European Journal of Taxonomy 968: 275–294
https://doi.org/10.5852/ejt.2024.968.2737
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ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2024 · Schröder O. *et al.*

Research article

urn:lsid:zoobank.org:pub:C38A1E04-4541-4BFD-92E7-DB615BE736CF

A new genus and species of spring snails (Caenogastropoda, Tateidae) from the ultramafic South of New Caledonia

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[3] urn:lsid:zoobank.org:author:FC9098A4-8374-4A9A-AD34-475E3AAF963A
[4] urn:lsid:zoobank.org:author:8CE4B347-14C5-464F-99C4-DE2263FC55D5

Abstract. During an expedition in 2016, a rich fauna of freshwater gastropods of the family Tateidae Thiele, 1925 was discovered on the ultramafic terrains of the Southeast of New Caledonia (NC). Hitherto, only three of the 62 known NC family members were reported from this type of bedrock. With less than 1.5 mm in length, many of the new species are particularly small. In order to establish a methodological setup for the description and phylogenetic analyses of these new species, we here describe *Viriiella touaouroua* gen. et sp. nov. and assess its relationships based on three gene fragments. *Viriiella* is morphologically well defined and resembles *Fluviopupa* Pilsbry, 1911 not present in NC. In the phylogenetic analyses, though, *Viriiella* appeared as a member of the *Hemistomia*-clade, the NC tateids occurring on non-ultramafic terrain. However, *Viriiella* had the longest branch and, sister group to different genera in maximum likelihood and Bayesian analyses, its position was unstable, probably an artifact due to long-branch attraction. Considering that *Viriiella* does not share the defining character states of *Hemistomia* s. lat., it may well be possible that inclusion of more related genera will show that the new taxa share a most recent common ancestor with the *Hemistomia*-clade, but as sister group.

Keywords. Long-branch attraction, micro-computed tomography, monotypy, ophiolitic nappe, ultrabasic rocks.

Schröder O., Schächinger P.M., Bouchet P. & Haase M. 2024. A new genus and species of spring snails (Caenogastropoda, Truncatelloidea, Tateidae) from the ultramafic South of New Caledonia. *European Journal of Taxonomy* 968: 275–294. https://doi.org/10.5852/ejt.2024.968.2737

Introduction

New Caledonia is regarded as one of the global hotspots of biodiversity, with a high proportion of endemic species (Myers *et al.* 2000; Kier *et al.* 2009; Caesar *et al.* 2017; Veron *et al.* 2019). The uniqueness of the biota is largely a consequence of the geology and the geological history of New Caledonia (Murienne 2009), which is an archipelago dominated by Grande Terre situated at the northern end of the largely sunken Gondwanan fragment Zealandia that separated from Australia about 80 Mya (Mortimer *et al.* 2017; Maurizot & Campbell 2020). A geological peculiarity are large portions of ultramafic rocks that cover about a third of the island's surface, especially in the Southeast – in New Caledonia referred to as "le Grand Sud" (Grandcolas *et al.* 2008; Folcher *et al.* 2015). According to Downes (2021), rocks are referred to as 'ultramafic' if they contain at least 90% mafic minerals, i.e., minerals comprising of substantial amounts of magnesium and iron. Many ultramafic rocks are also ultrabasic, meaning SiO_2 makes up less than 45% of their mass (Downes 2021). The ultramafic rocks of New Caledonia are the relics of a subduction event at the end of the Eocene, during which oceanic crust, the so called 'ophiolitic nappe' (Aitchison *et al.* 1995), was thrust across continental crust and reached the surface with the re-emergence of the island (Aitchison *et al.* 1995; Pelletier 2007; Maurizot & Campbell 2020). Around 50 % of the endemic flora of New Caledonia can be found on ultramafic soils, thus their contribution to the number of endemics is disproportionally high (Isnard *et al.* 2016). Ultramafic rocks contain, among other metals, a high amount of nickel, a metal that is extensively mined in New Caledonia, making the island the world's fourth largest exporter in 2021 (U.S. Geological Survey 2022). Mining, the increasing frequency of fires (Pascal *et al.* 2008), and land cover change (Haase & Zielske 2015) probably comprise the most imminent threats to the unique biota of New Caledonia.

In 2016, the two senior authors (MH, PB) surveyed these ultramafic terrains of the Southeast of New Caledonia for gastropods of the family Tateidae Thiele, 1925 during an expedition dedicated to the freshwater fauna of New Caledonia (https://www.mnhn.fr/fr/la-planete-revisitee-en-nouvelle-caledonie). Tateidae are a family of largely minute snails which mainly occur in freshwaters of Australia, including Tasmania and Lord Howe Island, New Guinea, Sulawesi, New Zealand, New Caledonia, Vanuatu, Fiji, the Austral Islands, and South America (Zielske *et al.* 2017; Ponder 2019). Many species dwell in springs or even groundwater and have very restricted ranges (Ponder 2019). The degree of micro-endemism is often astonishing (for New Caledonia see Haase & Bouchet 1998). In New Caledonia, 62 species of tateids have been described. Fifty-nine of them belong to what we dubbed the *Hemistomia*-clade (Haase & Bouchet 1998; Haase & Zielske 2015) of which all but one occur on non-ultramafic bedrock. Two species of the genus *Heterocyclus* Crosse, 1872 live in the large lakes of the Plaine des Lacs in the ultramafic Southeast and one wrongly ascribed to *Fluviopupa* Pilsbry, 1911 (Johl & Haase, unpublished data) is a crenobiont from the Ile des Pins (Franc 1957; Starmühlner 1970). In the 2016 survey, a considerable number of undescribed species, many of them with shell heights of less than 1.5 mm even for tateids very small, were discovered. As a pilot study for establishing a methodological setup for the description and phylogenetic analyses of these new species we here describe one of them in morphological/anatomical detail and try to assess its relationships with respect to the *Hemistomia*-clade and other Austral-Asian and Pacific tateids based on Sanger sequencing of three gene fragments.

Material and methods

Collection

Snails were collected in a stream draining a swamp below a slope dominated by Niauli trees on the western bank of the road in Touaourou South of Yaté washing Characeae Gray and leaves in a white tray (Figs 1–2). They were fixed in 96% ethanol and kept at 4°C upon return to our lab in Greifswald. The maps of Fig. 1 were created in ArcGIS 2.7.3 (ESRI: Environmental Systems Research Institute, Redlands, CA). The geological layer was made available by the Gouvernement de la Nouvelle-Calédonie/DIMENC/SGNC-BRGM (2010).

Morphology and anatomy

Twenty-two adult shells were photographed under a Zeiss SteREO Discovery V20 dissecting microscope with a Zeiss Axiocam 305 Color camera and measured by the first author using AxioVision 4.8.2.SP2. Shell height (SH) and aperture height (AH) were measured parallel to the coiling axis and the width of shell (SW), aperture (AW) and body (=penultimate) whorl (BWW) perpendicular to it. Photographs and measurements were taken twice with an interval of one week in order to control for repeatability. Whorls were counted to the nearest eighth of a whorl according to Kearney & Cameron (1979). Normal distribution was tested with the Shapiro-Wilk test. As a consequence, the measurement series of SH, SW, and AH were compared with a Wilcoxon signed-rank test and AW and BWW with a paired t-test. All tests were executed in R ver. 4.3.2 (R Development Core Team 2015). All comparisons were not

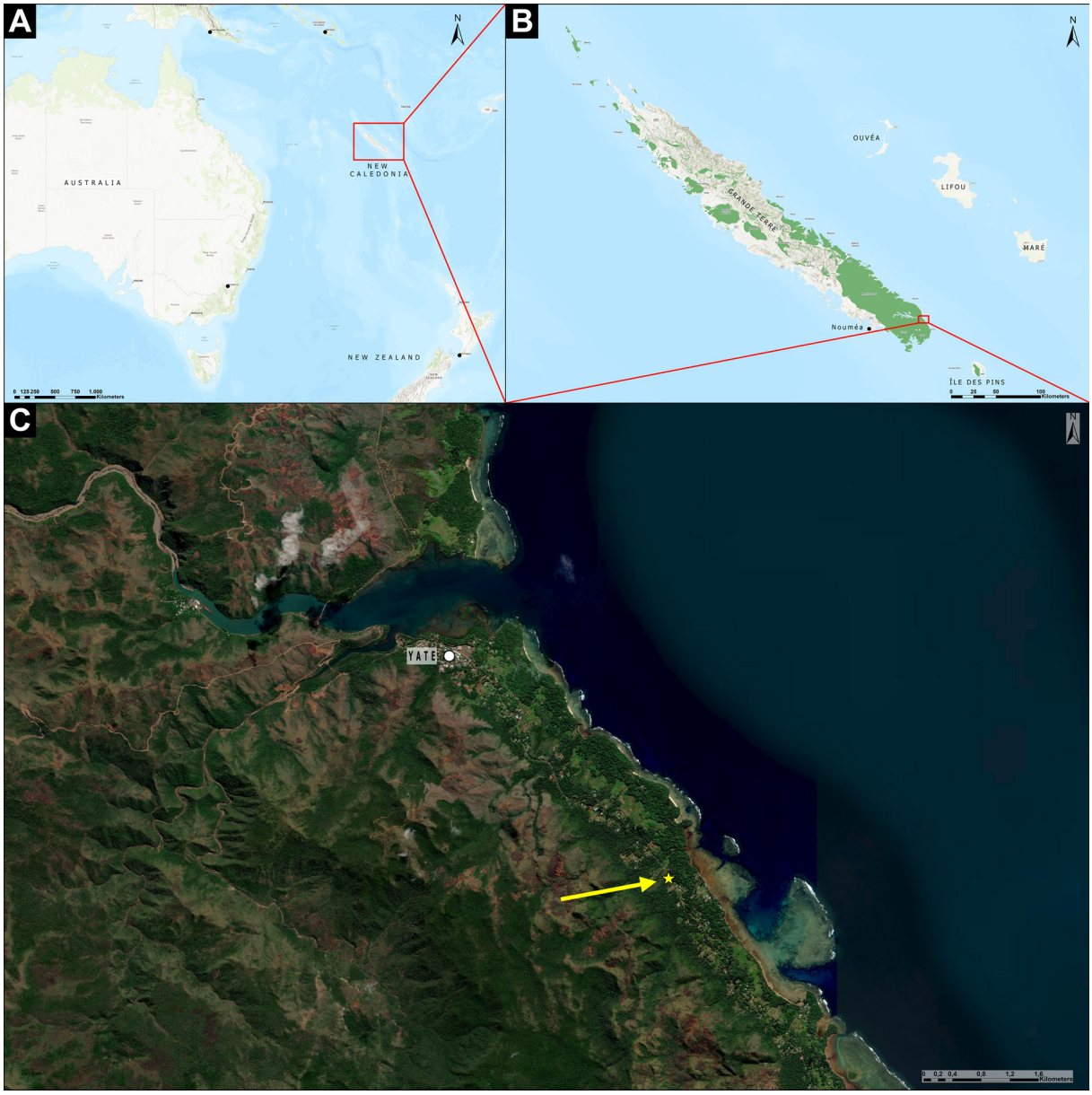

Fig. 1. Map showing the type locality of *Viriiella touaouroua* gen. et sp. nov. **A**. Southwest Pacific. **B**. New Caledonia with areas of ultramafic base rock indicated in green. **C**. Type locality Touaourou (arrow and asterisk).

significant ($p > 0.05$), hence, the procedure was consistent. The means of both series were used in the description.

The anatomy was investigated using micro computed tomography (µCT) following Verhaegen & Haase (2021). Shells of five adult snails (three females, two males) were dissolved in 0.5M ethylenediaminetetraacetic acid (EDTA) over five days with one change of EDTA. EDTA-residues were removed by placing the snails in distilled water for ten minutes before contrasting overnight in a solution of 1% phosphotungstic acid in 70% ethanol. For scanning in an Xradia Micro XCT-200 µCT at the Imaging Centre of the University of Greifswald, snails were individually placed in a plastic pipette tip filled with 99% ethanol and sealed off with hot glue at both ends. The pipette tip was subsequently attached to a plastic rod that could be mounted into the µCT. Recordings were taken at 40 kV current, 8 W power and 20 times magnification. Image stacks were loaded into Amira 2021.2 (Thermo Fisher) to reconstruct the genital system. One female and one male were reconstructed in full detail and the results compared visually to the other stacks. Two color schemes were applied, one for normal-sighted people, and another one for readers with red-green color blindness (Katsnelson 2021; Supp. files 1–2).

Six specimens with shells dissolved in 1N hydrochloric acid were traditionally dissected in order to investigate the mantle cavity and prepare cephalic tentacles, penis, and radula for scanning electron microscopy (SEM). Shells as well were investigated with SEM after dissolving the periostracum in ca 2.5% sodium hypochlorite. Hypochlorite-cleaned radulae were placed in a drop of deionized water onto conductive aluminum foil glued onto a SEM stub. Heads with cephalic tentacles and penes of three males were dried in hexamethyldisilazane (Nation 1983) and mounted on a stub with conductive carbon adhesive tab together with the shells. All specimens were coated with gold/palladium using a Fisons Polaron 7640 sputter coater and investigated in a Zeiss EVO LS10 SEM at the Imaging Centre of the University of Greifswald.

Due to the small size of the new species, preparations were not always successful. The actual number of specimens investigated may therefore deviate from the numbers given here and are stated in the species description.

DNA sequencing

DNA was extracted from three specimens with the E.Z.N.A® Mollusc DNA Kit (Omega Bio-Tek Inc.) crushing the entire snail and according to the manufacturer's protocol except that we did not use liquid nitrogen for homogenizing the tissue. We amplified fragments of the mitochondrial cytochrome c oxidase subunit I gene (COI) using Folmer *et al.*'s (1994) primers LCO1490 and H1298, the latter modified at position 12 (A instead of G) by Zielske *et al.* (2011) and the 16S rRNA gene (16S) with primers 16Sar (Palumbi *et al.* 1991) and 16Sb (Edgecombe *et al.* 2002; Palumbi *et al.*'s (1991) 16Sbr did not work), as well as of the nuclear 18S rRNA with primers 18Sf and 18Sr (Holland *et al.* 1991).

Polymerase chain reactions (PCR) were performed in a total volume of 25 µL for COI and 16S rRNA and 11 µl for 18S rRNA. For the mitochondrial genes, the reaction mixes consisted of 2.5 µl buffer, 2 µl MgCl2 (50 mM stock), 0.5 µl dNTPs (10 mM stock), 1 µl BSA (1% stock), 1 µl of each primer, 0.1 µl Taq (Bioline), water, and 20–80 ng DNA. For 18S rRNA, the mix contained 4.6 µL of HS MyTaqTM RedMix (Bioline), 0.2 µl of each primer, 5 µl water, and 20–80 ng DNA. The temperature profile for COI was 3 min of initial denaturation at 95°C followed by 40 cycles comprising 45 s denaturation at 95°C, 45 s annealing at 46°C, and 1 min extension at 72°C, and a final extension at 72°C for 5 min. For the rRNAs we ran touch-down protocols only differing in the annealing temperature: 1 min initial denaturation at 95°C, 10 cycles with 20 s denaturation at 95°C,

20 s annealing starting at 60°C and dropping by 1 degree in each cycle to 51°C for 16S rRNA and the same from 51 to 42°C for 18S rRNA, and 30 s extension at 72°C, then further 25 cycles consisting of 20 s denaturation at 95°C, 20 s of annealing, and 30 s extension at 72°C, and finally 10 min extension at 72°C.

PCR products were checked on a 1% agarose gel and purified with a mix of exonuclease I and shrimp alkaline phosphatase. For cycle sequencing we used the SupreDye v3.1 Cycle Sequencing Kit of AdvancedSeq and the PCR primers. The products were cleaned with magnetic beads using Beckman Coulter's Agencourt CleanSeq and sequenced on an ABI 3130xl Genetic Analyser (Applied Biosystems).

Phylogenetic analyses

The new sequences were edited in Geneious ver. 10.2.3 (https://www.geneious.com) and BioEdit 7.0.5.3 (Hall 1999). Since the three specimens differed at only a single position in the 16S gene, we selected one of them and aligned its sequences with those of 41 other tateids from Australia, the Austral Islands, Fiji, New Caledonia, New Zealand, Sulawesi, and Vanuatu as well as three beddomeiid (see Ponder *et al.* 2023) species as outgroups (Zielske *et al.* 2011; Zielske & Haase 2014a, 2014b; Zielske *et al.* 2017; see Table 1 for GenBank accession numbers) using MAFFT with the default settings (Katoh *et al.* 2019). The alignment was finally trimmed to 638 bp for COI, 550 bp for 16S rRNA, and 501 bp for 18S RNA. According to Xia *et al.*'s (2003) test for phylogenetic signal implemented in DAMBE 7 (Xia 2018), saturation of substitutions should not have been a problem. The three beddomeiids used as outgroup differed in base composition from the ingroup, though [Chi^2 test implemented in W-IQ-TREE (Chernomor *et al.* 2016; Trifinopoulos *et al.* 2016); $p < 0.05$]. We conducted partitioned maximum likelihood (ML) analyses in W-IQ-TREE and partitioned Bayesian analyses (BA) in MrBayes ver. 3.2.6 (Ronquist *et al.* 2012). For the former, the package's own ModelFinder (Kalyaanamoorthy *et al.* 2017) identified K3Pu+I+Γ for both, COI and 16S rRNA and K2P+I+Γ for 18s rRNA as best fitting models. For MrBayes, jModeltest 2.1.4 (Darriba *et al.* 2012) determined HKY+I+Γ for both mitochondrial partitions and SYM+I+Γ for the nuclear one. In W-IQ-TREE, robustness was assessed with 1000 ultrafast bootstrap replicates (Hoang *et al.* 2017). MrBayes was run for 2 Mio generations with every 1000th tree sampled, a burnin of 5000, and otherwise default settings. All diagnostics implemented in MrBayes indicated convergence of parameter estimates.

Fig. 2. Philippe Bouchet collecting *Viriiella touaouroua* gen. et sp. nov.

Table 1 (continued on next page). Species used in phylogenetic analyses and their GenBank accession numbers.

Species	COI	16S rRNA	18S rRNA
Austropyrgus niger (Quoy & Gaimard, 1834)	KT313290	KT313133	KT313166
Austropyrgus turbatus Ponder, Colgan, Clark & Miller, 1994	KT313291	KT313134	KT313167
Beddomeia krybetes Ponder & Clark, 1993	KT313292	KT313135	KT313168
Caldicochlea globosa Ponder, Colgan, Terzis, Clark & Miller, 1996	KT313293	KT313136	KT313169
Catapyrgus matapango Haase, 2008	KT313294	KT313137	KT313170
Crosseana melanosoma (Haase & Bouchet, 1998)	KJ490902	KJ490813	KT313206
Fluviopupa brevior (Ancey, 1905)	KC875084	KC875004	KT313171
Fluviopupa bula Zielske & Haase, 2014	KF939760	KF939677	KT313190
Fluviopupa dromodromo Zielske & Haase, 2014	KF939781	KF939698	KT313192
Fluviopupa espiritusantoana Haase, Fontaine & Gargominy, 2010	KC875095	KC875018	KT313175
Fluviopupa espiritusantoana Haase, Fontaine & Gargominy, 2010	KC875091	KC875011	KT313174
Fluviopupa gracilis pupa (Iredale, 1944)	KT313295	KT313138	KT313176
Fluviopupa herminae Zielske & Haase, 2014	KC875113	KC875042	KT313177
Fluviopupa irinimeke Haase, Ponder & Bouchet, 2006	KF939798	KF939715	KT313178
Fluviopupa jeanyvesi Haase, Gargominy & Fontaine, 2005	KT313296	KT313139	KT313179
Fluviopupa pascali Haase, Fontaine & Gargominy, 2010	KC875097	KC875022	KT313181
Fluviopupa raivavaeensis Haase, Gargominy & Fontaine, 2005	KT313297	KT313140	KT313183
Fluviopupa ramsayi royana (Iredale, 1944)	KT313298	KT313141	KT313184
Fluviopupa riva Zielske & Haase, 2014	KC875086	KC875006	KT313185
Fluviopupa rurutua Haase, Gargominy & Fontaine, 2005	KT313300	KT313143	KT313187
Fluviopupa seasea Haase, Ponder & Bouchet, 2006	KF939756	KF939673	KT313188
Fluviopupa torresiana Haase, Fontaine & Gargominy, 2010	KC875101	KC875029	KT313196
Fluviopupa tubuaia Haase, Gargominy & Fontaine, 2005	KT313302	KT313145	KT313198

Table 1. Continued.

Species	COI	16S rRNA	18S rRNA
Fluviopupa tunuloa Zielske & Haase, 2014	KF939793	KF939710	KT313194
Fluviopupa uka Zielske & Haase, 2014	KF939736	KF939653	KT313189
Fonscochlea accepta Ponder, Hershler & Jenkins, 1989	KT313303	KT313146	KT313199
Fonscochlea zeidleri Ponder, Hershler & Jenkins, 1989	AY622460	KT313148	KT313201
Halopyrgus pupoides (Hutton, 1882)	JX970616	KT313149	KT313202
Hemistomia cockerelli. Haase & Bouchet, 1998	KJ490853	KJ490768	KT313208
Hemistomia gemma gemma Ponder, 1982	KT313305	KT313150	KT313203
Hemistomia rusticorum Haase & Bouchet, 1998	KJ490836	KJ490755	KT313207
Kanakyella gentilsiana (Crosse, 1874)	KJ490914	KJ490825	KT313209
Leiorhagium kavuneva Haase & Bouchet, 1998	KJ490860	KJ490775	KT313211
Meridiopyrgus murihiku Haase, 2008	AY631086	KT313152	KT313212
Novacaledonia numee (Haase & Bouchet, 1998)	KJ490832	KJ490751	KT313210
Opacuincola delira Haase, 2008	KT313306	KT313154	KT313214
Phrantela daveyensis tristis Ponder & Clark, 1993	KT313307	KT313155	KT313215
Posticobia brazieri (E.A. Smith, 1882)	KT313309	KT313157	KT313217
Potamopyrgus estuarinus Winterbourn, 1971	AY631104	KT313158	KT313218
Rakiurapyrgus cresswelli (Climo, 1974)	KT313310	KT313159	KT313219
Sororipyrgus raki Haase, 2008	KT313311	KT313160	KT313221
Sulawesidrobia abreui Zielske, Glaubrecht & Haase, 2011	HM587351	HM587394	HM587420
Sulawesidrobia anceps Zielske, Glaubrecht & Haase, 2011	HM587346	HM587388	HM587417
Tatea huonensis (Tenison-Woods, 1876)	KT313312	JX970550	KT313222
Trochidrobia punicea Ponder, Hershler & Jenkins, 1989	KT313313	KT313161	KT313223
Victodrobia victoriensis Ponder & Clark, 1993	KT313314	KT313162	KT313224
Viriiella touaouroua gen. et sp. nov.	PP545377	PP545463	PP545464

Results

Systematic descriptions

Since the new genus is at this point monotypic, descriptions of both genus and species are in principle redundant. However, we restrict the description of the former to those characters and states which we assume to remain more or less invariant once more congeners might be discovered based on our experience with this group of gastropods (e.g., Haase & Bouchet 1998; Haase *et al.* 2005, 2006; Haase 2008; Zielske & Haase 2014a, 2014b). Reference to figures is only made in the species description.

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Family Tateidae Thiele, 1925

Genus ***Viriiella*** gen. nov. (by monotypy)
urn:lsid:zoobank.org:act:C856F38F-7BDC-4DD6-9B57-22E31943C654

Type species

Viriiella touaouroua sp. nov., by monotypy.

Diagnosis

Shell small (< 1.5 mm high), cylindrical to cylindro-conical, transparent, protoconch smooth; central tooth of radula with a single pair of basal cusps, lateral teeth with solid neck-region and square face; the operculum has neither smear nor peg in the attachment area; the stomach has no proximal caecum; the renal oviduct bends twice in opposite directions, first 180°, then 270° and bears distally a seminal receptacle; the bursa copulatrix is club-shaped and extends straight beyond the albumen gland; the penis is simple without glands or muscular appendages.

Etymology

Viriiella, feminine, is derived from 'virii', which means 'small' in nââ numèè, the language spoken in the region where the type species has been found.

Description

Shell. Small (< 1.5 mm high), cylindrical to cylindro-conical, transparent, periostracum practically colorless, protoconch smooth.

Operculum. Ovate, thin, yellowish, paucispiral, nucleus excentric, without smear or peg.

External features. Epidermis without pigment, eyes black, small.

Mantle cavity. Ctenidium with small number of filaments; osphradium ovate.

Digestive system. Typical taenioglossate radula with rhachis (= central), lateral, inner and outer marginal teeth; central tooth with a single, large pair of basal cusps; lateral tooth with solid neck and square face; stomach without proximal caecum; pallial rectal loop simple and wide.

Female genitalia. Ovary a simple sac; renal oviduct describing almost a triangle, bending first almost 180° backwards, descending almost straight and then bending forward, the descending part thickened, glandular, small receptaculum seminis arising anterior to these loops; bursa copulatrix elongate club-shaped extending straight behind albumen gland; capsule gland with two portions.

Male genitalia. Testis lobate, vas deferens entering prostate medio-ventrally, distal vas deferens originating on distal end of prostate; penis simple, without glands or lobes.

Remarks

Among tateid genera, *Viriiella* gen. nov. probably resembles most *Fluviopupa* occurring on Lord Howe Island and the archipelagos of Vanuatu, Fiji and the Australs with respect to the arrangement of the renal oviduct and the distal position of the seminal receptacle. However, the distal counter-clockwise loop of 270° seen in most *Fluviopupa* (e.g., Haase *et al.* 2005, 2006) is here at best insinuated. In *Fluviopupa*, the protoconch is wrinkled and not smooth, though the operculum may have a white smear, the central radular tooth bears two to five pairs of basal cusps instead of one, the neck region of the lateral tooth is membranous and not solid, and the face rectangular rather than square. From the genera of the New Caledonian *Hemistomia*-clade, *Viriiella* differs in the same shell and radular features. The operculum in *Hemistomia* Crosse, 1872, and allies, including *Leiorhagium* Haase & Bouchet, 1998, bears long pegs, and the proximal loop of the renal oviduct is bent anteriorly in *Leiorhagium*. The genetic and phylogenetic justification of the genus is presented below.

Viriiella touaouroua gen. et sp. nov.
urn:lsid:zoobank.org:act:18A13BF1-D46C-4A61-A0F8-17B86351C903
Figs 3–8

Diagnosis

Shell small, cylindrical to cylindro-conical, 1.8 to 2 times as high as wide, not more than four rather flat whorls; aperture semi-lunar, not extending far beyond the outline of the spire, lip continuous, slightly thickened, orthocline; umbilicus narrow; smooth protoconch with about 1.25 whorls.

Etymology

The epithetum refers to Touaourou, the name of the community of the type locality.

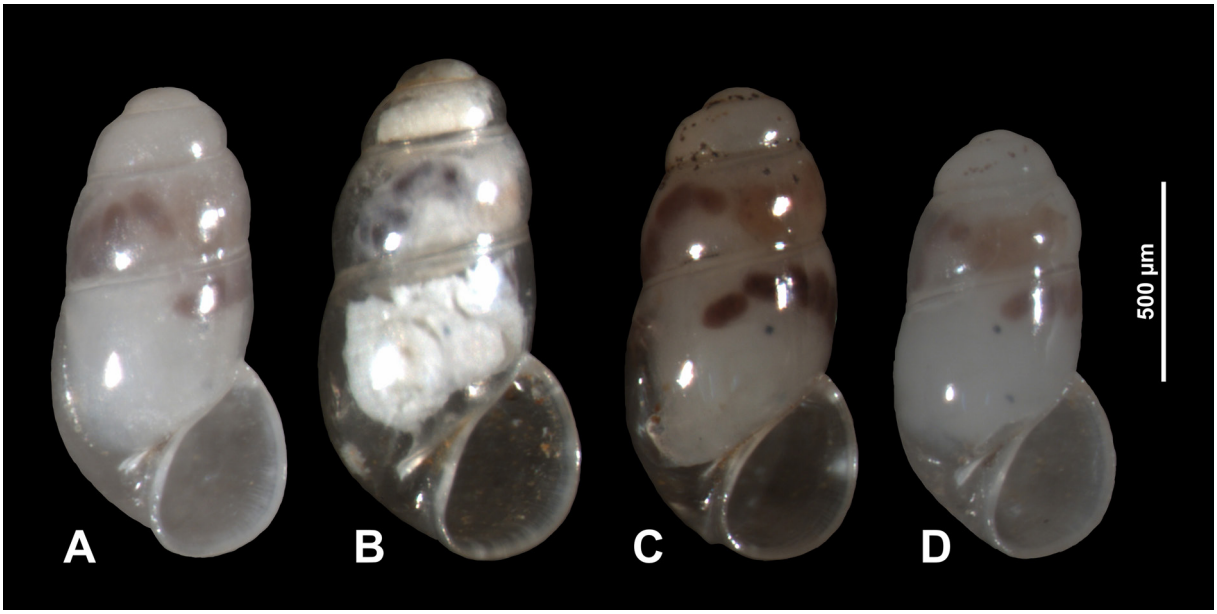

Fig. 3. Types of *Viriiella touaouroua* gen. et sp. nov. **A**. Holotype (MNHN-IM-2000-39460). **B-D**. Paratypes (MNHN-IM-2000-39461).

Type material

Holotype (Fig. 3A)
NEW CALEDONIA • Province Sud, district of Yaté, community Touaourou, small stream draining a swamp below a slope dominated by Niauli trees on the western bank of the road; 22°11′05.6″ S, 166°58′15.0″ E; 3 Nov. 2016; Bouchet and Haase leg.; MNHN-IM-2000-39460.

Paratypes (Figs 3B–D, 4)
NEW CALEDONIA • > 50 specimens; same collection data as for holotype; MNHN-IM-2000-39461.

Description

Shell (Figs 3–4; Table 2). Small (< 1.3 mm high), cylindrical to cylindro-conical, 1.8 to 2 times higher than wide, not more than four rather flat whorls; aperture semi-lunar, not extending far beyond the outline of the spire, lip continuous, slightly thickened, palatal thinner, apical angle acute, orthocline; umbilicus narrow; smooth protoconch with 1–1.25 whorls.

Operculum (N = 6). Ovate, thin, yellow, paucispiral, nucleus excentric, without smear or peg.

External features (N = 30). Epidermis without pigment; eyes black (Fig. 3), small; cephalic tentacles without ciliation.

Mantle cavity (N = 2). Ctenidium with 10 filaments; osphradium ovate.

Digestive system. Radula formula R: 4–5 1 4–5 / 1 1, L: 3–4 1 6–7, M1: 17–19, M2: 14–15 (N = 1; Fig. 5); stomach with two equally sized chambers, proximal without caecum (N = 5); pallial rectal loop in females wide adjoining the pallial oviduct, narrower in males, not adjoining the prostate (N = 30).

Female genitalia (N = 3; Fig. 6; Supp. file 1). Ovary a simple sack, starting at 1.5 whorls below the apex, comprising about ⅓ whorls, not reaching stomach; receptaculum seminis elongate, small with very short duct; bursa copulatrix large, elongate, club-shaped, reaching far behind albumen gland; anterior capsule gland much smaller than posterior one.

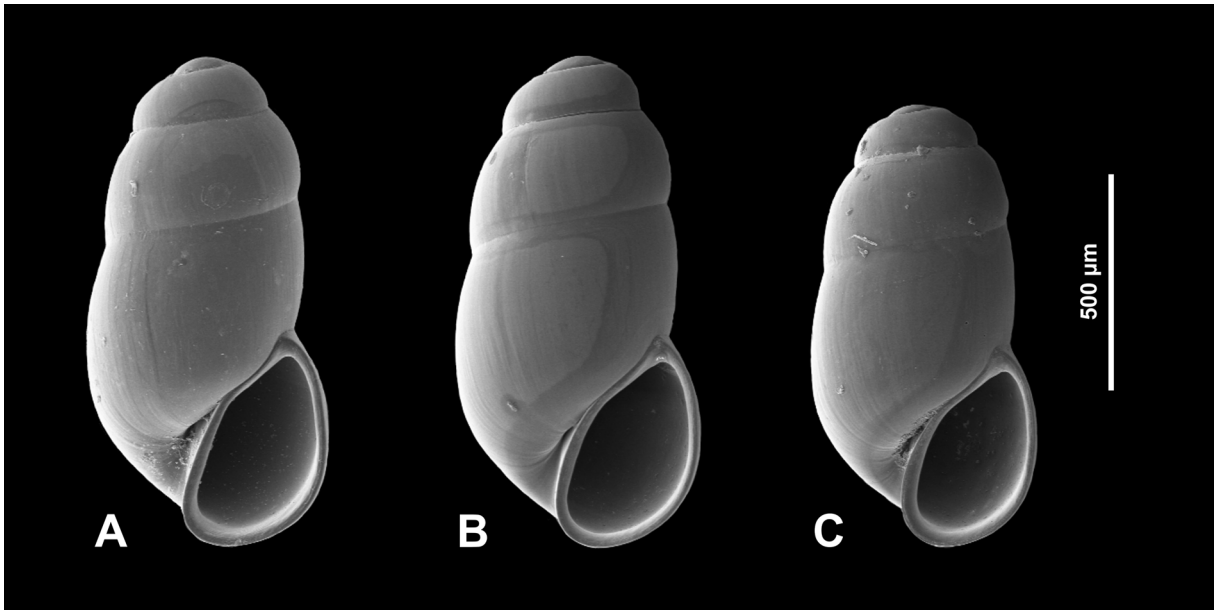

Fig. 4. SEM micrographs of paratypes of *Viriiella touaouroua* gen. et sp. nov. (MNHN-IM-2000-39461).

Male genitalia (N = 5; Figs 7–8; Supp. file 2). Testis lobate, starting 0.75 whorls below apex, comprising up to 0.75 whorls, almost reaching stomach; vesicula seminalis below testis fairly small; vas deferens proceeding along stomach reaching kidney-shaped prostate ventrally, distal vas deferens leaving prostate at anterior tip, initially straight then undulating before reaching penis; penis simple, elongate, slender, simple, distal end blunt.

Remarks

Viriiella touaouroua gen. et sp. nov. is the smallest freshwater gastropod so far known from New Caledonia. *Leiorhagium granum* Haase & Bouchet, 1998, and *L. granulum* Haase & Bouchet, 1998, both only known by their shells, thus with tentative generic allocation, measure at least 1.5 mm in height and are much more conical (Haase & Bouchet 1998). The type locality lies in a narrow strip of alluvial deposits between the coast and a range of ultramafic hills (see https://georep.nc/explorateur-cartographique provided by the Gouvernement de la Nouvelle Calédonie). These slope colluviums come from the dismantling of the peridotite massif located directly to the West of the type locality and form an aquifer at the foot of the massif (probably temporary and perched), which is fed by both the drainage of the massif and also by the creeks of the area (L. Russ, pers. com.).

Phylogenetic analyses

Both ML and BA yielded almost identical topologies (Fig. 9). The ingroup, i.e., Tateidae, received full support. A clade containing *Sulawesidrobia* Ponder & Haase, 2005 and *Tatea* Tenison-Woods, 1879 was sister group to all remaining taxa, which formed two larger clades, both with two subclades. One clade contained all species of *Fluviopupa* and all species from New Zealand, while in the other one, Australian genera were sister to all species from New Caledonia. Within clades, there were only two differences: 1) in the relationships of the New Zealand genera *Halopyrgus* Haase, 2008, *Potamopyrgus* Stimpson,

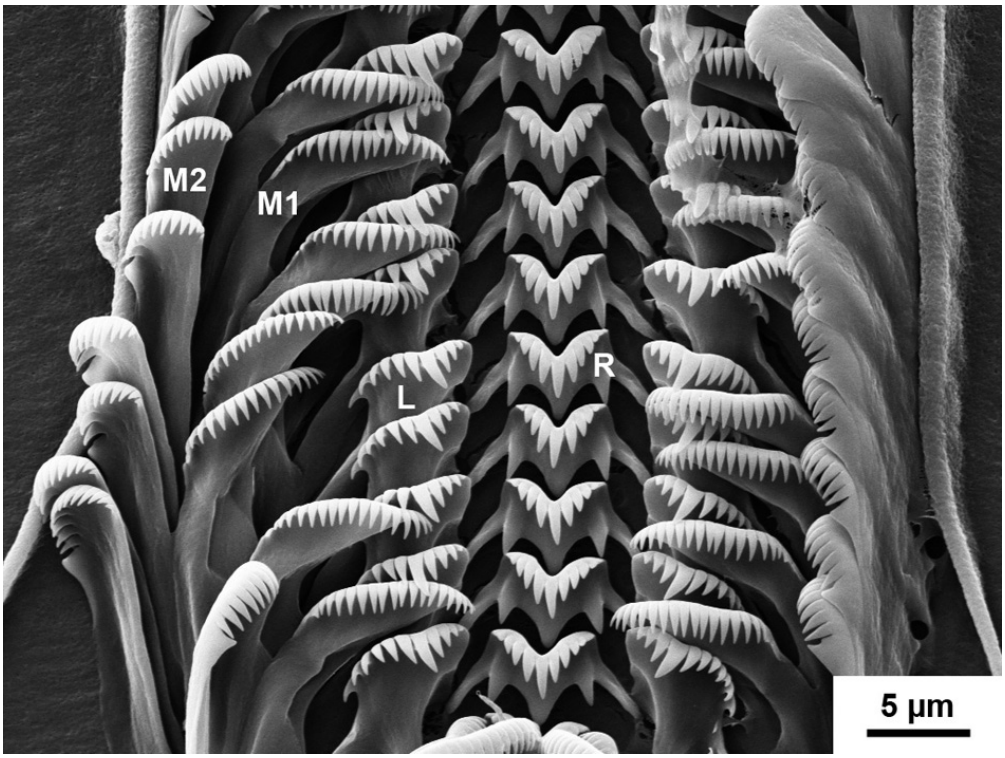

Fig. 5. Radula of *Viriiella touaouroua* gen. et sp. nov. Abbreviations: L = lateral teeth; M1 = inner marginal teeth; M2 = outer marginal teeth; R = rhachis (central) teeth.

1865, and *Sororipyrgus* Haase, 2008; 2) and most relevant for the present account, the relationship of the new genus *Viriiella*. In ML, *V. touaouroua* gen. et sp. nov. was sister species of *Crosseana melanosoma* (Haase & Bouchet 1998), in BA of *Leiorhagium kavuneva* Haase & Bouchet, 1998. Both relationships were only insignificantly supported. Some of the deeper nodes were not well supported, either.

Discussion

The new genus *Viriiella* gen. nov. has a number of apomorphies or an apomorphic combination of character states including the small, near cylindrical shell, the single pair of basal cusps on the central radular teeth, the square face of the lateral teeth, the lack of opercular pegs, the arrangement of the renal oviduct with its glandular, straightly descending portion, and the elongate, club-shaped bursa copulatrix. This combination of states justifies the introduction of the new genus. Some of these states appear similar in *Fluviopupa* from Lord Howe Island, Vanuatu, Fiji and the Austral Islands. However, relationships can rarely be inferred from morphology or anatomy in tateids or other families of similarly small species. This requires molecular phylogenetic analyses (Criscione & Ponder 2013; Wilke *et al.* 2013). In our analyses based on three gene fragments, *Viriiella* was associated with the New Caledonian taxa, a member of the so-called *Hemistomia*-clade (Haase & Bouchet 1998; Zielske & Haase 2015). It was either sister taxon to *Crosseana* (ML) or *Leiorhagium* (BA), but both relations were only poorly supported. Considering the morphological/anatomical differences to *Hemistomia* s. lat. it was somewhat surprising to see *Viriiealla* among the other New Caledonian genera. It is noteworthy, though, that *Viriiella* has the longest branch of all ingroup taxa and it is therefore, and because of the low node support, possible, that we see an artifact due to long-branch attraction (Felsenstein 1978). At this point, we would rather speculate that *Viriiella* possibly shares an immediate common ancestor with the *Hemistomia*-clade, thus will turn out to belong to the sister group, once congeneric species or more

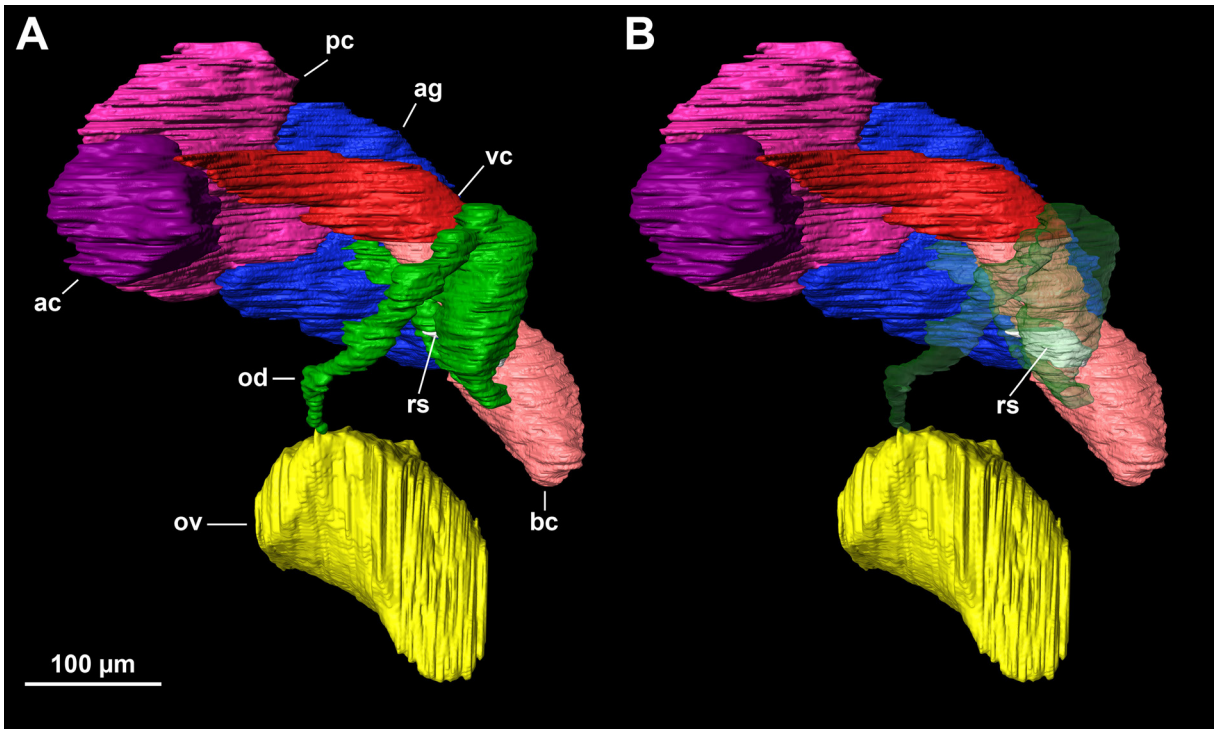

Fig. 6. Female genitalia of *Viriiella touaouroua* gen. et sp. nov. **A**. All parts opaque. **B**. Oviduct transparent revealing the seminal receptacle. Abbreviations: ac = anterior capsule gland; ag = albumen gland; bc = bursa copulatrix; od = oviduct; ov = ovary; pc = posterior capsule gland; rs = receptaculum semins; vc = ventral channel.

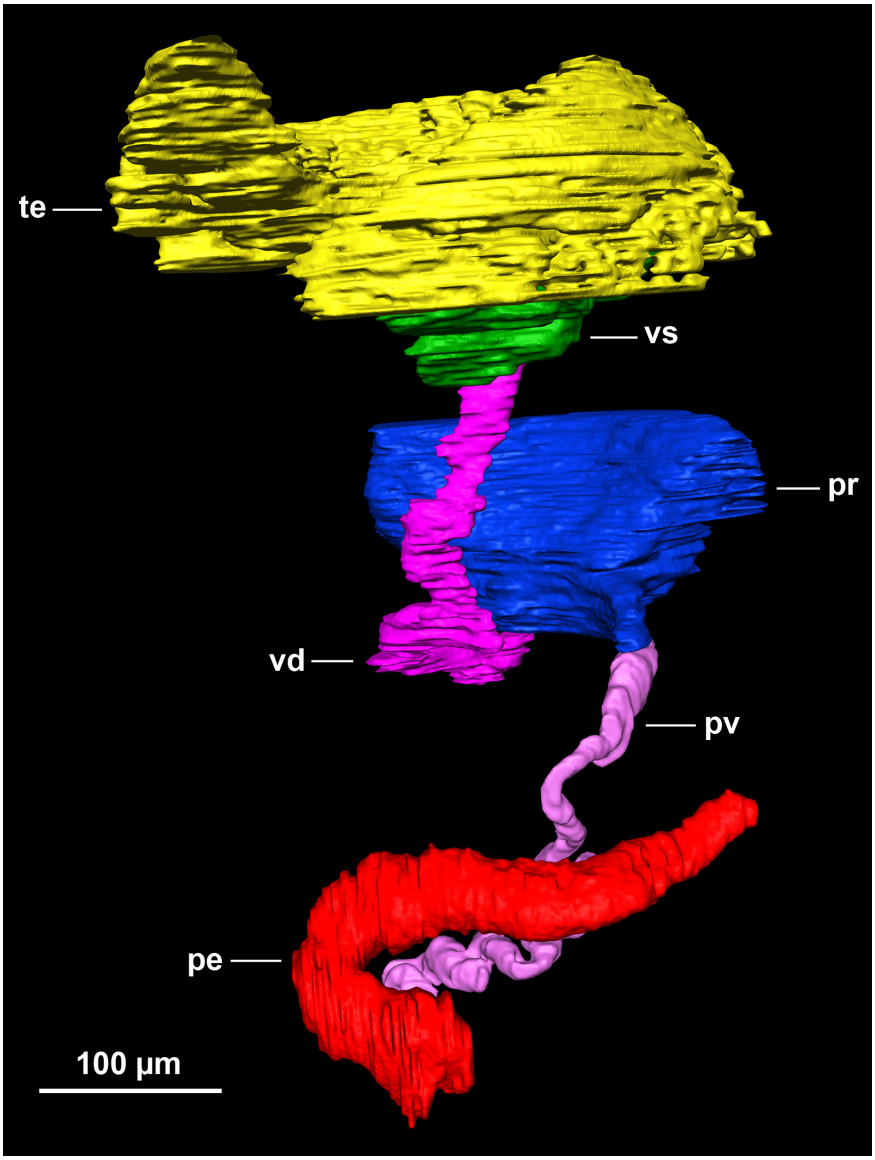

Fig. 7. Male genitalia of *Viriiella touaouroua* gen. et sp. nov. Abbreviations: pe = penis; pr = prostate; pv = pallial vas deferens; te = testis; vd = vas deferens; vs = vesicula seminalis.

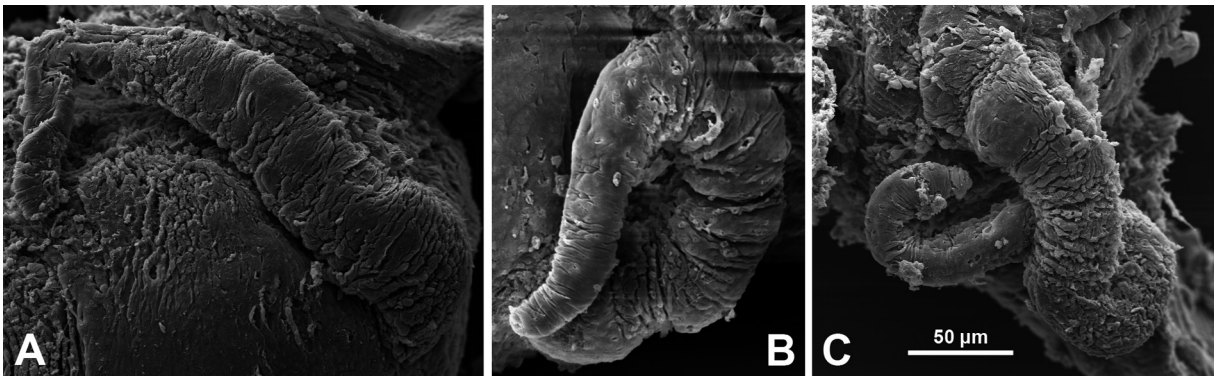

Fig. 8. Penes of three males of *Viriiella touaouroua* gen. et sp. nov.

closely related genera can be included. Also, inclusion of more genes may render the analyses more robust. In the analysis of Zielske *et al.* (2017), which used 28S rRNA and Histone 3 in addition to the three genes of our study, support was still unsatisfying, though suggesting that we probably have to aim for genomic analyses. In any case, the long branch in our present analysis also justifies the placement of the new species in a new genus.

Monotypic genera are certainly somewhat unsatisfactory from a cladist's point of view as they do not denote a more inclusive taxon, viz. clade (Platnick 1976). Platnick (1976) conceded, though, that monotypy may be due to the extinction or the outstanding discovery of congeneric species. In both cases, it is the degree of differentiation justifying the recognition of a monotypic genus. Here, taxonomic theory and practice are obviously in conflict. Only in case of the discovery of at least one congeneric species, which we expect to happen for *Viriiella*, will the monotypy be suspended.

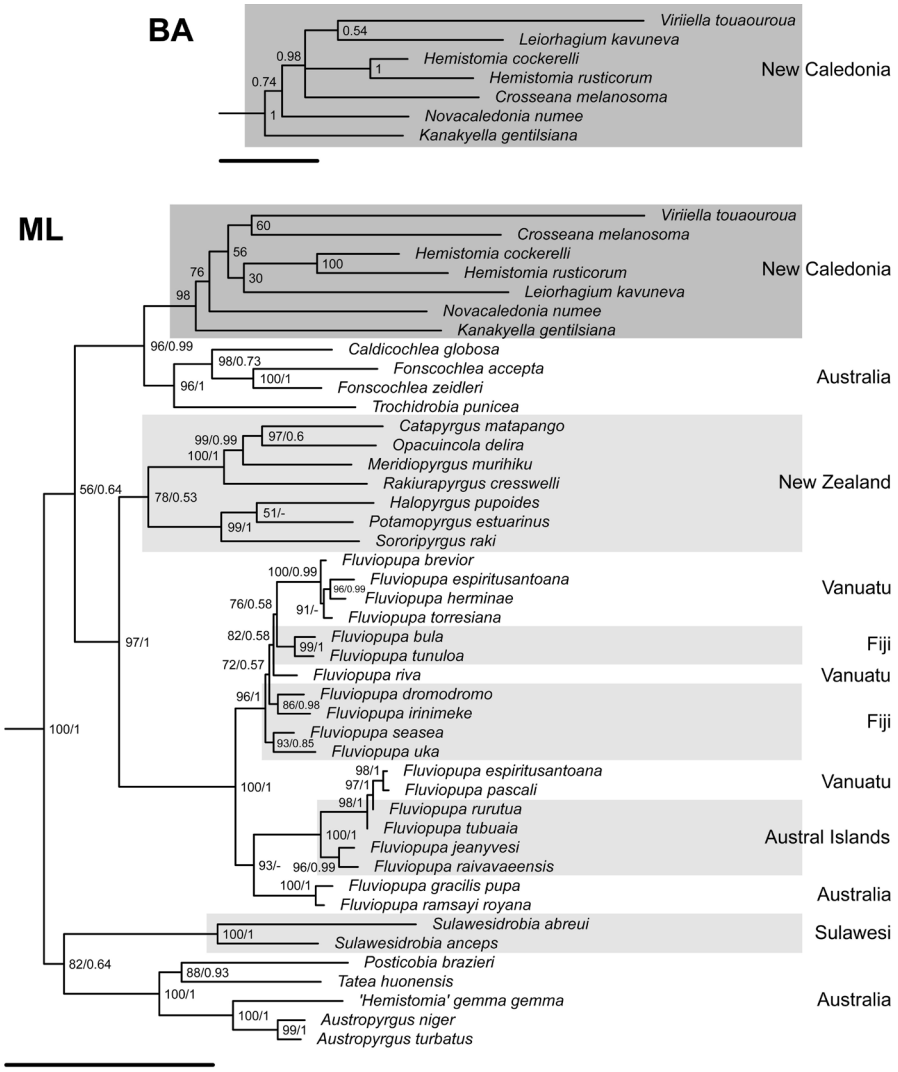

Fig. 9. Phylogenetic analyses. Maximum likelihood (ML) tree and section of Bayesian tree (BA). Support values are bootstrap support values/posterior probabilities; the latter are omitted for the New Caledonian taxa in the ML tree, the former in the Bayesian tree fragment. Scale bars = 0.1 substitutions/site.

Table 2. Measurements of 22 shells. Measurements in mm. Abbreviations: AH = aperture height; AW = aperture width; BWW = body whorl width; cv = coefficient of variation; max = maximum; min = minimum; sd = standard deviation; SH = shell height; SW = shell width; W = number of whorls.

	SH	SW	AH	AW	BWW	SH/SW	W
holotype	1.18	0.61	0.49	0.34	0.42	1.94	3.88
min	1.05	0.55	0.44	0.32	0.47	1.79	3.50
max	1.28	0.68	0.53	0.38	0.56	2.01	4.00
mean	1.18	0.62	0.49	0.35	0.62	1.90	3.78
sd	0.07	0.04	0.03	0.02	0.04	0.05	0.15
cv	5.69	6.10	5.83	4.67	6.10	2.63	3.96

Base frequencies of the mitochondrial genes of the outgroup taxa belonging to the family Beddomeiidae Ponder, Nimbs & Shea, 2023 differed from those of the ingroup Tateidae. Such heterogeneity may mislead phylogenetic analyses (Lockhart *et al.* 1994; Mooers & Holmes 2000; Jermiin *et al.* 2004), but the severity of the problem has been a matter of debate (van den Bussche *et al.* 1998; Rosenberg & Kumar 2003; Jermiin *et al.* 2004; Böckers *et al.* 2016). Anyway, the topology of the ingroup was identical to the analyses of Zielske *et al.* (2017), who, in addition to the three beddomeiids, also had an ascorhid and a pomatiopsid species in the outgroup and used two more nuclear gene fragments.

The small size of the new species was challenging for the anatomical investigations. Inner organs could only be investigated reconstructing µCT scans. However, also in the µCT image stacks, delicate structures like the proximal oviduct or the vasa deferentia were at times difficult to identify. As already discussed by Verhaegen & Haase (2021), this could possibly be improved by fixation with formalin, which, however, is impractical during expeditions. Considerably longer treatment with phosphotungstic acid over several days may also increase the contrast (Ziegler *et al.* 2018; Keklikoglou *et al.* 2019; Koç *et al.* 2019). However, for specimens too small to be dissected, which of course differs individually, µCT is a useful method for anatomical investigation. Another size dependent issue was the preparation of the radula as this has to be done under a dissecting microscope. Dissolving the surrounding tissue in sodium hypochlorite needs to be monitored to prevent the radula from being etched. The process has to be interrupted in time by transferring the radula into deionized water with a pipette. We normally repeat this three times – and this was when we lost several of these extremely small specimens. Therefore, we are considering to switch to a more costly but time-independent enzymatic approach to eliminate at least the time pressure (Holznagel 1998).

Acknowledgements

We are grateful to Lilian Horn (Greifswald) for sequencing. We thank the staff of the imaging center in Greifswald, Marie Hörnig and Stefan Bock, for operating tomograph and SEM, respectively. Geological expertise was generously provided by Lea Russ (DIMENC, Nouméa). The "Our Planet Reviewed" New Caledonia expedition (PIs: Philippe Bouchet, Olivier Pascal) was a joint project of Muséum national d'Histoire naturelle (MNHN) and Conservatoire d'espaces naturels (CEN) de Nouvelle-Calédonie [now Agence néo-Calédonienne de la Biodiversité (ANCB)]. It was funded through the mediation of Pascale Joannot by a cocktail of grants, mostly from the Gouvernement de la Nouvelle-Calédonie, Province Sud and Province Nord, and Office des Postes et Télécommunications (OPT), and with kind support from AirCalin and Toyota Nouvelle-Calédonie. The 2016 expedition operated under a permit issued by the Direction de l'Environnement (DENV) of Province Sud, and the organizers thank Isabelle Jurquet for facilitating its issuance. Fernand Ouetcho, President of the customary council of Truauru, is thanked for facilitating access to the study area. Our Planet Reviewed/La Planète Revisitée was a global initiative founded in 2007

by MNHN and Pro-Natura International (PNI). Comments by Canella Radea, two anonymous reviewers and the section editor Thierry Backeljau helped to improve the original version of the manuscript. MH acknowledges funding from the Deutsche Forschungsgemeinschaft, grant HA 4752/8-1.

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Manuscript received: 5 March 2024
Manuscript accepted: 9 July 2024
Published on: 18 November 2024
Topic editor: Magalie Castelin
Section editor: Thierry Backeljau
Desk editor: Chris Le Coquet-Le Roux

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Supplementary material

Supp. file 1. Female genitalia of *Viriiella touaouroua* gen. et sp. nov. with color scheme for red-green blind readers. **A.** All parts opaque. **B.** Oviduct transparent revealing the seminal receptacle. Abbreviations: ac = anterior capsule gland; ag = albumen gland; bc = bursa copulatrix; od = oviduct; ov = ovary; pc = posterior capsule gland; rs = receptaculum semins; vc = ventral channel. https://doi.org/10.5852/ejt.2024.968.2737.12557

Supp. file 2. Male genitalia of *Viriiella touaouroua* gen. et sp. nov. with color scheme for red-green blind readers. Abbreviations: pe = penis; pr = prostate; pv = pallial vas deferens; te = testis; vd = vas deferens; vs = vesicula seminalis. https://doi.org/10.5852/ejt.2024.968.2737.12559