.64 times higher than wide, no size dimorphism detected, whorls moderately convex; protoconch with about 0.9 whorls; aperture broadly pyriform, much higher than wide.
Operculum: Attachment area entirely covered by white smear, peg well developed (Fig. 5G).
External features: Mantle largely black except rim, area covering pallial glands and parts facing the columella; epidermis around and behind eyes, eventually also on snout and tentacles black.
Mantle cavity: Ctenidium with 18–21 filaments; osphradium ovate, under middle of ctenidium, about 1/3 length of ctenidium.
Digestive system: Radular formula (Fig. 6G): R: 3-4 1 3-4/3 3, L: 4 1 3-4, M1: 20–21, M2: 28–30; fan-shaped caecum well developed (Fig. 7D); rectum close to pallial genital glands in both sexes.
Female genitalia: Ovary lobate, starting 1.75 whorls below apex, comprising 0.5 whorls, not reaching stomach; bursa copulatrix a large, pyriform sac, bursal duct entering antero-centrally.
Male genitalia: Testis starting 1.0–1.25 whorls below apex, comprising 1.0–1.25 whorls; penis may be pigmented along most of its length.
Remarks: *F. walterlinii* sp. nov. is unique with its broadly conical shell shape and broadly pyriform aperture. It also has the largest opercular peg among the tateids of Vanuatu.

Fluviopupa narii sp. nov.

Type material: holotype MNHN; paratypes MNHN (>100).
Type locality: Fapon, Butmas, Espiritu Santo, Vanuatu. SAPB3. Stream. 420 m a.s.l. 15.3393°S, 166.9721°E. Coll. PB RP, 05.IV.2007.
Habitat and distribution: Stream on limestone. Only known from the type locality, i.e. endemic from the Butmas plateau (Mont Tankara).
Etymology: The new species is dedicated to Russell Nari, director at the Ministère des Terres in Port Vila, who supported SANTO 2006 in many ways.

Description

Shell (Figs. 2E, 3F): Light brown, conical, on average 1.75 times higher than wide, no size dimorphism detected, whorls moderately convex; protoconch with about 0.9 whorls; aperture ovate-pyriform, much higher than wide.
Operculum: Attachment area largely covered by white smear, peg distinct, but small (Fig. 5H).
External features: Mantle largely black except rim, area covering pallial glands and parts facing the columella; epidermis around and behind eyes, eventually also on snout and tentacles black.
Mantle cavity: Ctenidium with 21–25 filaments; osphradium ovate-elongate, under middle of ctenidium, about 1/3 length of ctenidium.
Digestive system: Radular formula: R: 3-4 1 3-4/4-5 4-5, L: 3-4 1 3-5, M1: 19–22, M2: 27–28; fan-shaped caecum relatively small (Fig. 7E); rectum close to pallial genital glands in both sexes.
Female genitalia: Ovary lobate, starting 1.0 whorls below apex, comprising 0.75–1.0 whorls, not reaching stomach; bursa copulatrix large, cubical to cuboidal, bursal duct entering antero-centrally to -ventrally.
Male genitalia: Testis starting 1.0–1.25 whorls below apex, comprising 1.0–1.5 whorls; penis may be pigmented along most of its length.

Remarks: *F. narii* sp. nov. occurs syntopically with *F. walterlinii* sp. nov. but is readily distinguished by its larger and more slender shell as well as the smaller opercular peg.

Fluviopupa snel sp. nov.

Type material: holotype MNHN.
Type locality: Fapon, Butmas, Espiritu Santo, Vanuatu. SAPB3. Stream. 420 m a.s.l. 15.3393°S, 166.9721°E. Coll. PB RP, 05.IV.2007.
Habitat and distribution: Stream on limestone. Only known from the type locality, i.e. endemic on the Butmas plateau (Mont Tankara).
Etymology: Snel, used as noun in apposition, means snail in Bislama, the lingua franca of Vanuatu.

Description

Shell (Fig. 2F): Colourless, slender-conical, spire short, 1.72 times higher than wide; no protoconch data; aperture ovoid, much higher than wide.
Remarks: *F. snel* sp. nov. is intermediate in shell shape between the stouter *F. titusi* and the more slender *F. smolwan*. It is also distinguished from these species by its ovoid aperture. Only a single shell has been found at Fapon indicating, that it had been washed there and its actual, possibly subterranean habitat is unknown.

Fluviopupa priei sp. nov.

Type material: holotype MNHN; paratypes MNHN (>100).
Type locality: Fapon cave, Butmas, Espiritu Santo, Vanuatu. SAVP13. In sand. 15.33102°S, 166.96488°E. Coll. VP, X.2007.
Habitat and distribution: Limestone. Apparently a stygobiont species, which is only known from the type locality, i.e. endemic on the Butmas plateau (Mont Tankara).
Etymology: This new species is dedicated to Vincent Prié, its collector, a French malacologist totally devoted to the aquatic, subterranean realm.

Description

Shell (Fig. 2G, 3G): Colourless, slender conical in the beginning, uncoiling after 3.0–4.125 whorls, whorls convex; protoconch with 0.9–1.0 whorls; aperture almost circular.
Remarks: This species has not been found alive so far. However, among the hundreds of colourless empty shells, many were fresh suggesting that this species is a true stygobiont actually living close to the locality where its shells have been collected. Uncoiling is not common among rissooidean gastropods (see e.g. Rex & Boss, 1976, Hershler & Longley, 1986), yet, *F. priei* sp. nov. appears to have a perfect Doppelgänger in the cochliopid *Heleobia mirum* (Haas, 1957) from Lake Titicaca in Peru (Hershler & Thompson, 1992).

Fluviopupa torresiana sp. nov.

Type material: holotype MNHN; paratypes MNHN (>100).
Type locality: North of Riara Bay, Toga, Torres Islands, Vanuatu. To28. Stream at the base of a cliff, open area. 16 m a.s.l. 13.42663°S, 166.68162°E. Coll. PB OG BF, 25.XI.2007.
Additional material: Southern tip of Toga island, Torres islands, Vanuatu. To24. Resurgence at base of cliff. 10 m a.s.l. 13.44652°S, 166.6909°E. Coll. PB, 24.XI.2007; Northeast of Mt Wonvara, Hiu, Torres Islands, Vanuatu. To2. Spring at the base of a cliff, edge of plantation. 149 m a.s.l. 13.1431°S, 166.56884°E. Coll. OG BF, 19.XI.2007; Hiu, Torres islands, Vanuatu. To5. Small permanent spring. 13.1552°S, 166.576°E. Coll. PB, 19.XI.2007. Yuwutu Bay, West coast, Hiu, Torres Islands, Vanuatu. To15. Stream running from a taro field at the base of a cliff. 10 m a.s.l. 13.15498°S, 166.5471°E. Coll. PB OG BF, 21.XI.2007.
Habitat and distribution: Springs and streams in limestone sometimes close to plantations. Endemic on Hiu and Toga, Torres Islands.
Etymology: The new species is named after its area of distribution, the Torres Islands in the far North of the Vanuatu archipelago.

Description

Shell (Figs. 2H, 3H): Light brown, conical, 1.79–1.89 times higher than wide, males significantly smaller than females (Mann–Whitney *U*-test, $P = 0.003$ and $P < 0.001$ for To28 and To2, respectively), whorls

moderately convex; protoconch with 0.9–1.0 whorls; aperture ovate-pyriform, slightly higher than wide.
Operculum: Attachment area may bear traces of a white smear; in the majority of specimens from all populations a smear was lacking (Fig. 5I).
External features: Mantle largely black except rim, area covering pallial glands and parts facing the columella; epidermis around eyes as well as on snout and tentacles black.
Mantle cavity: Ctenidium with 13–21 filaments; osphradium ovate-elongate, behind middle of ctenidium, about 1/3 length of ctenidium.
Digestive system: Radular formula: R: 3-4 1 3-4/3-4 3-4, L: 4-5 1 4, M1: 21–23, M2: 28–29; fan-shaped caecum well developed (Fig. 7F); rectum close to pallial genital glands in both sexes.
Female genitalia: Ovary lobate, starting 1.25–1.5 whorls below apex, comprising 0.5–1.0 whorls, eventually reaching stomach; bursa copulatrix pyriform, bursal duct entering antero-centrally.
Male genitalia: Testis starting 1.0–1.5 whorls below apex, comprising 0.75–1.0 whorls; penis without pigment.
Remarks: The species most similar to *F. torresiana* sp. nov. is *F. espiritusantoana* sp. nov. The latter has a higher number of denticles on M2 and a less pronounced size dimorphism than the former. In addition, *F. torresiana* sp. nov. has a more central origin of the bursal duct. Other conical species differ in having a defined opercular peg. *F. torresiana* sp. nov. would be the only species among Pacific Tateidae occurring on more than one island. However, there is some variation in terms of shell and opercular morphology among the populations from Toga and Hiu, which are 25 km distant from each other. Whether they are indeed conspecific has to be confirmed using molecular methods.

Fluviopupa titusi sp. nov.

Type material: holotype MNHN; paratypes MNHN (5).
Type locality: Hiu, Torres islands, Vanuatu. To5. Small permanent spring. 13.1552°S, 166.576°E. Coll. PB, 19.XI.2007.
Habitat and distribution: Spring on limestone. Only known from the type locality, on the east coast of Hiu Island.
Etymology: This species is dedicated to Titus Noel, customial chief and Vanuatu Kultural Senter Field Worker resident in Torres, who helped us in the field.

Description

Shell (Figs. 2I, 3I): Colourless, short-conical to pupiform, only 1.67 times higher than wide, whorls moderately convex; protoconch with 0.8 whorls; aperture ovate-pyriform, as high as wide.
Operculum: Attachment area without smear and peg.
External features: Epidermis without pigment, only eyes black.
Mantle cavity ($N = 1$ male): Ctenidium with 8 filaments; osphradium ovate-elongate, behind middle of ctenidium, about 1/2 length of ctenidium.
Digestive system ($N = 2$ males): Radula and stomach not prepared; rectum bending in pallial roof (Fig. 8C).
Male genitalia ($N = 2$): Testis starting 1.25 whorls below apex, comprising 0.75 whorls; penis without pigment.
Remarks: Together with *F. smolwan* sp. nov. described below this species is the smallest known from Vanuatu. It has a stouter appearance than *F. smolwan* sp. nov. and has pigmented, thus functional eyes in contrast to the latter.

Fluviopupa smolwan sp. nov.

Type material: holotype MNHN.
Type locality: Hiu, Torres islands, Vanuatu. To5. Small permanent spring. 13.1552°S, 166.576°E. Coll. PB, 19.XI.2007.
Habitat and distribution: Only known from the type locality, on the east coast of Hiu Island.
Etymology: Smolwan means small in Bislama, the lingua franca of Vanuatu.

Description

Shell (Fig. 2J): Colourless, slender conical, 1.88 times higher than wide, whorls convex; no protoconch data available; aperture ovoid, slightly higher than wide.
External features: Epidermis without pigment, no eyes observed.
Digestive system: No radula and stomach data available; rectum bending in pallial roof.

Remarks: *F. smolwan* sp. nov. is more slender than the similar-sized *F. titusi* sp. nov. and is also distinguished by the lack of eyes. The species is certainly stygobiont and the single specimen found has been washed out of its habitat.

Multivariate comparison of shell morphology

In a discriminant analysis across seven species—*F. snel* sp. nov. and *F. smolwan* sp. nov. were excluded because of their small sample size and *F. priei* sp. nov. could not be directly compared because of its detached final whorl(s)—including *F. espiritusantoana* sp. nov. and *F. torresiana* sp. nov. represented by each two populations, the species allocations were confirmed. With Wilk's $\lambda = 0.0193$, $df_1 = 40$, $df_2 = 687.1$ and $F = 25.33$, the null hypothesis of identical samples was rejected with $P \ll 0.001$. Inspecting the CVA (Fig. 11), this result might be largely attributed to the influence of *F. titusi* sp. nov., which is much smaller than the remaining species. However, in Bonferroni-corrected Hotelling's pairwise post hoc comparisons, only conspecific populations were not significantly differentiated (data not shown).

Discussion

The tateids from Vanuatu fit very well into the dispersal scenario across the Pacific outlined in the "Introduction" section (Fig. 12). The general Bauplan and in particular the white opercular smear, the membranous neck region of the radular lateral tooth

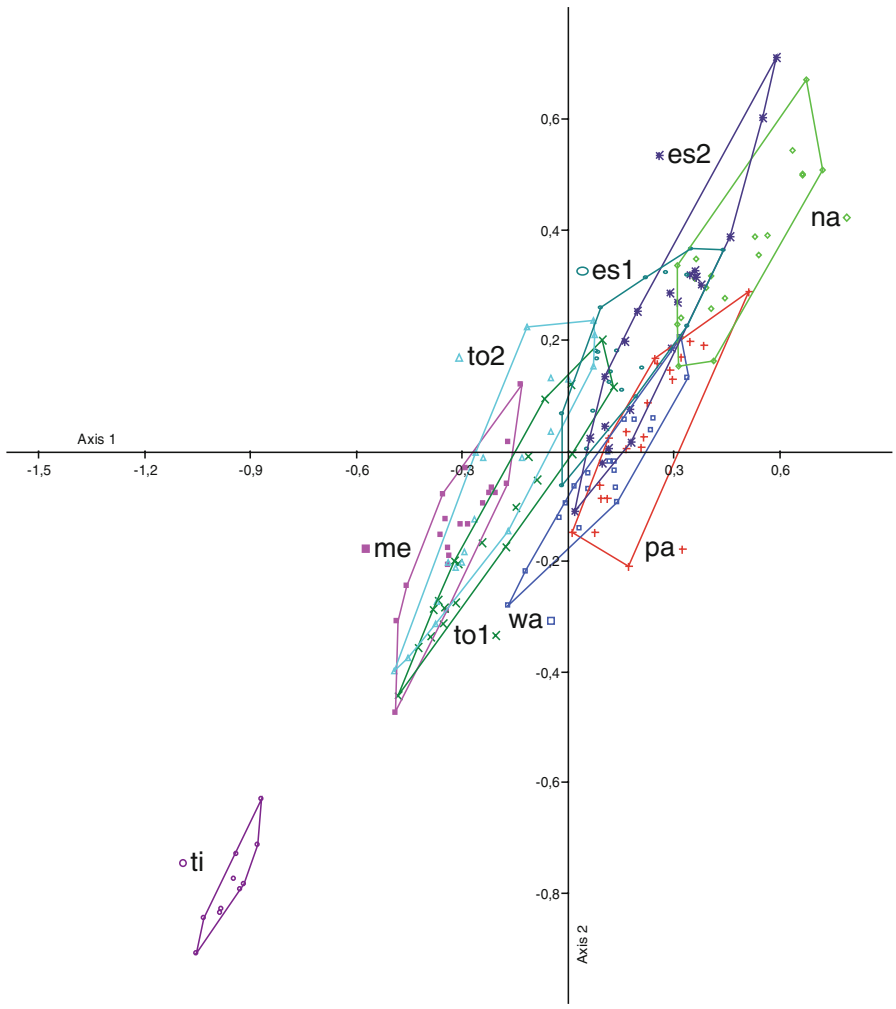

Fig. 11 Canonical variates analysis based on five shell measurements. Dominant variables were sw, ah, aw, bww on Axis 1 and sh on Axis 2, respectively (see Table 1 for abbreviations). *me*, *F. melissae* sp. nov.; *wa*, *F. walterlinii* sp. nov.; *ti*, *F. titusi* sp. nov.; *es1*, *F. espiritusantoana* sp. nov., type locality; *es2*, *F. espiritusantoana* sp. nov., SAPB1; *na*, *F. narii* sp. nov.; *pa*, *F. pascali* sp. nov.; *to1*, *F. torresiana*, type locality; *to2*, *F. torresiana*, To2

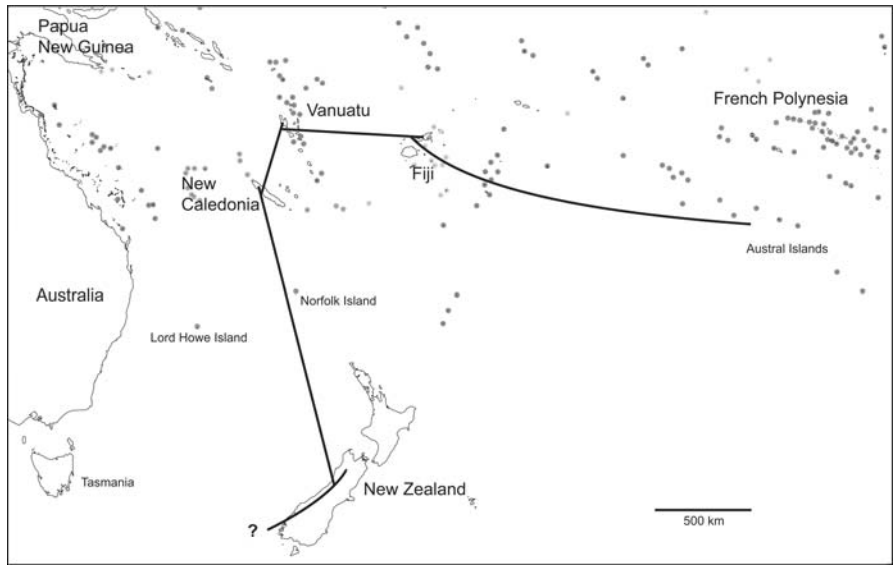

Fig. 12 Cladogram plotted onto the South Pacific exemplifying the phylogeographic hypothesis developed based on morphological data assuming monophyly of the extant species

as well as the presence of a fan-shaped caecum on the proximal end of the stomach confirm their relationship to the previously investigated species from New Zealand, New Caledonia, Fiji and the Austral Islands (Haase & Bouchet, 1998; Haase et al., 2005, 2006; Haase, 2008). The presence of the fan-shaped caecum at least in two species (*Hemistomia rusticorum* Haase & Bouchet, 1998 and *Caledoconcha mariapetrae* Haase & Bouchet, 1998) has now also been confirmed for the New Caledonian *Hemistomia*-clade, which has not been reported previously (Haase & Bouchet, 1998). *H. fallax* Haase & Bouchet, 1998 as well as *Kankyella gentilsiana* (Crosse, 1874) showed structures, which may be interpreted as rudiments of a caecum. An addditional eight species re-investigated (*H. caledonica* Crosse, 1872, *H. fabrorum* Haase & Bouchet, 1998, *H. minor* Haase & Bouchet, 1998, *H. yuaga* Haase & Bouchet, 1998, *Leiorhagium cathartes* Haase & Bouchet, 1998, *L. kavuneva* Haase & Bouchet, 1998, *L. montfaouense* Haase & Bouchet, 1998 and *L. mussorgskyi* Haase & Bouchet 1998) lacked any trace of a caecum. These findings suggest that the fan-shaped caecum was present in the ancestor of the New Caleonian species and was lost probably in parallel in several lineages. Another characterestic state linking the species from New Caledonia, Vanuatu, Fiji and the Austral Islands is the blunt penis. Although not present in all the species, this peculiar shape suggests a single origin and subsequent parallel loss. The simple opercular peg apparently in a stage of reduction assuming homology with the elaborate formations observed in New Caledonia (Haase & Bouchet, 1998) places the species from Vanuatu not only geographically but also evolutionarily in between the relatives from New Caledonia and Fiji, where pegs have not been observed (Haase et al., 2006). In conclusion, we do see anatomical evidence for an evolutionary scenario that links the Pacific islands in a stepping stone-like fashion (Fig. 12). However, considering the general paucity of anatomical characters in rissooidean freshwater gastropods and the pervasive homoplasies, this scenario should probably only be regarded as a hypothesis that needs to be tested using molecular data.

Although our and earlier collecting efforts on the archipelago of Vanuatu were far from comprehensive, the diversity pattern conforms to the general pattern of freshwater rissooideans on other islands and in other parts of the world. Only two species seem to have a wider distribution, and only three localities harboured more than one species. All *Fluviopupa* species seem to be restricted to springs or little streams not far from the spring and have never been collected in larger rivers. One species (*F. priei* sp. nov.) may be exclusively stygobiont (troglobitic). All the species were exclusively collected on limestone or marl limestone substrate, except *F. espiritusantoana* sp. nov. which was found on both limestone and volcanic substrate.

None of these species seems to be threatened at present, and most of them are living in relatively undisturbed habitats. In the Torres islands, they live at sea level, a remarkable situation illustrating the state of preservation of these islands. At To2, *F. torresiana* sp. nov. was found in a spring which is used by local people to get drinking water. Similarly, the only known locality of *F. pascali* sp. nov. is a spring on the edge of an irrigated taro field, i.e. a disturbed habitat. In both cases, the current impact of human activity does not seem to be incompatible with *Fluviopupa* survival. No species of *Fluviopupa* was found in the eastern part of Santo, which is the most degraded by agriculture, but it is not known whether they used to thrive in this area. Nonetheless, we propose the following categorization under the IUCN Red List criteria (IUCN, 2001): None of the Vanuatu *Fluviopupa* satisfies the conditions to be classified as either EN (endangered) or CR (critically endangered), as no decline of either population size or range is known and can even be suspected. However, as all but *F. espiritusantoana* sp. nov. and *F. torresiana* sp. nov., which are certainly of Least Concern (LC), occur on less than 20 km^2 and are known from five or less localities, they can be classified as Vulnerable (VU D2). However, it should be emphasized that most species have been found at single sites and *F. smolwan* sp. nov. and *F. titusi* sp. nov. in particular are endemic in a single spring in already disturbed habitat. Therefore, it is well imaginable that they become extinct by a single pollution or destruction event, i.e. going from Vulnerable to Extinct without passing through EN and CR status. Similar human-caused extinction events are documented for a number of crenobiontic gastropods (e.g. Haase, 1996). As a consequence, we strongly endorse to extend the criteria for EN by consideration of the scale of potential human impact or stochastic natural events relative to the habitat size of small species with restricted ranges such as many crenobiontic organisms.

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References

Ancey, C. F., 1905. Remarks on some land and fresh-water shells from the New Hebrides, with description of new species. Nautilus 19: 42–46.

Bonneville, A. R., R. Le Suavé, L. Audin, V. Clouard, L. Dosso, P.-Y. Gillot, P. Janney, A. Jordahl Kelsey & K. Maamaatuaiahutapu, 2002. Arago Seamount: the missing hot spot found in the Austral Islands. Geology 30: 1023–1026.

Haase, M., 1996. The radiation of spring snails of the genus *Belgrandiella* in Austria (Mollusca: Caenogastropoda: Hydrobiidae). Hydrobiologia 319: 119–129.

Haase, M., 2005. Rapid and convergent evolution of parental care in hydrobiid gastropods from New Zealand. Journal of Evolutionary Biology 18: 1078–1086.

Haase, M., 2008. The radiation of hydrobiid gastropods in New Zealand: a revision including the description of new species based on morphology and mtDNA sequence information. Systematics and Biodiversity 6: 99–159.

Haase, M. & P. Bouchet, 1998. Radiation of crenobiontic gastropods on an ancient continental island: the *Hemistomia*-clade in New Caledonia (Gastropoda: Hydrobiidae). Hydrobiologia 367: 43–129.

Haase, M. & P. Bouchet, 2006. The radiation of hydrobioid gastropods (Caenogastropoda, Rissooidea) in ancient Lake Poso, Sulawesi. Hydrobiologia 556: 17–46.

Haase, M., O. Gargominy & B. Fontaine, 2005. Rissooidean freshwater gastropods from the middle of the Pacific: the genus *Fluviopupa* on the Austral Islands (Caenogastropoda). Molluscan Research 25: 145–163.

Haase, M., W. F. Ponder & P. Bouchet, 2006. The genus *Fluviopupa* Pilsbry, 1911 from Fiji (Caenogastropoda, Rissooidea). Journal of Molluscan Studies 72: 119–136.

Hammer, Ø., D. A. T. Harper & P. D. Ryan, 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4: 9 pp. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Hershler, R. & G. Longley, 1986. *Hadoceras taylori*, a new genus and species of phreatic Hydrobiidae (Gastropoda: Rissoacea) from South-Central Texas. Proceedings of the Biological Society of Washington 99: 121–136.

Hershler, R. & F. G. Thompson, 1992. A review of the aquatic gastropod subfamily Cochliopinae (Prosobranchia: Hydrobiidae). Malacological Review Supplement 5: 1–140.

IUCN, 2001. IUCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission. IUCN Gland, Switzerland and Cambridge, UK, pp. ii + 30.

Kroenke, L. W., 1996. Plate tectonic development of the western and southwestern Pacific: mesozoic to the present. In Keast, A. & S. E. Miller (eds), The Origin and Evolution of Pacific island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes. SPB Academic Publishing, Amsterdam: 19–34.

Nation, J. L., 1983. A new method using hexamethyldisilazane for preparation of soft insect tissues for scanning electron microscopy. Stain Technology 58: 347–351.

Ponder, W. F., 1981. *Posticobia norfolkensis* (Sykes), an apparently extinct fresh-water snail from Norfolk Island (Gastropoda: Hydrobiidae). Proceedings of the Linnean Society of New South Wales 105: 17–21.

Ponder, W. F., 1982. Hydrobiidae of Lord Howe Island (Mollusca: Gastropoda: Prosobranchia). Australian Journal of Marine and Freshwater Research 33: 89–159.

Rex, M. A. & K. J. Boss, 1976. Open coiling in recent gastropods. Malacologia 15: 289–297.

Solem, A., 1959. Systematics of the land and freshwater mollusca of the New Hebrides. Fieldiana Zoology 43: 1–359.

Starmühlner, F., 1976. Beiträge zur Kenntnis der Süsswasser-Gastropoden pazifischer Inseln. Annalen des Naturhistorischen Museums Wien 80: 473–656.

Verduin, A., 1982. How complete are dagnoses of coiled shells of regular build? A mathematical approach. Basteria 45: 127–142.