



Morphological proxies for taxonomic decision in turrids (Mollusca, Neogastropoda): a test of the value of shell and radula characters using molecular data

Yuri I Kantor, Nicolas Puillandre, Baldomero M Olivera, Philippe Bouchet

► To cite this version:

Yuri I Kantor, Nicolas Puillandre, Baldomero M Olivera, Philippe Bouchet. Morphological proxies for taxonomic decision in turrids (Mollusca, Neogastropoda): a test of the value of shell and radula characters using molecular data. *Zoological science*, 2008, 25 (11), pp.1156-1170. 10.2108/zsj.25.1156 . hal-02458051

HAL Id: hal-02458051

<https://hal.science/hal-02458051>

Submitted on 28 Jan 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Morphological proxies for taxonomic decision in turrids
(Mollusca, Neogastropoda):
a test of the value of shell and radula characters using molecular data

Yu. I. Kantor*, N. Puillandre**, B. M. Olivera***, P. Bouchet**

*A.N. Severtzov Institute of Ecology and Evolution of Russian Academy of Sciences,
Leninski prosp. 33, Moscow 119071, RUSSIA, kantor@malaco-sevin.msk.ru;

**Muséum National d'Histoire Naturelle, 55, Rue Buffon, 75005 Paris, FRANCE,
puillandre@mnhn.fr, pbouchet@mnhn.fr;

*** Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, UT
84112, Utah, USA.

Abstract

The state of the art of turrid (= Turridae s.l.) systematics is that shells - when it includes the protoconch - are reliable species-level identifiers, but inadequate proxies for allocation to genera or subfamilies. Generally, the radula is used for allocation to a (sub)family, but the hypothesis that the radula is a more adequate proxy than the shell for relationships has not yet been tested by molecular data. Species of *Xenuroturris* may have drastically different radulae, with either "semi-enrolled" or "duplex" marginal teeth, although their shells are very similar or even almost indistinguishable. Molecular data confirm that specimens with different types of radulae constitute different species, but two species of a pair with respectively "semi-enrolled" and "duplex" teeth end up being not closely related. However, it is still unresolved whether species with "semi-enrolled" [= *Iotyrriis*] and "duplex" teeth [= *Xenuroturris*] form two supported monophyletic clades. *Iotyrriis devoizei* n.sp., and *I. musivum* n.sp., are described from Vanuatu, where they occur sympatrically with *I. cingulifera* and *Xenuroturris legitima*.

Key-words: shell, radula, COI, 28S, convergence, new species.

Running head: Morphological proxies for taxonomic decision in turrids

Introduction

Among the gastropod superfamily Conoidea, "Turridae" (sensu Powell, 1966) is the most speciose group of marine mollusks, with estimates of about 340 Recent valid genera and subgenera (Taylor *et al.*, 1993) and 4,000 named living species (Tucker, 2004). Tropical and deep-water faunas are reservoirs of vast numbers of undescribed species: Bouchet *et al.* (2004) estimated that 58-72% of the 1,726 "turrid" species sampled in New Caledonia is undescribed, and the real number of Recent "turrid" species worldwide may be in the 10-20,000 species range. As is the case with other specialist predators, the vast majority of species occur in low abundance. As a result of a very large number of species and small number of specimens, turrid systematics is intimidating, and turrids are much less studied

than other marine gastropods of comparable size. In the history of turrid systematics, shell, radula and anatomy have been given different value and emphasis at different taxonomical levels. Shells - when it includes the protoconch - are usually considered reliable species-level identifiers. However, convergence and homoplasy renders them much less reliable predictors of relationships at higher taxonomic levels (family, genus). For instance, shells of *Toxicochlespira* Sysoev and Kantor, 1990 (Conidae) strongly resemble representatives of *Cochlespira* Conrad, 1865 (Turridae) (Sysoev and Kantor, 1990); shells of *Strictispira* McLean, 1971 (Strictispiridae), are hardly distinguishable from those of many species of *Crassispira* Swainson, 1840 (Turridae, Crassispirinae) (Tippett, 2006); and the radula-less species *Cenodagreutes aethus* Smith, 1967 is said to be conchologically indistinguishable from the radulate *Raphitoma leufroyi* (Michaud, 1828) (both Conidae, Raphitominae).

At higher taxonomic levels, anatomical characters, especially foregut anatomy, are used to define subfamilies and families (Taylor *et al.*, 1993). However, as these are accessed only after time consuming serial histological sectioning and reconstruction (e.g. Kantor, 1990), the radula is routinely used as a proxy for the rest of foregut anatomy. Radulae have also the advantage that they can be extracted from animals with dried soft parts. Most of the currently recognized (Taylor *et al.*, 1993) subfamilies within Turridae and Conidae were erected (e.g., McLean, 1971), or subsequently redefined, on the basis of radular characters.

The state of the art of turrid systematics is thus based on the shell for species delimitation and/or identification, and on the radula for allocation to a (sub)family. These traditionally held beliefs were shattered when, during the course of routine radular preparations from New Caledonia "turrids", we found two distinct radular types in different specimens of what we initially classified as a single species, generally identified as *Xenuroturris cingulifera* (Lamarck, 1822), a species widely distributed in the Indo-Pacific (Powell 1964). These differences in radulae would be considered to imply at least generic rank when applying conventional taxonomic decision, but in this case the specimens involved have shells so similar that they would hardly be separated as discrete morphs, and even less so as species, even by the most hardy conchologist. This prompted examination of radula and molecular characters of conchologically similar animals from the South and West Pacific, which resulted in evidence of further species "pairs" with similar shells and different radulae.

This is the first time such a case is reported in "turrids", and it brings new questions: is this an isolated case of radula polymorphism? Or is this a textbook case of shell convergence? A molecular analysis confirms that differences indicated by radulae are profound, but it does not rule out that similarities in shell morphologies are the result of conserved patterns rather than the result of convergence of evolved patterns.

Material and methods

Material for this study was collected over the course of several years during expeditions organized by the Muséum National d'Histoire Naturelle, Paris (MNHN) to New Caledonia (Expédition Montrouzier, 1993), the Loyalty Islands (LIFOU 2000), the Philippines (PANGLAO 2004), and Vanuatu (SANTO 2006). Material for molecular studies was preserved in 90 or 100% ethanol by clipping pieces of the head-foot from anesthetized specimens.

Radulae were extracted from the specimens (from those with dried bodies – after rehydration), cleaned with diluted bleach, rinsed in distilled water, mounted on the stubs, air dried, coated with a gold-palladium and investigated with a JEOL JSM 840A Scanning

Microscope. Terminology and homology of the central teeth in Turrinae follows Kantor (2006).

The following samples were examined in terms of radular morphology and also, where specifically mentioned, molecular sequences:

***Xenuroturris* identified as “*X. cingulifera*” based on shell characters**

Specimens with "duplex" radular type [= *Xenuroturris legitima* Iredale, 1929]

PHILIPPINES, Bohol Province, PANGLAO 2004, sta. G1, 09°41.9'N, 123°9.5'E, 100 m (2 spms – Fig. 2B-C).

NEW CALEDONIA, Koumac, sta. 913, 20°58'S, 164°32'E, 10-13 m (1 spm – Fig. 2E), sta. 944, 20°35'S, 164°12'E, 14-15 m (1 spm – Fig. 2F).

LOYALTY ISLANDS, LIFOU 2000, sta. 1465, 20°47.7'S, 167°07.0'E, 35-45 m (1 spm – Fig. 2D).

ESPIRITU SANTO, VANUATU. SANTO 2006, sta. DR87, 15°38.5'S, 167°15.1'E, 13 m (1 specimen sequenced, MNHN 17684) (Fig. 2A, 8A).

Specimens with "semi-enrolled" radular type [= *Iotyrris cingulifera* Lamarck, 1822]

NEW CALEDONIA, Nouméa, sta. 255, 22°25'S, 166°20'E, 11 m (1 spm); Nouméa, Grand Récif Aboré, 5 m (1 spm); Touho, sta. 1240 (Expedition Montrouzier), 20°46.5'S, 164°14'E, 0-2 m (1 spm – Fig. 3G); Koumac, sta. 941, 20°39'S, 164°13'E, 15-16 m (1 spm – Fig. 3F), sta. 1303 (Expedition Montrouzier), 20°37.7'S, 164°15.9'E, 0-8 m (1 spm – Fig. 3A); sta. 1304 (Expedition Montrouzier), 20°38.6'S, 164°13.2'E, 12-15 m (1 spm); LAGON, sta. 549, 22°58'S, 166°56'E, 26 m (1 spm – Fig. 3H, 8B); Atoll de Surprise, sta. 445, 18°18'S, 163°02'E, 41 m (1 spm – Fig. 3E),

LOYALTY ISLANDS, LIFOU 2000, sta. 1422, 20°47.1'S, 167°07.4'E, 4 m (1 spm) (Fig. – Fig. 3B), sta. 1423, 20°54.0'S, 167°07.3'E, 12 m (2 spms – Fig. 3C-D); sta. 1425, 20°46.8'S, 167°07.2'E, 4-5 m (1 spm).

VANUATU, ESPIRITU SANTO. SANTO 2006, sta. FS84, 15°33.6'S, 167°16.6'E, 5 m (2 spms sequenced, MNHN 17685 and 17686) (Fig. 3I).

Iotyrris devoizei n.sp.

VANUATU, ESPIRITU SANTO. SANTO 2006, sta. FB72, 15°36.1'S, 166°58.5'E, 16 m (1 specimen, sequenced, MNHN 20014) (Fig. 6 A-B); sta. DS04, 15°31.5'S, 167°14.5'E, depth unknown (2 specimens, sequenced, MNHN 17681 – Fig. 6D, MNHN 17682 – Fig. 6E).

Iotyrris musivum n.sp.

VANUATU, ESPIRITU SANTO. SANTO 2006, sta. DS04, 15°31.5'S, 167°14.1'E, 25 m (2 specimens sequenced: MNHN 17683 – Fig. 7C, MNHN 20015 – Fig. 7A).

Xenuroturris kingae (Powell, 1964)

NEW CALEDONIA. Koumac, sta. 1319 (Expedition Montrouzier), 20°44.1'S, 164°15.1'E, 15-20 m (2 specimens – Fig. 6 H-I, 8E).

Molecular study

Sequencing

DNA was extracted from a piece of foot, using 6100 Nucleic Acid Prepstation system (Applied Biosystem). A fragment of 658 bp of Cytochrome Oxidase I (COI) mitochondrial gene was amplified using the universal primers LCO1490 and HCO2198 developed by Folmer *et al.* (1994). One nuclear gene fragment was also analyzed: 900 bp of the rDNA 28S gene, involving D1, D2 and D3 domains (Hassouna *et al.*, 1984), using the primers C1 and D3 (Jovelín and Justine, 2001). All PCR reactions were performed in 25 µl, containing 3 ng of DNA, 1X reaction buffer, 2.5 mM MgCl₂, 0.26 mM dNTP, 0.3 µM of each primer, 5% DMSO and 1.5 units of Q-Bio Taq (Qbiogene) for all genes. For 28S gene, thermocycles consisted of an initial denaturation step at 94°C for 4', followed by 30 cycles of denaturation

at 94°C for 30'', annealing at 52°C and extension at 72°C for 1'. The final extension was at 72°C for 10'. Thermocycles used for COI gene are described in Hebert *et al.* (2003).

PCR products were purified and sequenced by the Genoscope, a French National Sequencing Center. Because of the length of the 28S PCR product, two internal primers (D2 and C2', Dayrat *et al.*, 2001) were used for sequencing, in addition of primers used for PCR. All genes were sequenced for both directions to confirm accuracy of each sequences. Sequences were deposited in GenBank. Genbank accession numbers for corresponding specimens are provided in Tables 1 and 2.

Phylogenetic Analyses

Three species of Turridae (each represented by a single specimen) were used as outgroups for phylogenetic analyses: *Lophiotoma albina* (Lamarck, 1822) [Turridae] (Vanuatu, SANTO 2006 expedition, sta. DR68, 15°22.9'S, 167°13.1'E, 7-27 m, MNHN 17756), as a closely related species (Olivera 2002); *Turris crispa* (Lamarck, 1816) [Turridae] (Philippines, PANGLAO 2004 expedition, sta. R42, 9°37.1'N, 123°52.6'E, 8-22 m, MNHN 17754) and *Crassispira* sp. [Crassispirinae] (Philippines, PANGLAO 2004 expedition, sta. L46, 9°30.9'N, 123°41.2'E, 90-110 m, MNHN 17755).

COI gene sequence was manually aligned, and 28S was automatically aligned using ClustalW multiple alignment implemented in BioEdit version 7.0.5.3 (Hall, 1999), and the accuracy of the alignment was confirmed by eye. Genetic pairwise distances were calculated with PAUP 4.0b10 (Swofford, 2002), using the best fitting model of nucleotide substitution for each gene as defined by the program Modeltest (Posada & Crandall, 2001), in conjunction with PAUP 4.0b10, following the Akaike information criterion (AIC).

Phylogenetic reconstruction were conducted using Bayesian analysis, consisting of two Markov chains (2000000 generations each with a sampling frequency of one tree each hundred generations) run in six parallel analyses using Mr. Bayes (Huelsenbeck *et al.*, 2001). The same model of substitution used for computing the genetic distances was used for the Bayesian analysis. When the log-likelihood scores were found to stabilize, a consensus tree was calculated after omitting the first 25% trees as burn-in.

Results

Radulae and Shells

Two morphologically distinct types of radulae were found in the species initially identified as "*Xenuroturris cingulifera*" based on shell characters.

The first radular type is characterized by the so-called "duplex" marginal teeth, typical for the family Turridae (*sensu* Taylor *et al.*, 1993) (Fig. 1A-C). The anterior part of the tooth (closer to the tip), constituting about 0.42-0.5 of total tooth length, is solid, while the posterior part has two thickened edges, a thinner dorsal one and thicker ventral one attached to the radular membrane (Fig. 1B). The central tooth is very small, narrow, and spear shaped. The lateral teeth absent. The ratio between marginal tooth length and shell length varies from 0.47 to 0.57 % (mean 0.52, $\sigma=0.03$, $n=9$), that between tooth length and aperture length varies from 1.67 to 2.05 % (mean 1.90, $\sigma=0.14$, $n=9$).

The second radular type is characterized by "semi-enrolled" marginal teeth (Fig. 1D-F). Both edges of the marginal tooth are elevated and equally developed along the entire tooth length, and they delimit a trough between them. The anterior solid part of the tooth is absent. Central and lateral teeth are absent. The marginal teeth are proportionally slightly longer than in the duplex type: the ratio between marginal tooth length and shell length

varies from 0.54 to 0.67 % (mean 0.63, $\sigma=0.05$, $n=8$), that between tooth length and aperture length varies from 1.90 to 2.37 % (mean 2.21, $\sigma=0.18$, $n=8$).

The two forms occur sympatrically, although not syntopically, in Koumac, an intensively sampled site (Bouchet *et al.*, 2002) in New Caledonia; at Lifou in the Loyalty Islands; and on Espiritu Santo in Vanuatu. The shells of both forms are extremely similar and fall within the hitherto accepted (Powell, 1964; Olivera, 2002) range of intraspecific variation of "*Xenuroturrus cingulifera*" (Figs. 2-3). However, after we had evidence of the two radular types, close examination of the shells revealed subtle differences.

(i) All specimens of "*Xenuroturrus cingulifera*" have paired peripheral cords, the adapical one becoming subdivided into two by a groove with increasing shell height. In specimens with "semi-enrolled" teeth this subdivision is slightly less obvious (Fig. 3 A, D, F, H) than in specimens with "duplex" teeth. The abapical, initially single and undivided, cord also becomes subdivided at certain shell size, but only in the form with "duplex" teeth. This is shown on the specimen on Fig. 2 A, in which the abapical cord is single on the adapical whorl and becomes subdivided on subsequent whorl. Large specimens of the form with "duplex" tooth thus have a peripheral zone with four nearly even thin cords (Fig. 2 A, C); specimens with the "duplex" marginal teeth tend to have slightly less convex peripheral cords.

(ii) Another difference is the shell base and the canal. Although observations are difficult to quantify and descriptions tend to be somewhat subjective, the form with "semi-enrolled" teeth has slightly more attenuated siphonal canal than in the "duplex" form.

Both *Iotyrriis devoizei* n. sp. and *I. musivum* n. sp. also have radulae with "semi-enrolled" teeth. In *I. devoizei* radular teeth are very similar to the form of "*X. cingulifera*" (Fig. 6 F-G) with the "semi-enrolled" teeth [= true *I. cingulifera*]. The central and lateral teeth were absent in one specimen, but rather well developed in another (Fig. 6 G). The marginal teeth are nearly twice as long as in *I. cingulifera*: the ratio between marginal tooth length and shell length varies from 0.94 to 1.15 % (mean 1.02, $\sigma=0.09$, $n=5$), that between tooth length and aperture length varies from 2.96 to 3.54 % (mean 3.18, $\sigma=0.24$, $n=5$). In *Iotyrriis musivum* the shape of marginal teeth is also similar. The central tooth is either very small and sharp (Fig. 7 E-F) or is obtuse and fused with vestigial laterals (Fig. 7G). The marginal teeth are of intermediate length: the ratio between marginal tooth length and shell length varies from 0.75 to 0.87 % (mean 0.79, $\sigma=0.05$, $n=5$), that between tooth length and aperture length varies from 2.37 to 2.76 % (mean 2.58, $\sigma=0.17$, $n=5$).

Molecular study

For COI and 28S genes, alignments resulted in sequences of 658 and 903 bp length respectively. No indel was found for COI. Within ingroups, 97 sites were variable for COI gene, and only 14 for 28S. The Tamura-Nei model (TrN+G, with $G = 0.1047$) model for the COI gene and the General Time Reversible model (GTR+I, with $I = 0.8579$) model for the 28S gene were defined as the best fitting models.

Genetic distances are low (0.003, table 1) between specimens specimens of "*Xenuroturrus cingulifera*" with "semi-enrolled" teeth [= true *Iotyrriis cingulifera*], and are similar to the genetic distances found between specimens of *I. devoizei*, or of *I. musivum* (from 0 to 0.010). On the contrary, genetic distances found between specimens of "*X. cingulifera*" with "semi-enrolled" teeth and the specimen of "*X. cingulifera*" with "duplex" teeth [= *X. legitima*] are very high (0.551), in fact higher than the genetic distances between specimens of *I. devoizei* and *I. musivum* (0.131).

All specimens of *Xenuroturris-Iotyrriis* clustered together for COI, but this result is not supported (Posterior Probability PP = 0.52, Fig. 4). Specimens with a "semi-enrolled" teeth are found to form a monophyletic clade (although weakly supported) that excludes the specimen with the "duplex" teeth. Within the "semi-enrolled" clade, three clades are recognized, each containing two or three specimens. Those three clades each included only specimens hypothesized to be conspecific based on shell and radula characters. Consequently, on the molecular tree, specimens of "*X. cingulifera*" with "semi-enrolled" teeth appear more closely related to *Iotyrriis devoizei* and *I. musivum* than to the specimen of "*X. cingulifera*" with "duplex" teeth.

Similar results are found for 28S gene, with low genetic distances between specimens with "semi-enrolled teeth" (0.001, table 2) and higher genetic distances (0.005, table 2) between specimens of "*X. cingulifera*" with "semi-enrolled" teeth [true *Iotyrriis cingulifera*] and "duplex" teeth [= *X. legitima*]. Monophyly of the *Xenuroturris-Iotyrriis* clade is weakly supported (0.93). Within "semi-enrolled" clade, the three clades defined with the COI gene are found again, but only one of them is strongly supported. Relationships between those three clades and the specimen of "*X. cingulifera*" with "duplex" teeth [= *X. legitima*] are not resolved.

Discussion

Taxonomic rank of the different forms

The genetic distances between specimens of "*Xenuroturris cingulifera*" and the phylogenetic relationships between those specimens provide two strong arguments that confirm the hypothesis based on the observation of the radulae:

(a) with both COI and 28S gene, genetic distances between specimens displaying different radulae are very high, corresponding at least to distances found between specimens of different species,

(b) with COI gene, specimens of "*X. cingulifera*" with "semi-enrolled" teeth are found to be more closely related to other species of *Iotyrriis* than to the specimens of "*X. cingulifera*" with duplex teeth. As specific status of *I. devoizei* and *I. musivum* is not questioned, two species must be recognized within "*X. cingulifera*".

The species level status of the two other species, *Iotyrriis devoizei* and *I. musivum* also leaves no doubt. All four species under consideration were found sympatrically in Santo, and *I. devoizei* and *I. musivum* were even found syntopically in a single underwater vacuum-cleaning collecting effort. *I. devoizei* and *I. musivum* are described as new species.

Taxonomic and nomenclatural implications

Although the species considered in this paper are not unambiguously recognizable from their shells (compare, e. g., Fig. 2 F and 3 E, or 2 B and 3 C), we examined the type material of the nominal species currently subsumed in "*Xenuroturris cingulifera*", to ascertain which names, if any, might be applicable. Two available names are applicable to two of our species, the other two are described as new.

The type material of *Xenuroturris legitima* Iredale, 1929 has a short recurved siphonal canal and both peripheral cords are subdivided (Fig. 5 C, E). The name is thus applicable to the form with "duplex" radular teeth.

The syntypes of *Pleurotoma cingulifera* Lamarck, 1822 are badly worn specimens that render their identification difficult. The only significant character is in the peripheral cords, of which the abapical one is not subdivided, even in the largest syntype (shell length 65 mm). In our specimens of similar size with "duplex" radular teeth, that cord is always subdivided. Although some ambiguity persists, we apply the name *cingulifera* to the form with "semi-

enrolled" marginal radular teeth. We are of the opinion that this is nomenclaturally more stable than leaving *cingulifera* as a *nomen dubium* and describing the form with "semi-enrolled" marginal radular teeth as a new species.

Ideally, the current name-bearing types of *Pleurotoma cingulifera* Lamarck, 1822 and *Xenuroturris legitima* Iredale, 1929 should be replaced by live-taken neotypes with known radular and molecular characteristics. This can be done only by a decision of the International Commission on Zoological Nomenclature, but we are of the opinion that this is unnecessary as long as the systematic and nomenclatural conclusions of this paper are accepted by zoologists.

The type species of *Xenuroturris*, by monotypy, is *X. legitima* Iredale, 1929, and this name is thus applicable to *Xenuroturris*-type shells with "duplex" teeth. Medinskaya and Sysoev (2001) proposed the monotypic new genus *Iotyrris* for what they had identified as *Xenuroturris cerithiformis* Powell, 1964 (misidentified; = *Iotyrris marquesensis* Sysoev, 2002), a species very similar to other species of *Xenuroturris* in shell characters and possessing a radula with "semi-enrolled" teeth. Although we did not include the type species of *Iotyrris* in our analysis, we suggest that the name *Iotyrris* is applicable to these turrids with *Xenuroturris*-type shells and "semi-enrolled" radular teeth.

Xenuroturris Iredale, 1929

Iredale, 1929: 283.

Type species (by monotypy): *Xenuroturris legitima* Iredale, 1929

Xenuroturris legitima Iredale, 1929

Iredale, 1929: 283, pl. 31, figs. 3-4.

Selected synonymy: *Xenuroturris cingulifera cingulifera* – Powell, 1964 (part.): plate 175, figs. 19-20, non fig. 12. *Xenuroturris cingulifera* – Medinskaya and Sysoev, 2002: 9, fig. 3?, fig. 6A. *Lophiotoma cingulifera* – Olivera, 2002, figs. 1 F, 1 G, H1, H2.

Syntypes: Two type specimens of *Xenuroturris legitima* housed in the Australian Museum are labeled as holotype (C.57823) and paratypes (C.110457). However, in the original description, Iredale did not fix a holotype and therefore all type specimens should be considered syntypes.

Type locality: Michaelmas Cay, Queensland, Australia.

Distribution: The distribution ascertained by us includes New Caledonia, the Loyalty Islands, Vanuatu, and the Philippines. The species is also recorded from South Africa (Kilburn 1983: 564-565, figs 30, 32) and Japan (Okutani 2000: 631, pl. 314, fig. 57), but this now require confirmation based on radula and/or molecular characters.

Iotyrris Medinskaya et Sysoev, 2001

Medinskaya and Sysoev, 2001: 12.

Type species: *Iotyrris marquesensis* Sysoev, 2002 (Fig. 8F), by fixation by Sysoev (2002) under Art. 70.3 of the Code of Nomenclature.

Iotyrris cingulifera (Lamarck, 1822)

Pleurotoma cingulifera Lamarck, 1822: 94.

Selected synonymy: *Xenuroturris cingulifera cingulifera* – Powell, 1964 (part.): plate 175, fig. 12, non figs. 19-20. *Lophiotoma cingulifera* – Olivera, 2002 (part.), fig. H3.

Syntypes: 3 possible syntypes of *Pleurotoma cingulifera* are housed in the Muséum d'histoire naturelle de la ville de Genève (MHNG 1097/62) (Fig. 5 E-G). The largest specimen, possibly illustrated by Kiener (1839), has a shell length of 65 mm (MHNG 1097/62/1), which more or less matches Lamarck's indication of a size of "2 pouces 4 lignes", i.e. 63 mm.

Type locality: not stated. Powell (1964) restricted it to Mauritius, a restriction that has no standing under the ICZN.

Distribution: The distribution ascertained by us includes New Caledonia, the Loyalty Islands, Vanuatu, and the Philippines. Records from Zanzibar (Powell 1964) and Guam (Olivera (2002: fig. H3) require confirmation based on radula and/or molecular characters.

Iotyrris devoizei n. sp.

(Fig. 6 A-G)

TYPE MATERIAL. Holotype MNHN 20014 and 2 paratypes MNHN 17681, 17682.

TYPE LOCALITY. Vanuatu, south of Espiritu Santo, Elia Island, 15°36.1'S, 166°58.5'E, 16 m [SANTO 2006 expedition, sta. FB72].

ETYMOLOGY. The species is named after Patrice Petit-Devoize, biologist and diver, and a pillar of the MNHN expeditions diving team.

OTHER MATERIAL EXAMINED. Vanuatu, Espiritu Santo, SANTO 2006 expedition, sta. DS04, wreck of *President Coolidge*, 15°31.5'S, 167°14.1'E, 25 m (2 lv, paratypes).

New Caledonia, LAGON sta. 888, 20°22'S, 164°38'E, 20 m, 1 dd; Expedition Montrouzier, sta. 1269, 20°35.1'S, 165°08.1'E, 15-20 m, 1 dd; sta. 1271, 20°52.7'S, 165°19.5'E, 5-25 m, 4 dd; sta. 1311, 20°40.4'S, 164°14.9'E, 10-60 m, 1 dd; sta. 1318, 20°41.4'S, 164°14.8'E, 20-30 m, 1 dd. Loyalty Islands, LIFOU 2000 expedition, sta. 1421, 20°52.4'S, 167°08.5'E, 4 m, 2 dd; sta. 1422, 20°47.1'S, 167°07.4'E, 4 m, 2 dd; sta. 1423, 20°54.0'S, 167°07.3'E, 12 m, 1 dd; sta. 1429, 20°47.5'S, 167°07.1'E, 8-18 m, 4 dd; sta. 1435, 20°55.2'S, 167°00.7'E, 5-30 m, 2 dd; sta. 1442, 20°46.4'S, 167°02.0'E, 47 m, 1 dd; sta. 1448, 20°45.8'S, 167°01.7'E, 20 m, sta. 1450, 20°45.8'S, 167°01.7'E, 27-31 m, 1 dd; sta. 1451, 20°47.3'S, 167°06.8'E, 10-21 m, 3 dd; sta. 1453, 20°54.6'S, 167°02.1'E, 21-30 m, 3 dd, 1 lv (Fig. 6C, 8C); sta. 1455, 20°56.8'S, 167°02.7'E, 15-20 m, 2 dd; sta. 1457, 20°46.8'S, 167°02.8'E, 5-10 m, 3 dd.

DISTRIBUTION. New Caledonia, Loyalty Islands, Vanuatu, shallow water, alive in 16 to 30 m, shells from 4 to 47 m. It is possible that the species also occurs in Hawaii and the Marquesas.

DESCRIPTION (holotype). Shell conical, consisting of 7 teleoconch whorls, with high spire, shell diameter to shell height 0.35, aperture height to shell height 0.33, spire height to shell height 0.49. Protoconch overgrown and eroded, light brown, of more than 3 whorls, sculptured with closely spaced axial threads. Teleoconch whorls slightly convex, spire whorls are slightly angulated on the periphery. Last whorl sharply narrowing towards attenuated, nearly straight, siphonal canal. Suture shallowly adpressed, slightly wavy. Subsutural ramp narrow, convex, with single bulging keel subdivided by two narrow and shallow grooves. The keel is strongly marked by rectangular, unevenly sized, dark red-brown spots. Immediately below the ramp are two narrow but tall, closely spaced, cords, forming the shoulder. Below them are three broadly spaced cords, equal to those on the shoulder, separated by smooth interspaces, except one narrow thread between the lower shoulder cord and upper periphery one. There are 5 more closely spaced cords on the shell base and 5 narrower and closer spaced threads on the canal. Axial sculpture absent except for

inconspicuous growth lines. Aperture narrowly oval. Outer lip broken, judging from the growth lines anal sinus deep, situated on the shoulder. Inner lip nearly straight, columellar part straight, callus very narrow not extending on the parietal wall. Color creamy white, with dark strong spots on the subsutural ramp, much lighter yellow narrow spots, covering all the cords of the periphery, tessellate dark closely spaced spots on the cords of the shell base, smaller and slightly lighter spots on the threads of the canal.

Shell height (holotype) 17.8 mm, shell diameter 6.3 mm, last whorl height 9.0 mm, aperture height 5.9 mm.

REMARKS. Paratypes are similar to the holotype in shell outline and sculpture, and appear to be juveniles. However, one of them (MNHN 17681, Fig. 6 D), with a shell length of only 11.8 mm, is already a mature male with a long penis equal in length to that of the mantle cavity. That specimen has more pronounced color spots on the shoulder and shell periphery, so that the contrast between the shell base and periphery is much less pronounced. The protoconch of the second paratype (Fig. 6 E) is best preserved, but its nucleus missing; the number of whorls is thus at least 4.

The largest specimen we attribute to *I. devoizei* has a shell length of 27.1 mm.

Iotyrriis devoizei is conchologically very similar to *X. kingae* (Powell, 1964) in terms of sculpture and colour pattern, down to the finest details. The only differences between the two is the more elongate shell of *I. devoizei*, with a clearly longer siphonal canal, and the slightly less bulging subsutural rim. The two species have a radula of a different type – while *I. devoizei* possesses semi-enrolled marginal radular teeth, *X. kingae* has duplex teeth (Fig. 6J).

Iotyrriis musivum n. sp.

(Fig. 7)

TYPE MATERIAL. Holotype MNHN 20015 and 1 paratype MNHN 17683.

TYPE LOCALITY. Vanuatu, Espiritu Santo, wreck of *President Coolidge*, 15°31.5'S, 167°14.1'E, 25 m [SANTO 2006 expedition, sta. DS04].

ETYMOLOGY. *Musivum*, Latin meaning mosaic, with reference to the colour pattern; used as a noun in opposition.

OTHER MATERIAL EXAMINED. New Caledonia, Expedition Montrouzier, Koumac, sta. 1286, 20°38'-20°39'S, 164°16'-164°17'E, intertidal, 1 lv. Loyalty Islands, LIFOU 2000 expedition, sta. 1421, 20°52.4'S, 167°08.5'E, 4 m, 1 lv (Fig. 7D, 8D); sta. 1424, 20°54.9'S, 167°03.0'E, 4 m.

DISTRIBUTION. New Caledonia, Loyalty Islands, Vanuatu, shallow water, intertidal to 16 m.

DESCRIPTION (holotype). Shell conical, consisting of 5.75 teleoconch whorls, with high spire, shell diameter to shell height 0.34, aperture height to shell height 0.31, spire height to shell height 0.48. Protoconch brown, consists of 4.25 convex whorls, sculptured with closely spaced axial threads, which are slightly prosocline on most whorls, but turned to strongly opisthocline on the posteriormost part of the last protoconch whorl. There are around 25 threads on the last protoconch whorl. Teleoconch whorls nearly flat, slightly angulated at the shoulder. Last whorl sharply narrowing towards attenuated nearly straight siphonal canal. Suture shallowly impressed, slightly wavy. Subsutural ramp narrow, with single strong sharp keel, followed by narrow thread. Immediately below the ramp there are two narrow but tall triangular in section closely spaced cords, forming the shoulder. Below there are four broadly spaced subequal cords, separated by smooth interspaces. There are 5 thinner and more closely spaced cords on the shell base and 8 narrower and closer spaced threads on the canal. Axial sculpture absent except for inconspicuous growth lines. Aperture narrowly oval.

Outer lip thin, evenly rounded. Anal sinus deep, situated on the shoulder. Inner lip slightly convex, columellar part straight, callus very narrow not extending on the parietal wall. Color creamy white, with regularly spaced light brown spots, covering cords of the entire shell surface and much more pronounced and more dark strong subrectangular spots on the shoulder cords.

Operculum yellow, transparent, leaf-shaped, with terminal nucleus.

Shell height (holotype) 12.6 mm, shell diameter 4.3 mm, last whorl height 6.6 mm, aperture height 3.9 mm.

REMARKS. The holotype is a juvenile specimen. We nevertheless chose to fix it as the name-bearing type, since it is clearly recognizable, because we know its radula and DNA sequence. The paratype (Fig. 7C), which is very similar to the holotype in shell outline and sculpture, has a length of 13.9 mm. The largest specimen has a shell length of 29.1 mm. In large specimens the subsutural ramp has additional thin but sharp spiral thread immediately below the suture. There are additional thin threads between the major cords on the shell periphery.

Iotyrris musivum resembles *Iotyrris marquesensis* Sysoev, 2002 (which also has "semi-enrolled" marginal radular teeth) but differs in having a broader shell with relatively shorter canal. Besides, the color marks on the shoulder keels are much less pronounced in *I. marquesensis* and do not differ from the spots on the rest of the shell. The subsutural ramp in *I. marquesensis* is separated from the shoulder keels by a deep cleft, while in *X. sp.* only by narrow and shallow groove. From small specimens of *I. cingulifera* the new species differs in much larger and color spots of the shell, brighter color spots on the shoulder cords and more coarse spiral sculpture. Another species which is remotely similar to *I. musivum* is *Lophiotoma olangoensis* Olivera, 2002. The new species differs in having a much more brightly colored subsutural rim and nearly straight canal, which in *L. olangoensis* is clearly curved to the left in apertural view. We examined the radula of a specimen from Lifou (Loyalty Islands) which we identified as *L. olangoensis* and it appeared to be similar to that of *Xenuroturrus legitima*, that is consisting of duplex marginal teeth, very small and narrow central one and vestigial laterals.

Radula as a taxonomic character in "Turridae"

Since McLean's (1971) classification of the Turridae s.l., the radula has routinely been used for subfamily and genus level allocation within Conoidea. However, relatively little correlation between foregut anatomy and shell and radular characters was found in many groups (e. g., Kantor *et al.*, 1997; Kantor and Taylor, 2002). For instance, several genera of Crassispirinae (Turridae) having very similar shells (*Inquisitor* Hedley, 1918, *Funa* Kilburn, 1988, and *Ptychobela* Thiele, 1925) differ significantly in radular teeth shape. In practice, similarity in shell together with dissimilarity in radula was interpreted as shell homeomorphy. For instance, Bouchet and Sysoev (2001) established the new genus *Leiosyrinx* (Conidae, Raphitominae), conchologically very similar to *Typhlosyrinx* Thiele, 1925, based on differences in their radulae. The subfamily Zonulispirinae McLean, 1971 (Turridae) was proposed mainly on the basis of its radula with "semi-enrolled" marginal teeth only, while in shell characters it is rather similar to the subfamily Crassispirinae (Turridae). However, the hypothesis that the radula better reflects relationships than the shell had never been tested by molecular data.

Kantor and Taylor (2000) showed that very different marginal radular teeth in Turridae s.s. are formed in a similar way by thickening of the tooth edges, longitudinal folding and progressive elevation of the posterior edge of the tooth from the membrane in the course of tooth maturation. They illustrated this process for what they called *Xenuroturrus cingulifera* with "duplex" teeth [= *X. legitima*] (Kantor and Taylor, 2000: fig. 3 g-h). Comparison of the

process of maturation in both teeth types revealed that, at some point, the semi-matured teeth are rather similar in shape, and the final differences are the result of extra sclerotization of the duplex teeth that is responsible for the long anterior solid tip. The difference between "duplex" and "semi-enrolled" teeth might therefore be less profound than it seems, and its phylogenetic value was only speculative. An important result of this study is thus that species such as *Iotyrris cingulifera*, *I. devoizei* and *I. musivum*, with rather different shells but with similar radulae (in this case, "semi-enrolled" marginal teeth) form a clade, thus confirming that radular type is indeed reliable for revealing relationships.

The radulae of two further species with *Xenuroturrus*-type shells were examined from animals with dried soft parts, and reveal further species pairs with "duplex" and "semi-enrolled" teeth. One case is *Xenuroturrus kingae* (Powell, 1964) [with "duplex" teeth] and *Iotyrris devoizei* [with "semi-enrolled" marginal teeth] (Fig. 6). Both are conchologically very similar in terms of sculpture and even identical in the finest details of coloration, the only significant difference being a more elongate shell, with distinctly longer siphonal canal, in *X. devoizei*. Such differences were earlier considered to be of intraspecific value. Thus, pending confirmation, we think that Olivera's (2002) figs 2B1 and 2B4 represent *Iotyrris devoizei*, while figs 2B2-3 and 2B5 represent *X. kingae*. The two species co-occur in Hawaii and the Marquesas (based on Olivera's illustrations) and in New Caledonia (this paper). Another case is *Iotyrris marquesensis* Sysoev, 2002 [with "semi-enrolled" marginal teeth] (Fig. 8F) and *Xenuroturrus cerithiformis* Powell, 1964 [with "duplex" teeth] (Fig. 8G), which differ so little in shell shape that Medinskaya and Sysoev (2001) initially confused them.

It is remarkable that within the subfamily Turrinae a "semi-enrolled" radular tooth is found only in this clade, and it raises the question of whether they originated once in the genus - and *Iotyrris* is indeed monophyletic, and conchologically similar species with different radular types are the result of convergence or homoplasy -, or they appeared several times - and *Iotyrris* is polyphyletic and conchologically similar species with different radular types are indeed sister taxa. Regrettably, our study includes only one case where both members of the pair - *X. legitima* and *I. cingulifera* - were included in the analysis, and they ended up being not closely related in the molecular tree. Thus, although the molecular analysis confirms that differences indicated by radulae are profound, it does not rule out that similarities in shell morphologies are the result of conserved patterns rather than the result of convergence of evolved patterns.

Currently, *Xenuroturrus* is considered a mere subgenus of *Lophiotoma* Casey, 1904 (Kilburn, 1983; Taylor *et al.*, 1993; Higo *et al.*, 1993), the main difference being the truncated base of *Xenuroturrus*. Olivera (2002) even expressed serious doubts that *Xenuroturrus* should be recognized as a valid subgenus, pointing out the strong similarities in shell sculpture between *Lophiotoma albina* (Lamarck, 1822) and "*X. cingulifera*". Our study included a single species conchologically attributable to *Lophiotoma*, and is not relevant on the phylogenetic relationships between the two genera.

In conclusion, and despite these reservations, our working hypothesis is that *Lophiotoma*, *Xenuroturrus* and *Iotyrris* are all valid genera, a view that could not have been predicted from shells alone. Currently, most "turrid" genera are defined purely based on shell characters and there are anatomical or radula data for fewer than 10% of the described species. As long as molecular data exist only for a desperately small proportion of that diversity, we must be prepared that many of the currently accepted taxa are poly- or paraphyletic, at all taxonomic levels: specific, generic, and subfamilial.

Acknowledgements

The present research was carried out during a visiting curatorship of YK in MNHN and the senior author wants to express his thanks to Philippe Maestrati, Virginie Héros, and especially Pierre Lozouet, for expertise and assistance during his stay in Paris. Key material for molecular studies originates from the MNHN-IRD-PNI Santo 2006 expedition, and we thank Patrice Petit de Voize, Laurent Albenga and Jacques Pelorce for collecting the specimens during daily dives during 6 weeks of sustained bad weather. Preliminary sorting of the material to morphospecies was accomplished by Alexander Sysoev and Richard Kilburn, as part of the New Caledonia "turrid factory" project. We express our thanks to Dr. Jason Biggs who shared with us unpublished information and photographs of different species of *Xenuroturris*, and to two anonymous reviewers for the valuable comments and suggestions. The Total Foundation supported the LIFOU 2000, PANGLAO 2004 and SANTO 2006 expeditions. The work was partially supported by a grant of the Russian Foundation for Basic Research, No. 06-04-48462.

REFERENCES

- Bouchet P, Sysoev A (2001) *Typhlosyrinx*-like tropical deep-water turritiform gastropods (Mollusca, Gastropoda, Conoidea). *J Nat Hist* 35(11):1693-1715
- Bouchet P, Lozouet P, Maestrati P, Heros V (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biol J Linn Soc* 75: 421-436
- Bouchet P, Sysoev A, Lozouet P (2004) An inordinate fondness for turrids. *Molluscan Megadiversity: Sea, Land and Freshwater. World Congress of Malacology (Perth, Western Australia, 11-16 July 2004), Abstracts*: 12
- Dayrat B, Tillier A, Lecointre G, Tillier S (2001) New clades of Euthyneuran Gastropods (Mollusca) from 28S rRNA sequences. *Mol Phylogenetics Evol* 19: 225-235
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol Mar Biol Biotechnol* 3: 294-299
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl Acids Symp Ser* 41: 95-98
- Hassouna M, Michot B, Bachellerie J-P (1984) The complete nucleotide sequence of mouse 28SrRNA gene. Implications for the process of size increase of the large subunit rRNA of higher eukaryotes. *Nucleic Acids Res* 12: 3563-3583
- Hebert PDN, Cywinska A, Ball SL, deWaard JR (2003) Biological identifications through DNA Barcodes. *Proc R Soc Lond B* 270: 313-321
- Higo S, Callomon P, Gotō Y (1999) Catalogue and bibliography of the marine shell-bearing Mollusca of Japan. Elle Scientific Publications, Osaka
- Huelsenbeck JP, Ronquist F, Hall B (2001) MBayes: bayesian inference of phylogeny. *Bioinformatics* 17: 754-755
- Iredale T (1929) Queensland molluscan notes, No. 1. *Mem Queensland Mus* 9: 261-295
- Jovelin R, Justine J-L (2001) Phylogenetic relationships within the Polyopisthocotylean monogeneans (Plathyhelminthes) inferred from partial 28S rDNA sequences. *Int J Parasitol* 31: 393-401
- Kantor YuI (1990) Anatomical basis for the origin and evolution of toxoglossan mode of feeding. *Malacologia* 32(1): 3-18
- Kantor YuI (2006) On the morphology and homology of the "central tooth" in the radulae of Turridae (Conoidea: Turridae). *Ruthenica* 16(1-2): 47-52
- Kantor YuI, Medinskaya AI, Taylor JD (1997) Foregut anatomy and relationships of the Crassispirinae (Gastropoda, Conoidea). *Bull Nat Hist Mus, London (Zoology)* 63(1): 55-92
- Kantor YuI, Taylor JD (2000) Formation of marginal radular teeth in Conoidea (Neogastropoda) and the evolution of the hypodermic envenomation mechanism. *J Zool, London* 252: 251-262
- Kantor YuI, Taylor JD (2002) Foregut anatomy and relationships of raphitomine gastropods (Gastropoda: Conoidea: Raphitominae). In "Systematics, Phylogeny and Biology of the Neogastropoda" Ed by M Oliverio, R Chemello. *Boll Malacologico, Suppl* 5: 161-174
- Kilburn RN (1983) Turridae (Mollusca: Gastropoda) of southern Africa and Mozambique. Part 1. Subfamily Turridae. *Ann Natal Mus* 25(2): 549-585

- Kiener LC (1839) Genre Pleurotome. (*Pleurotoma*, Lam.). In "Spécies général et Iconographie des coquilles vivantes" 5: 17-84
- Lamarck JB (1822) Histoire naturelle des animaux sans vertèbres, 6(2). Paris, Verdière. 1-232
- McLean J (1971) A revised classification of the family Turridae, with the proposal of new subfamilies, genera, and subgenera from the Eastern Pacific. *Veliger* 14: 114-130
- Medinskaya AI, Sysoev AV (2001) The foregut anatomy of the genus *Xenuroturrus* (Gastropoda, Conoidea, Turridae), with a description of a new genus. *Ruthenica* 11(1): 7-14
- Okutani T (2000) (ed.) Marine mollusks in Japan. Tokai University Press
- Olivera BM (2002) The gastropod genus *Xenuroturrus* (Iredale, 1929) evaluated and a new turrid *Lophiotoma olangoensis* described from the central Philippines. *Science Dillman* 14(2): 40-50
- Posada D, Crandall KA (2001) Selecting models of nucleotide substitution: an application to human immunodeficiency virus 1 (HIV-1). *Molecular Biology and Evolution* 18: 897-906
- Powell AWB (1964) The family Turridae in the Indo-Pacific. Part 1, The subfamily Turrinae. *Indo-Pacific Mollusca* 1(5): 227-345
- Sowerby GB (1908) Descriptions of new species of *Terebra*, *Pleurotoma*, *Trochus*, *Tellina*, *Dosinia*, and *Modiola*. *Proc Malac Soc London* 8(4): 198-201
- Swofford DL (2002) PAUP*. Phylogenetic Analysis Using Parsimony* and other methods. Sunderland: Sinauer Associates
- Sysoev AV (2002) On the type species of *Iotyrris* Medinskaya et Sysoev, 2001 (Gastropoda, Turridae). *Ruthenica* 12(2): 169-171
- Sysoev AV, Kantor YuI (1990) A new genus and species of "*Cochlespira*-like" turrids (Gastropoda, Toxoglossa, Turridae). *Apex* 5(1-2): 1-6
- Taylor JD, Kantor YuI, Sysoev AV (1993) Foregut anatomy, feeding mechanisms, relationships and classification of Conoidea (Toxoglossa) (Gastropoda). *Bull Nat Hist Mus, London (Zoology)* 59: 125-169
- Tippett DL (2006) The genus *Strictispira* in the western Atlantic (Gastropoda: Conoidea). *Malacologia* 48(1-2): 43-64
- Tucker JK (2004) Catalog of Recent and fossil turrids (Mollusca: Gastropoda). *Zootaxa* 682: 1-1295
- Wilson B (1994) Australian Marine Shells, Vol. 2—Prosobranch Gastropods. Part two (Neogastropoda). Odyssey Publishing, Kallaroo, Australia

Figure captions.

Fig. 1. Two radular types found in specimens originally identified as "*Xenuroturris cingulifera*". A-C – radula with "duplex" marginal teeth, from specimen (PANGLAO 2004, sta. S22, SL 28.4 mm, shell see Fig. 2 B) now identified as *Xenuroturris legitima*. D-F – radula with "semi-enrolled" marginal teeth, from specimen (LIFOU 2000, sta. 1422, SL 28.4 mm, shell see Fig. 3 B) now identified as *Iotyrris cingulifera*. Scale bars A, D – 100 μ m; B, C, E, F – 10 μ m.

Fig. 2. *Xenuroturris legitima*. A – Vanuatu, SANTO 2006, sta. DR 087 (MNHN 17684), whole shell SL 57.0 mm, and close-up view of sculpture; B and C – Philippines, Panglao 2004, sta. S22, B – SL 28.4 mm, C – whole shell SL 50.5 mm, and close-up view of sculpture; D – Loyalty Islands, LIFOU 2000, sta. 1465, SL 51.5 mm; E – New Caledonia, Koumac, sta. 913, SL 39.5 mm; F – New Caledonia, Koumac, sta. 944, whole shell SL 32.5 mm, and close-up view of sculpture. All shells at the same scale, scale bars of close-ups 2 mm.

Fig. 3. *Iotyrris cingulifera*. A – New Caledonia, Koumac, sta. 1303, whole shell SL 38.4 mm, and close-up view of sculpture; B – Loyalty Islands, LIFOU 2000, sta. 1422, SL 28.4 mm; C-D – Loyalty Islands, LIFOU 2000, sta. 1423, C – SL 22.4 mm, D – whole shell SL 23.0 mm, and close-up view of sculpture; E – New Caledonia, Surprise Atoll, sta. 445, SL 31.2 mm; F – New Caledonia, Koumac, sta. 941, whole shell SL 32.5 mm, and close-up view of sculpture; G – New Caledonia, Touho, sta. 1240, SL 41.5 mm; H – New Caledonia, sta. 549, whole shell SL 44.5 mm, and close-up view of sculpture; I – Vanuatu, Santo 2006, sta. FS 084, SL 15.6 mm. All shells at the same scale, scale bars of close-ups 2 mm.

Fig. 4. Trees obtained with COI gene (on the left) and 28S gene (on the right), using Bayesian approach. Posterior probabilities are indicated above nodes.

Fig. 5. A-E – syntypes of *Xenuroturris legitima* Iredale, 1929: A-C – AMS C57823, SL 55.7 mm; D-E – AMS C220457, SL 72 mm. E-G – syntypes of *Pleurotoma cingulifera* Lamarck, 1822: E-F – MHNG 1097/62/1, SL 65.0 mm, G – MHNG 1097/62/3, SL 54.0 mm.

A-E, photos by A.C. Miller, copyright: Australian Museum. E-G, photos courtesy of Y. Finet, MHNG.

Fig. 6. A-G. *Iotyrris devoizei* n. sp. A-B – holotype, MNHN 20014 (the hole in the back results from drilling to extract the radula). C – Loyalty Islands, LIFOU 2000, sta. 1453, 21-30 m, SL 19.9 mm. D – paratype, MNHN 17681, SL 11.8 mm; E – apertural and dorsal views of paratype, MNHN 17682, SL 10.2 mm. F – radula of holotype. G – radula of the specimen in Fig. 6 C. H-J. *Xenuroturris kingae* Powell, 1964, New Caledonia, Koumac, 15-20 m. H – SL 17.4 mm. I – apertural and dorsal views, SL 18.0 mm. J – radula of the specimen in Fig. 6 I. All shells at the same scale. Scale bars for the radulae 50 μ m.

Fig. 7. *Iotyrris musivum* n. sp. A-B – holotype (B – enlarged), MNHN 20015, SL 12.6 mm (the hole in the back results from drilling to extract the radula). C – paratype, MNHN 17683, SL 13.9 mm. D – Loyalty Islands, LIFOU 2000, sta. 1421, 4 m, SL 24.5 mm. E-

F – radula of holotype. G – central field of the radula of the specimen in Fig. 7 D. All shells (except B) at the same scale. Scale bars for E and G 50 μ m, for F 10 μ m.

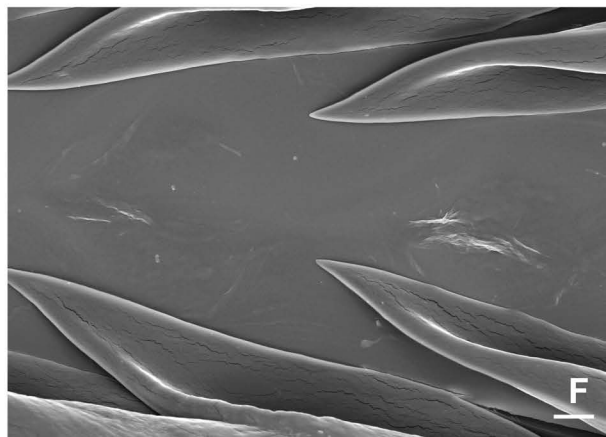
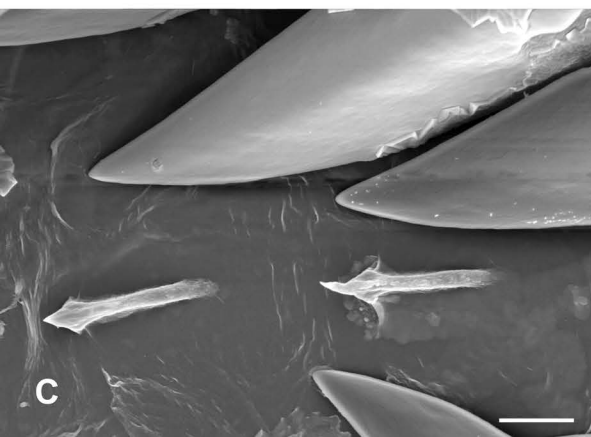
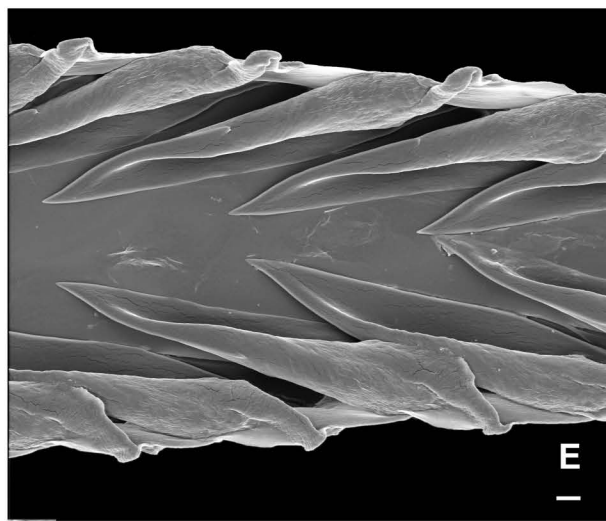
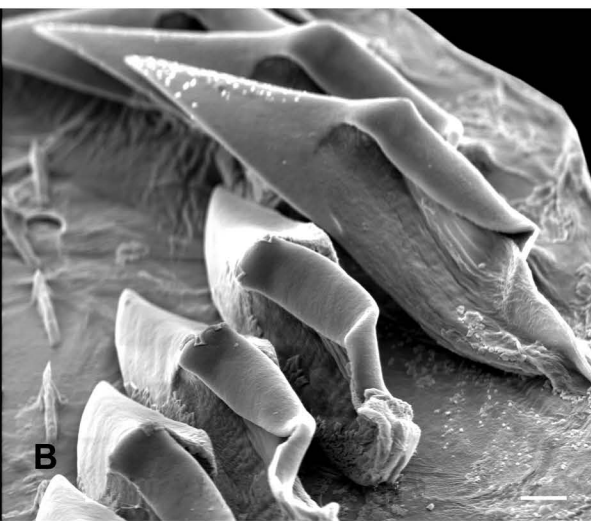
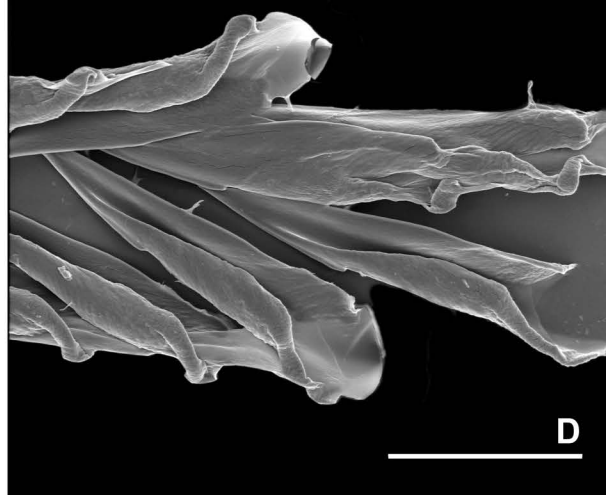
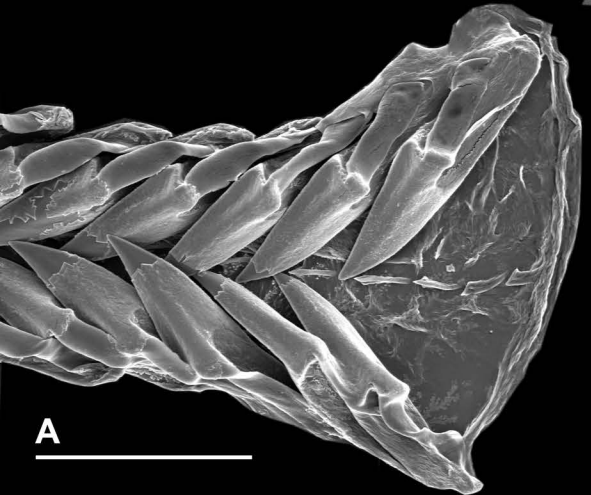
Fig. 8. Colour patterns of type or authenticated specimens of the species addressed in this study. A – *Xenuroturrus legitima*, SL 57.0 mm, same specimen as Fig. 2A. B – *Iotyrris cingulifera*, SL 44.5 mm, same specimen as Fig. 3H. C – *Iotyrris devoizei*, SL 19.9 mm, same specimen as Fig. 6C. D – *Iotyrris musivum*, SL 24.5 mm, same specimen as Fig. 7D. E – *Xenuroturrus kingae*, SL 18.0 mm, same specimen as Fig. 6I. F – *Iotyrris marquensensis*, holotype, SL 28.8 mm. G – *Xenuroturrus cerithiformis*, holotype, SL 38.5 mm.

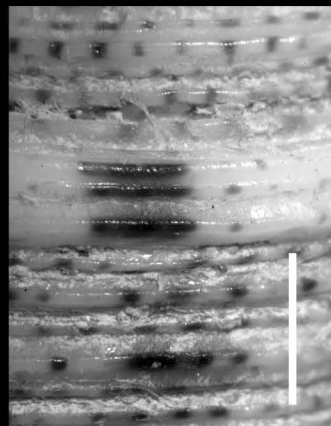
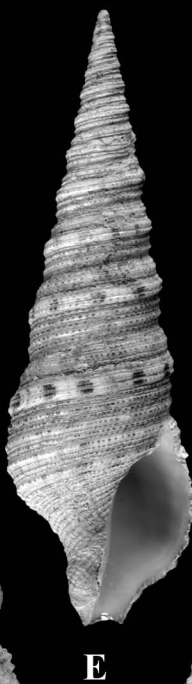
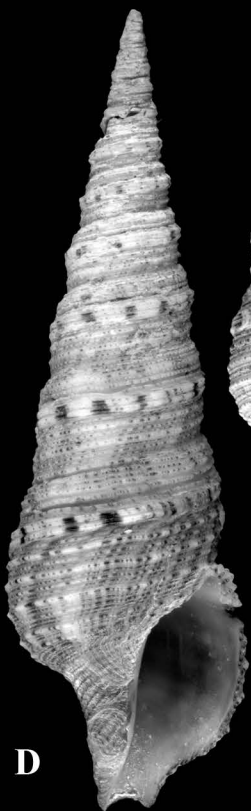
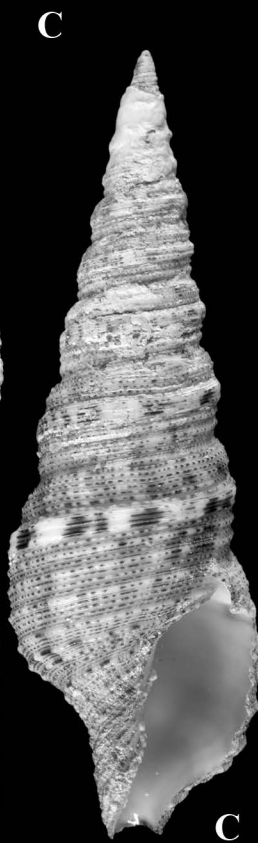
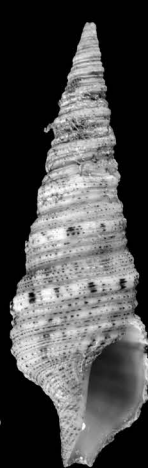
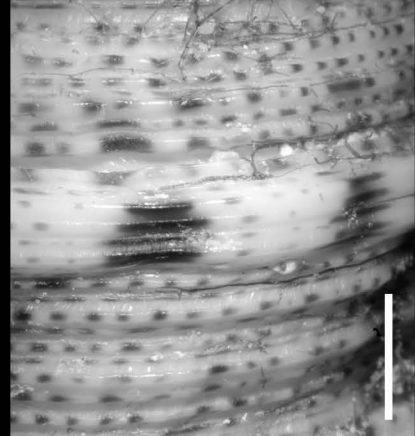
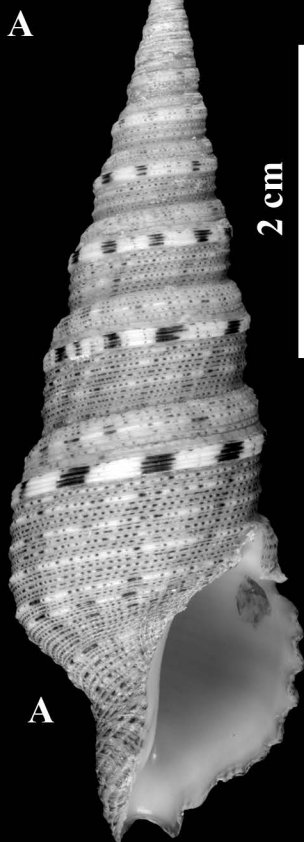
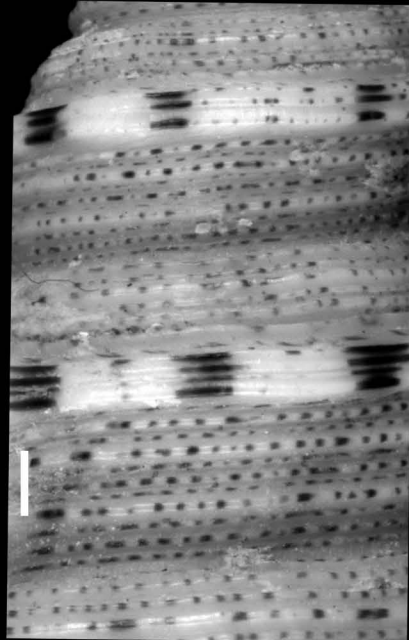
Table 1. Genetic pairwise distances for COI gene. The last line for each entry in first column represents the Genbank accession number.

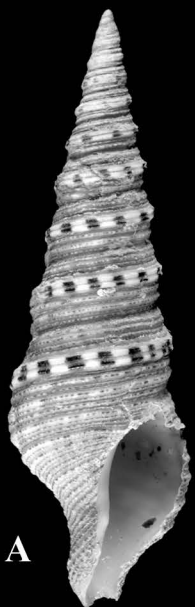
	17683	20015	17682	17681	17684	20014	17686	17685	17756	17754
MNHN 17683 <i>Iotyrris musivum</i> (EU127874)										
MNHN 20015 <i>Iotyrris musivum</i> (EU127875)	0.000									
MNHN 17682 <i>Iotyrris devoizei</i> (EU127877)	0.132	0.132								
MNHN 17681 <i>Iotyrris devoizei</i> (EU127876)	0.131	0.131	0.010							
MNHN 17684 <i>Xenuroturrus legitima</i> (EU127878)	0.821	0.821	0.734	0.717						
MNHN 20014 <i>Iotyrris devoizei</i> (EU127879)	0.125	0.125	0.008	0.005	0.721					
MNHN 17686 <i>Iotyrris cingulifera</i> (EU127880)	0.080	0.080	0.125	0.163	0.551	0.149				
MNHN 17685 <i>Iotyrris cingulifera</i> (EU127881)	0.089	0.089	0.137	0.179	0.551	0.163	0.003			
MNHN 17756 <i>Lophiotoma albina</i> (EU127882)	0.259	0.259	0.328	0.281	0.553	0.284	0.329	0.329		
MNHN 17754 <i>Turris crista</i> (EU015677)	0.526	0.526	0.710	0.755	0.678	0.762	0.517	0.563	0.425	
MNHN 17755 <i>Crassispira</i> sp. (EU015707)	1.557	1.557	2.024	1.876	2.939	1.835	2.027	2.027	1.419	1.811

Table 2. Genetic pairwise distances for 28S gene. The last line for each entry in first column represents the Genbank accession number.

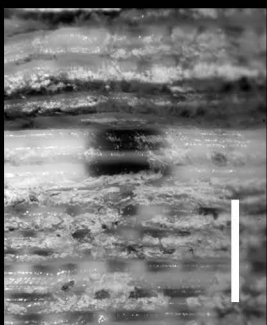
	17683	20015	17682	17681	17684	20014	17686	17685	17756	17754
MNHN 17683										
<i>Iotyrris musivum</i>										
(EU127874)										
MNHN 20015										
<i>Iotyrris musivum</i>										
(EU127875)	0.000									
MNHN 17682										
<i>Iotyrris devoizei</i>										
(EU127877)	0.002	0.002								
MNHN 17681										
<i>Iotyrris devoizei</i>										
(EU127876)	0.002	0.002	0.000							
MNHN 17684										
<i>Xenuroturrus legitima</i>										
(EU127878)	0.004	0.004	0.004	0.004						
MNHN 20014										
<i>Iotyrris devoizei</i>										
(EU127879)	0.002	0.002	0.000	0.000	0.004					
MNHN 17686										
<i>Iotyrris cingulifera</i>										
(EU127880)	0.005	0.005	0.005	0.005	0.006	0.005				
MNHN 17685										
<i>Iotyrris cingulifera</i>										
(EU127881)	0.004	0.004	0.004	0.004	0.005	0.004	0.001			
MNHN 17756										
<i>Lophiotoma albina</i>										
(EU127882)	0.011	0.011	0.011	0.011	0.016	0.011	0.015	0.016		
MNHN 17754										
<i>Turris crista</i>										
(EU015677)	0.019	0.019	0.019	0.019	0.024	0.019	0.027	0.024	0.011	
MNHN 17755										
<i>Crassispira</i> sp.										
(EU015707)	0.050	0.050	0.050	0.050	0.061	0.050	0.067	0.061	0.053	0.056





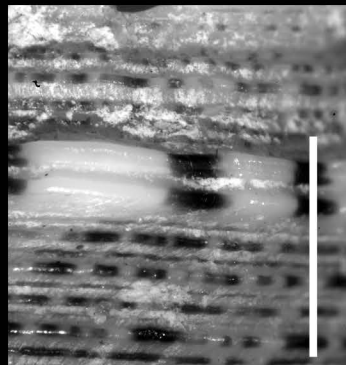


A

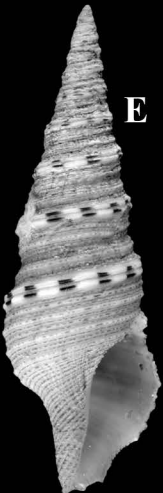


B

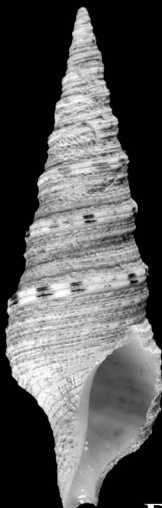
C



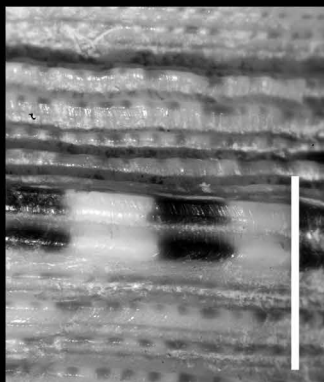
D



E



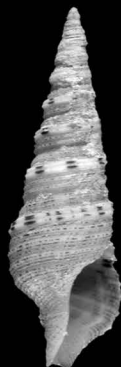
F



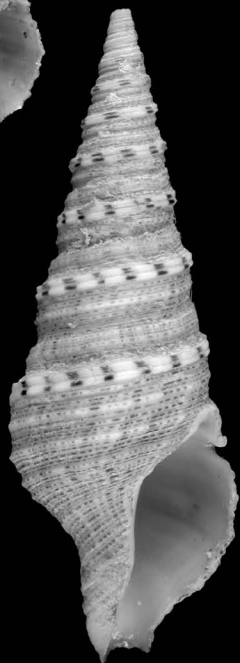
F



G



D



H

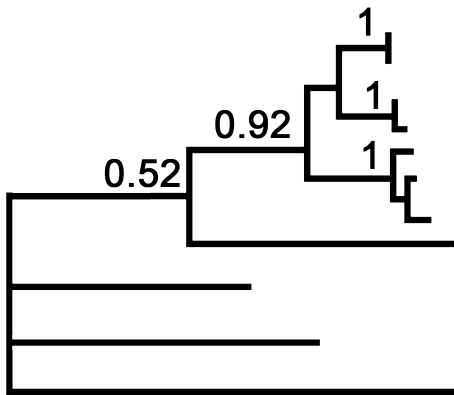


2 cm

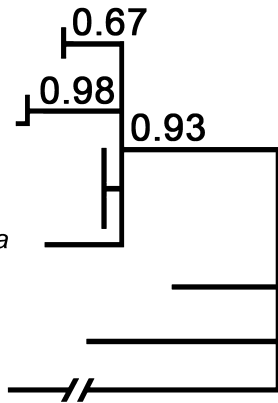
H

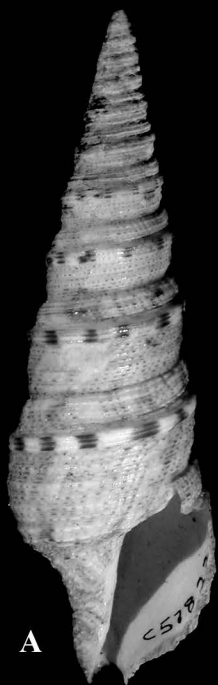


I

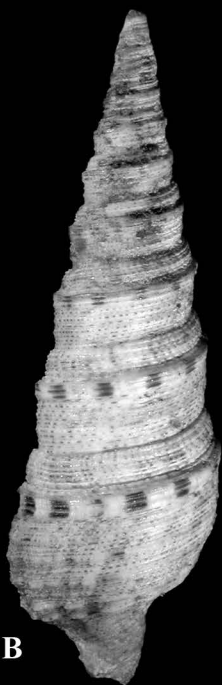


MNHN 17683 *lotyrris musivum*
 MNHN 20015 *lotyrris musivum*
 MNHN 17686 *lotyrris cingulifera*
 MNHN 17685 *lotyrris cingulifera*
 MNHN 17682 *lotyrris devoizei*
 MNHN 17681 *lotyrris devoizei*
 MNHN 20014 *lotyrris devoizei*
 MNHN 17684 *Xenuroturreis legitima*
 MNHN 17756 *Lophiotoma albina*
 MNHN 17754 *Turris crista*
 MNHN 17755 *Crassispira*





A



B



C



D



E



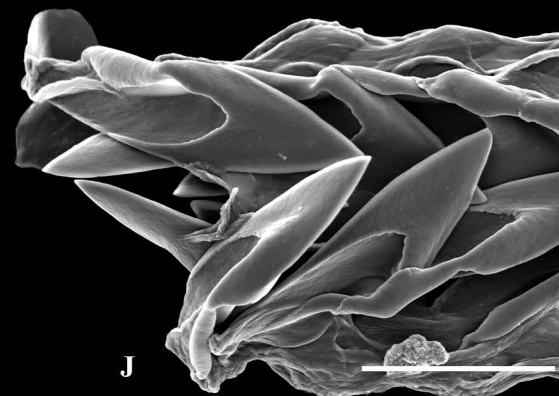
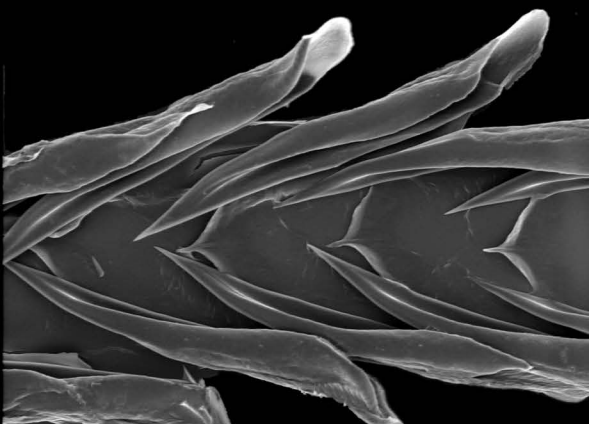
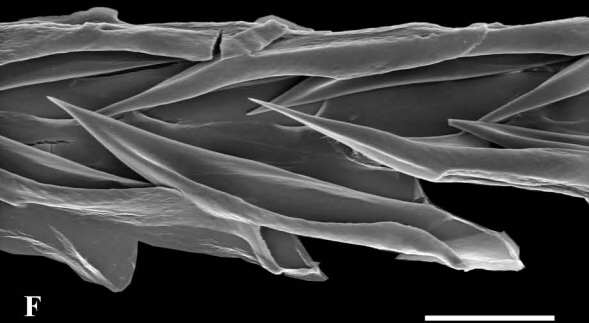
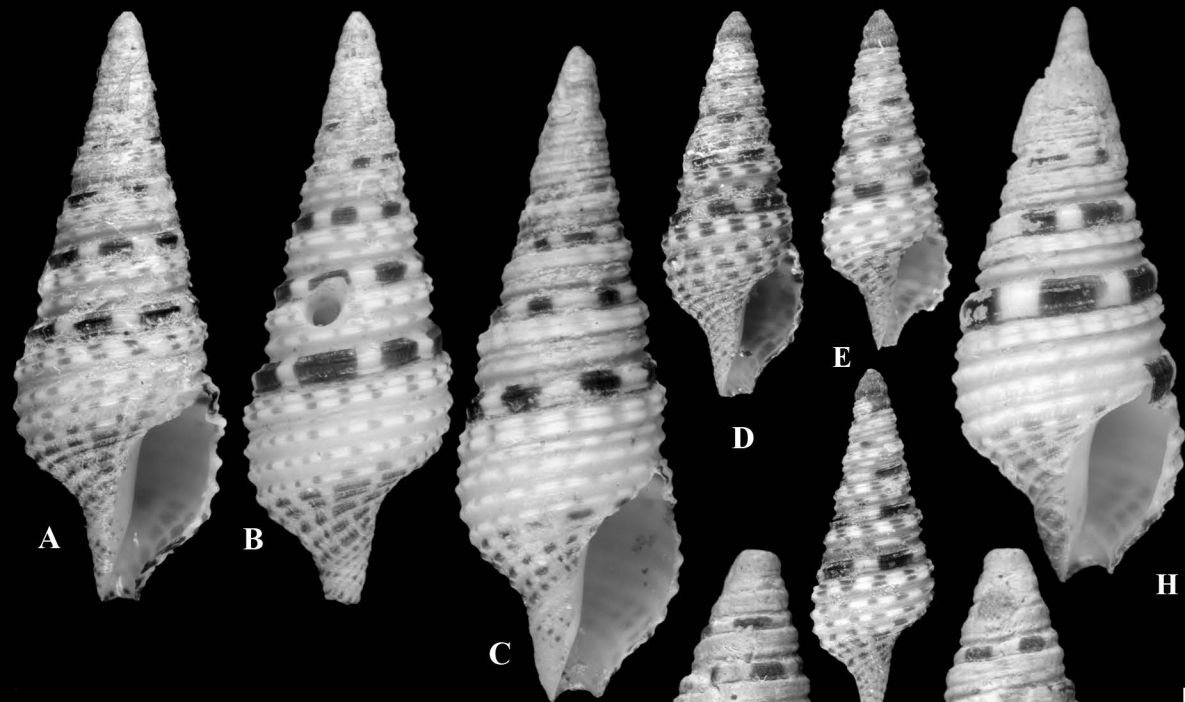
F



G



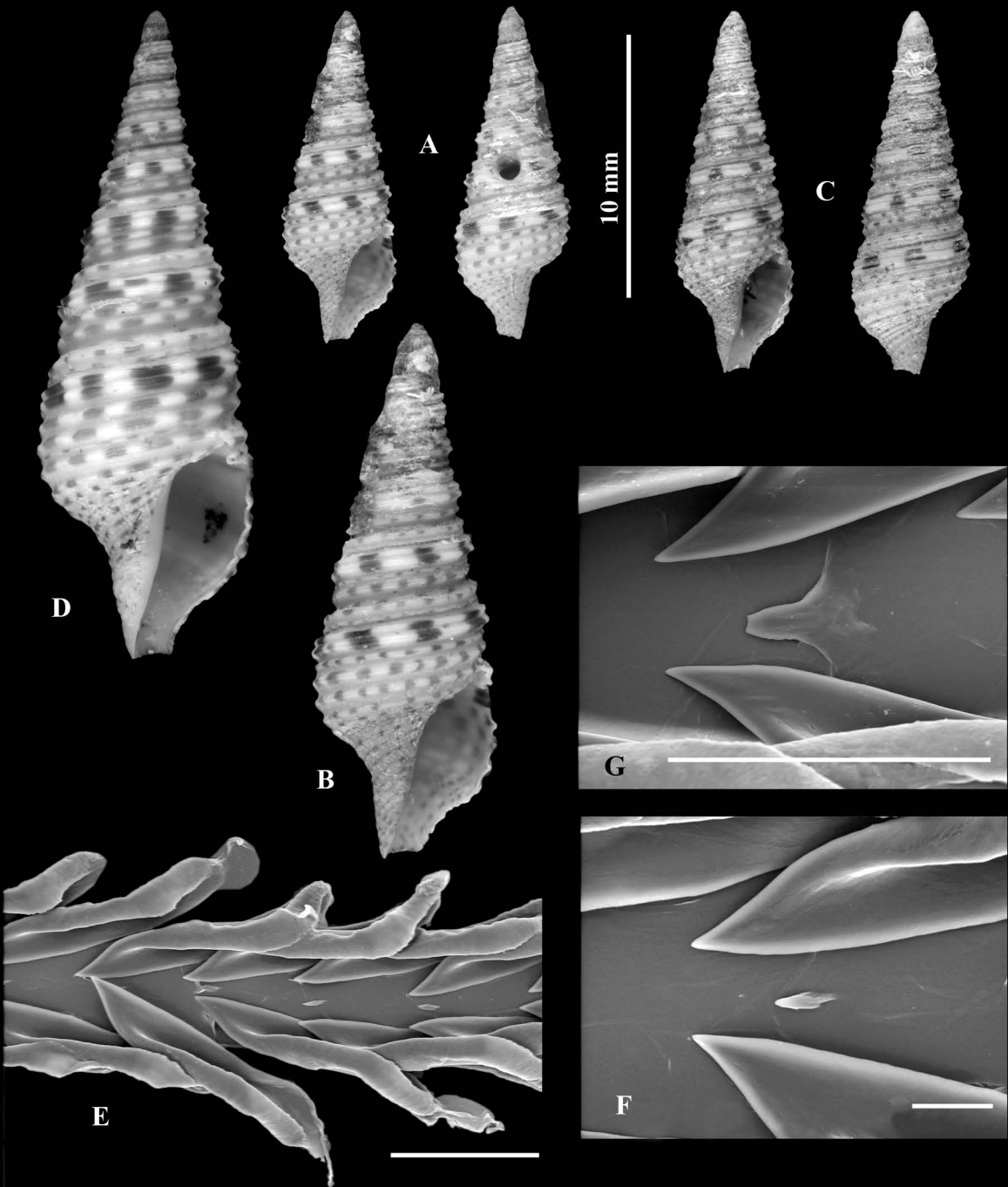
H



G

J

10 mm





A



B



C



E



G



D



F