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Morphological Proxies for Taxonomic Decision in Turrids (Mollusca, Neogastropoda): a Test of the Value of Shell and Radula Characters Using Molecular Data

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The state of the art of turrid (=Turridae s. l.) systematics is that shells — when they include 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 (=*Iotyrris*) and duplex teeth (=*Xenuroturris*) form two supported monophyletic clades. *Iotyrris 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

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 turriform Conoidea species worldwide may be in the 10,000–20,000 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 have been 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 they include the protoconch — are usually considered reliable species-level identifiers. However, convergence and homoplasy render 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 (Turrridae, 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

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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 has been 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.

MATERIALS 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 stubs, air dried, coated with gold-palladium, and investigated with a JEOL JSM 840A scanning electron microscope. Terminology and homology of the central teeth in Turrinae follow Kantor (2006).

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

Specimens examined

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 specimens (Fig. 2B, C).

New Caledonia. Koumac, Sta. 913, 20°58'S, 164°32'E, 10–13 m, 1 specimen (Fig. 2E); Sta. 944, 20°35'S, 164°12'E, 14–15 m, 1 specimen (Fig. 2F).

Loyalty Islands. LIFOU 2000, Sta. 1465, 20°47.7'S, 167°07.0'E, 35–45 m, 1 specimen (Fig. 2D).

Vanuatu, Espiritu Santo. SANTO 2006, Sta. DR87, 15°38.5'S, 167°15.1'E, 13 m, 1 specimen sequenced (MNHN 17684) (Figs. 2A, 8A).

Xenuroturris identified as "X. *cingulifera*" based on shell characters: specimens with semi-enrolled radular type (=*Iotyrris cingulifera* Lamarck, 1822).

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

Loyalty Islands. LIFOU 2000, Sta. 1422, 20°47.1'S, 167°07.4'E, 4 m, 1 specimen (Fig. 3B); Sta. 1423, 20°54.0'S, 167°07.3'E, 12 m, 2 specimens (Fig. 3C, D); Sta. 1425, 20°46.8'S, 167°07.2'E, 4–5 m, 1 specimen.

Vanuatu, Espiritu Santo. SANTO 2006, Sta. FS84, 15°33.6'S, 167°16.6'E, 5 m, 2 specimens 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. 6A, 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 (Figs. 6H, I, 8E).

DNA Sequencing

DNA was extracted from a piece of foot, using the 6100 Nucleic Acid Prepstation system (Applied Biosystem). A fragment of 658 bp of the mitochondrial cytochrome oxydase I (COI) gene was amplified with the universal primers LCO1490 and HCO2198 (Folmer et al., 1994). One nuclear gene fragment was also analyzed, 900 bp of the 28S rRNA gene, involving the D1, D2, and D3 domains (Hassouna et al., 1984), with primers C1 and D3 (Jovelin and Justine, 2001). All PCR reactions for both genes were performed in 25-μl volumes, containing 3 ng of DNA, 1X reaction buffer, 2.5 mM $MgCl_2$, 0.26 mM each dNTP, 0.3 μM each primer, 5% DMSO, and 1.5 units of Q-Bio Taq (Qbiogene). For 28S, thermal cycling conditions were 94°C for 4 min; 30 cycles of 94°C for 30 sec, 52°C for 1 min, and 72°C for 1 min; and 72°C for 10 min. Thermal cycling conditions for COI are described in Hebert et al. (2003).

PCR products were purified and sequenced by 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 to the primers used for PCR. All genes were sequenced for both directions to confirm accuracy of each sequence. Sequences were deposited in GenBank (see Tables 1 and 2 for accession numbers).

Phylogenetic analysis

Three species of Turridae (each represented by a single specimen) were used as outgroups for phylogenetic analyses: *Lophiotoma albina* (Lamarck, 1822) (Turrinae) (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) (Turrinae) (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 sequences were manually aligned, and 28S sequences were automatically aligned by using ClustalW multiple-alignment software implemented in BioEdit version 7.0.5.3 (Hall, 1999); the accuracy of the alignments 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 and Crandall, 2001), in conjunction with PAUP 4.0b10, following the Akaike information criterion (AIC).

Phylogenetic reconstruction were conducted by Bayesian analysis, consisting of two Markov chains (2,000,000 generations each with a sampling frequency of one tree each hundred generations) run in six parallel analyses in Mr. Bayes (Huelsenbeck et al., 2001). The same model of substitution used for computing 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% of 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 of the family Turridae (sensu Taylor et al., 1993) (Fig. 1A–

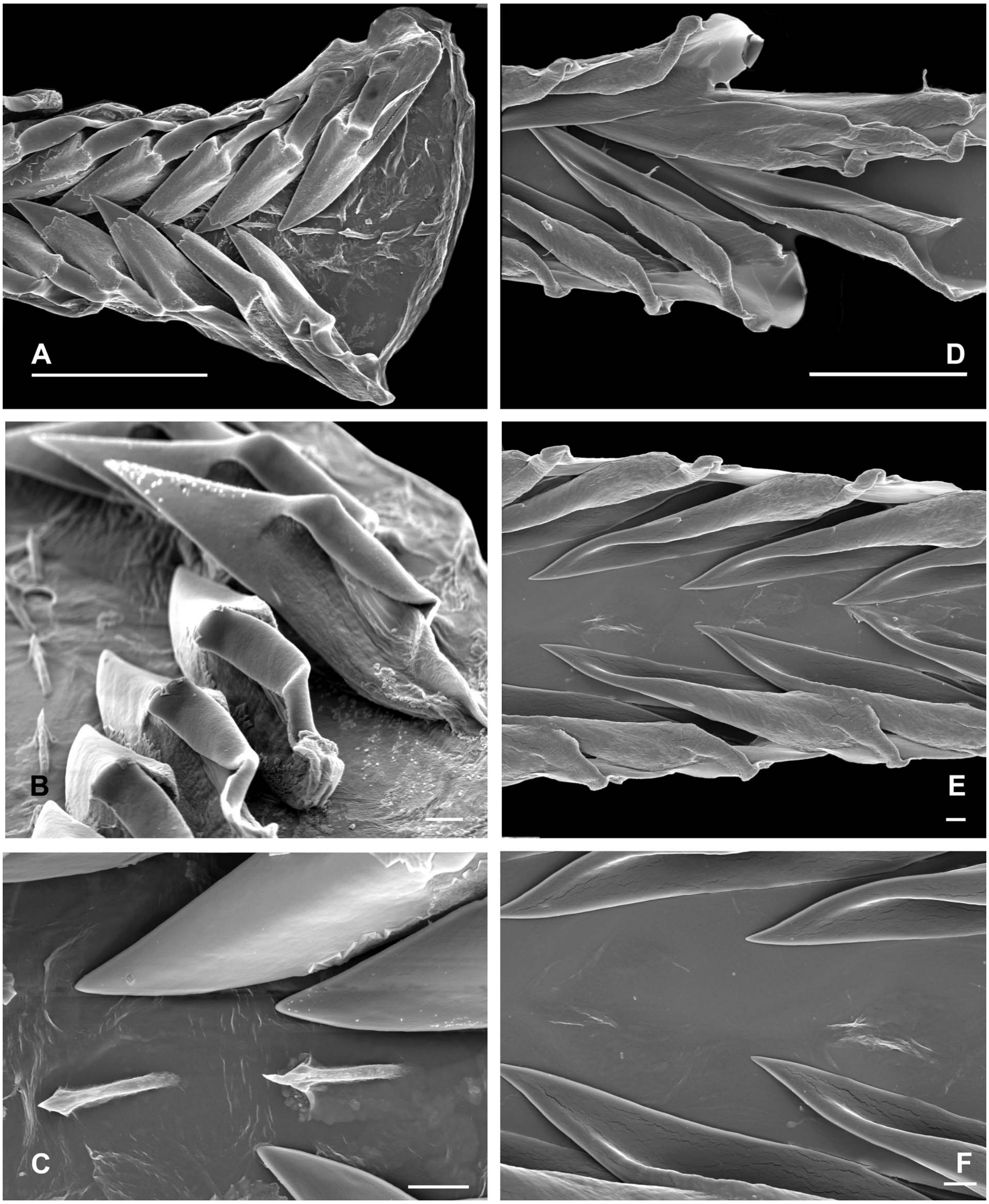

Fig. 1. Two radular types found in specimens originally identified as "*Xenuroturris cingulifera*". **(A–C)** Radula with duplex marginal teeth, from specimen (PANGLAO 2004, Sta. S22, SL 28.4 mm; for shell, see Fig. 2B) now identified as *Xenuroturris legitima*. **(D–F)** Radula with semi-enrolled marginal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

C). The anterior part of the tooth (closer to the tip), constituting about 0.42–0.50 of total tooth length, is solid, while the posterior part has two thickened edges, a thinner dorsal one and a thicker ventral one attached to the radular membrane (Fig. 1B). The central tooth is very small, narrow, and spear shaped. Lateral teeth are absent. The ratio between marginal tooth length and shell length varies from 0.47–0.57% (mean 0.52%, σ=0.03, n=9); that between tooth length and aperture length varies from 1.67–2.05% (mean 1.90%, σ=0.14, n=9).

The second radular type is characterized by "semi-enrolled" marginal teeth (Fig. 1D–F). Both edges of the marginal teeth are elevated and equally developed along the entire tooth length, and they delimit an intervening trough. 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 0.54–0.67% (mean 0.63%, σ=0.05, n=8), that between tooth length and aperture length varies from 1.90–2.37% (mean 2.21%, σ=0.18, n=8).

The two forms occur sympatrically, although not syntopically, at 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 "*Xenuroturris cingulifera*" (Figs. 2, 3). However, after we had evidence of the two radular types, close examination of the shells revealed subtle differences, as follows.

(1) All specimens of "*Xenuroturris 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. 3A, D, F, H) than in specimens with duplex teeth. The abapical, initially single and undivided, cord also becomes subdivided at a certain shell size, but only in the form with duplex teeth. This is shown in the specimen on Fig. 2A, in which the abapical cord is single on the adapical whorl and becomes subdivided on subsequent whorls. Large specimens of the form with duplex tooth thus have a peripheral zone with four thin, nearly even cords (Fig. 2A, C); specimens with the duplex marginal teeth tend to have slightly less convex peripheral cords.

(2) 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 a siphonal canal slightly more attenuated than that in the duplex form.

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

Molecular study

For COI and 28S, alignments resulted in sequences of 658 and 903 bp length respectively. No indel was found for COI. Within the ingroup, 97 sites were variable for COI, but only 14 for 28S. The Tamura-Nei model (TrN+G, with G=0.1047) model for COI and the general time reversible model (GTR+I, with I=0.8579) for 28S were identified as the best-fitting models.

Genetic distances are low (0.003; Table 1) between specimens of "*Xenuroturris cingulifera*" with semi-enrolled teeth (=true *Iotyrris cingulifera*), and are similar to the genetic distances between specimens of *I. devoizei*, or those of *I. musivum* (0 to 0.010). In contrast, 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* and *Iotyrris* clustered together for COI, but this result is not well supported (posterior probability=0.52; Fig. 4). Specimens with semi-enrolled teeth form a monophyletic group (although weakly supported) that exludes the specimen with duplex teeth. Within the semi-enrolled clade, three clades are evident, each containing two or three specimens. These three clades each include only specimens hypothesized to be conspecific based on shell and radula characters. Consequently, in the molecular tree, specimens of "*X. cingulifera*" with semi-enrolled teeth appear more closely related to *Iotyrris devoizei* and *I. musivum* than to the specimen of "*X. cingulifera*" with duplex teeth. Similar results were found for 28S, 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 *Iotyrris cingulifera*) and duplex teeth (=*X. legitima*). Monophyly of the *Xenuroturris*-*Iotyrris* clade is weakly supported (0.93). Within the semi-enrolled clade, the three clades defined with the COI gene are found again, but only one of them is strongly supported. Relationships between these three clades and the specimen of "*X. cingulifera*" with duplex teeth (=*X. legitima*) are not resolved.

Taxonomy

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 (in part): 322, Plate 175, Figs. 19, 20, non Fig. 12.

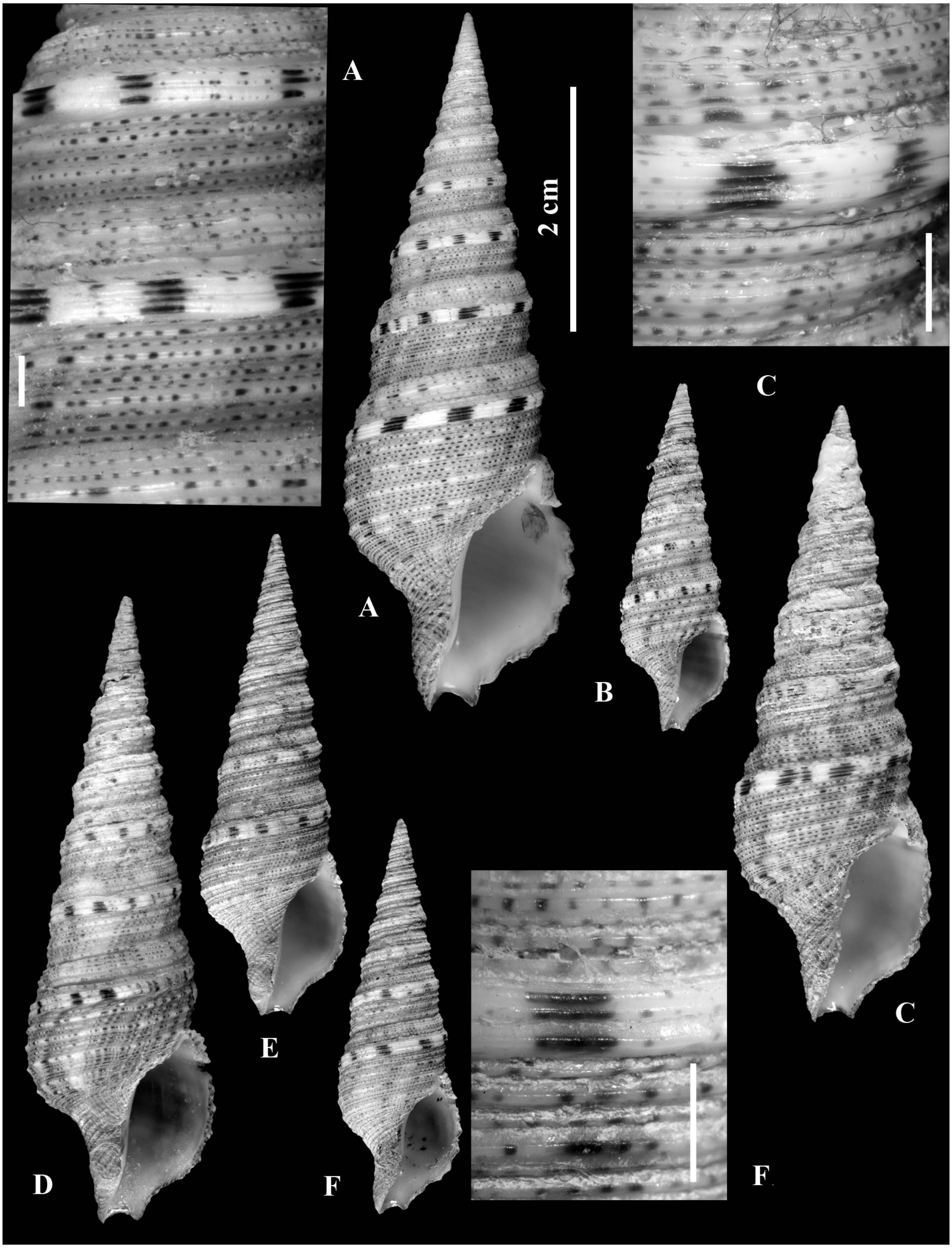

Fig. 2. *Xenuroturris legitima*. **(A)** MNHN 17684, Vanuatu, SANTO 2006, Sta. DR 087, whole shell (SL 57.0 mm) and close-up view of sculpture. **(B, C)** Philippines, Panglao 2004, Sta. S22; **(B)** SL 28.4 mm, **(C)** whole shell (SL 50.5 mm) and close-up view of sculpture. **(D)** Loyalty Islands, 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 are at the same scale; scale bars for close-ups, 2 mm.

Xenuroturris cingulifera, Medinskaya and Sysoev, 2002: 9, Fig. 3?, Fig. 6A.
Lophiotoma cingulifera, Olivera, 2002: Figs. 1F, 1G, H1, H2.

Syntypes. Two type specimens of *Xenuroturris legitima* housed in the Australian Museum are labeled as the 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 syn-

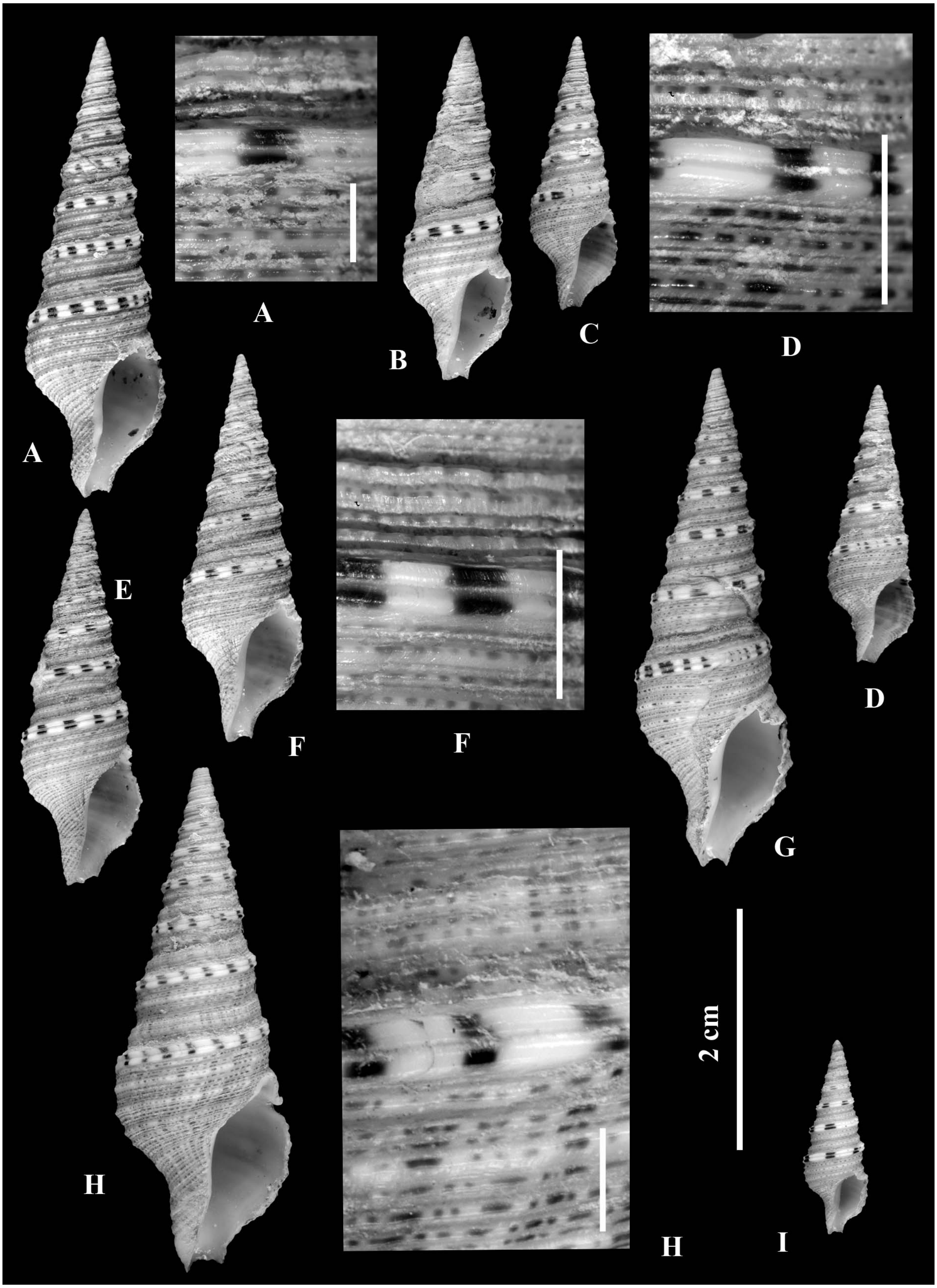

Fig. 3. *Iotyrris cingulifera.* **(A)** New Caledonia, Koumac, Sta. 1303, whole shell (SL 38.4 mm) and close-up view of sculpture. **(B)** Loyalty Islands, LIFOU 2000, Sta. 1422, SL 28.4 mm. **(C, D)** Loyalty Islands, LIFOU 2000, Sta. 1423; **(C)** SL 22.4 mm, **(D)** whole shell (SL 23.0 mm) and close-up 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 are at the same scale; scale bars of close-ups, 2 mm.

Table 1. Pairwise genetic distances for COI. The Genbank accession number for each entry in the first column is in parentheses.

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

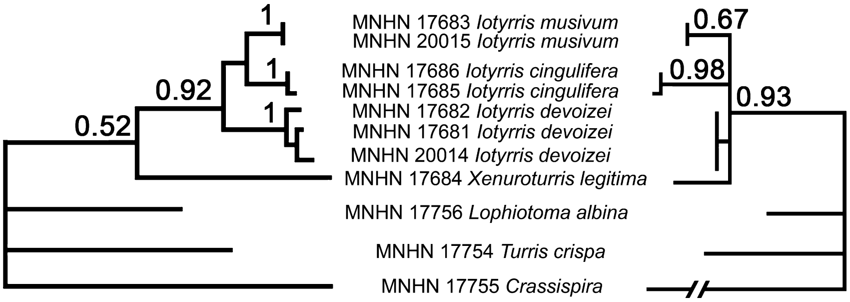

Fig. 4. Trees obtained for COI (left) and 28S (right), using Bayesian analysis. Posterior probabilities are indicated above branches.

Table 2. Pairwise genetic distances for 28S. The Genbank accession number for each entry in the first column is in parentheses.

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

types.

Type locality. Michaelmas Cay, Queensland, Australia.

Distribution. The distribution we ascertained includes New Caledonia, the Loyalty Islands, Vanuatu, and the Philippines. The species has also been reported from South Africa (Kilburn, 1983: 564, Figs. 30, 32) and Japan (Okutani, 2000: 631, Pl. 314, Fig. 57), but these records 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 Article 70.3 of the Code of Nomenclature.

Iotyrris cingulifera **(Lamarck, 1822)**

Pleurotoma cingulifera Lamarck, 1822: 94.

Selected synonymy:

Xenuroturris cingulifera cingulifera, Powell, 1964 (in part): 322, Plate 175, Fig. 12, non Figs. 19, 20.

Lophiotoma cingulifera, Olivera, 2002 (part.): 41, Fig. H3.

Syntypes. Three possible syntypes of *Pleurotoma cingulifera* are housed in the Muséum d'Histoire Naturelle de la Ville de Genève (MHNG 1097/62) (Fig. 5E–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) believed it to be restricted to Mauritius, a restriction that has no standing under the ICZN.

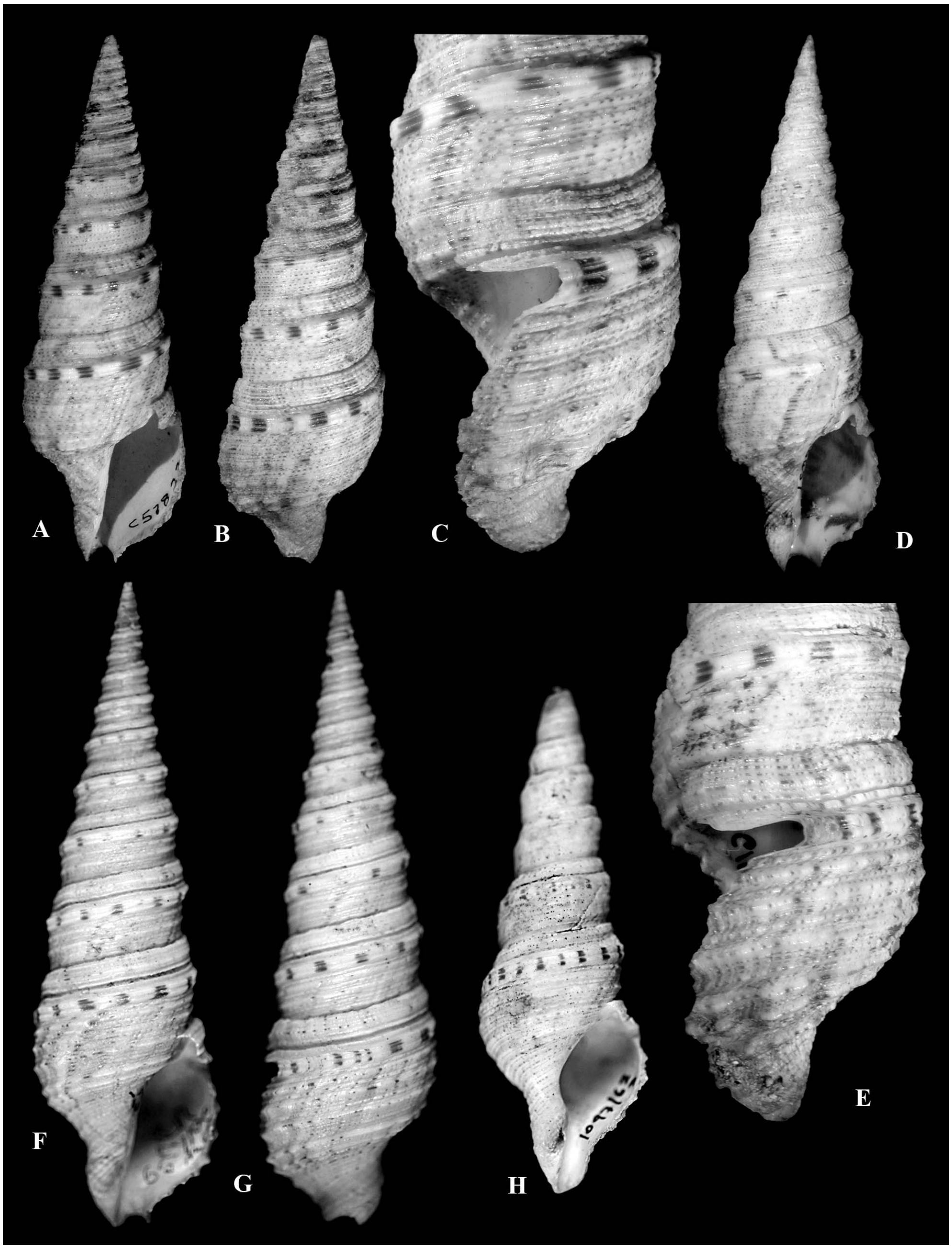

Fig. 5. **(A–E)** Syntypes of *Xenuroturris legitima* Iredale, 1929; **(A–C)** AMS C57823, SL 55.7 mm, **(D, E)** AMS C220457, SL 72 mm. **(F–H)** Syntypes of *Pleurotoma cingulifera* Lamarck, 1822; **(F, G)** MHNG 1097/62/1, SL 65.0 mm, **(H)** MHNG 1097/62/3, SL 54.0 mm. A–E, photos by A. C. Miller, copyright Australian Museum; F–H, photos courtesy of Y. Finet, MHNG.

Distribution. The distribution we ascertained 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. 6A–G)

Type material. Holotype MNHN 20014 and two 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 (dd, collected as shell only; lv, collected alive). 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,

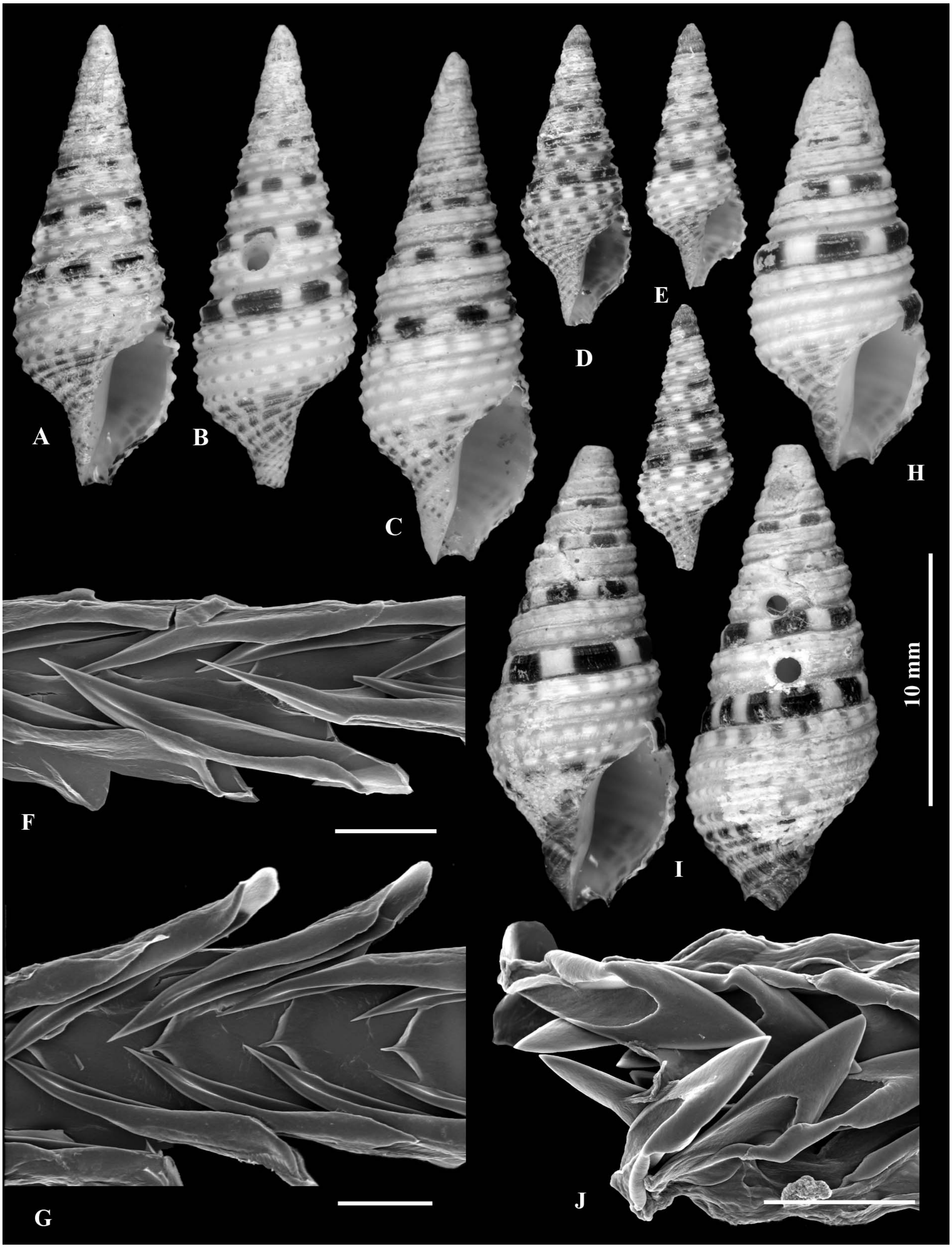

Fig. 6. **(A–G)** *Iotyrris devoizei* n. sp. **(A, B)** Holotype, MNHN 20014 (the hole in the back is the result of drilling to extract the radula. **(C)** Loyalty Islands, LIFOU 2000, Sta. 1453, 21–30 m, SL 19.9 mm. **(D)** Paratype, MNHN 17681, SL 11.8 mm. **(E)** Apertural and dorsal views of paratype, MNHN 17682, SL 10.2 mm. **(F)** Radula of holotype. **(G)** Radula of the specimen in Fig. 6C. **(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. 6I. All shells are at the same scale; scale bars for the radulae, 50 µm.

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 (Figs. 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 16–30 m, shells from 4–47 m. It is possible that the species also occurs in Hawaii and the Marquesas.

Description (holotype). Shell height 17.8 mm, shell diameter 6.3 mm, last whorl height 9.0 mm, aperture height 5.9 mm. 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 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 for one narrow thread between the lower shoulder cord and upper peripheral 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 onto the parietal wall. Color creamy white, with strong, dark spots on the subsutural ramp; much lighter yellow narrow spots covering all the cords of the periphery; tessellate, closely spaced dark spots on the cords of the shell base; and smaller, slightly lighter spots on the threads of the canal.

Remarks. Paratypes are similar to the holotype in shell outline and sculpture, and appear to be juveniles. However, one of them (MNHN 17681) (Fig. 6D), with a shell length of only 11.8 mm, is already a mature male with a long penis equal in length to 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. 6E) is best preserved, but its nucleus missing; the number of whorls is at least 4. The largest specimen we attribute to *I. devoizei* has a shell length of 27.1 mm. *Iotyrris 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 are 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).

Iotyrris musivum **n. sp.**

(Fig. 7)

Type material. Holotype (MNHN 20015) and one 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 color pattern; used as a noun in apposition.

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 (Figs. 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 height 12.6 mm, shell diameter 4.3 mm, last whorl height 6.6 mm, aperture height 3.9 mm. 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, two narrow, closely spaced cords that are tall and triangular in section form 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 onto the parietal wall. Color creamy white, with regularly spaced, light brown spots covering cords of the entire shell surface and much more pronounced, strong, darker subrectangular spots on the shoulder cords. Operculum yellow, transparent, leaf-shaped, with terminal nucleus.

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 an additional thin, sharp spiral thread immediately below the suture, and 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 a relatively shorter canal. In addition, the color marks on the shoulder keels are much less pronounced in *I. marquesensis*

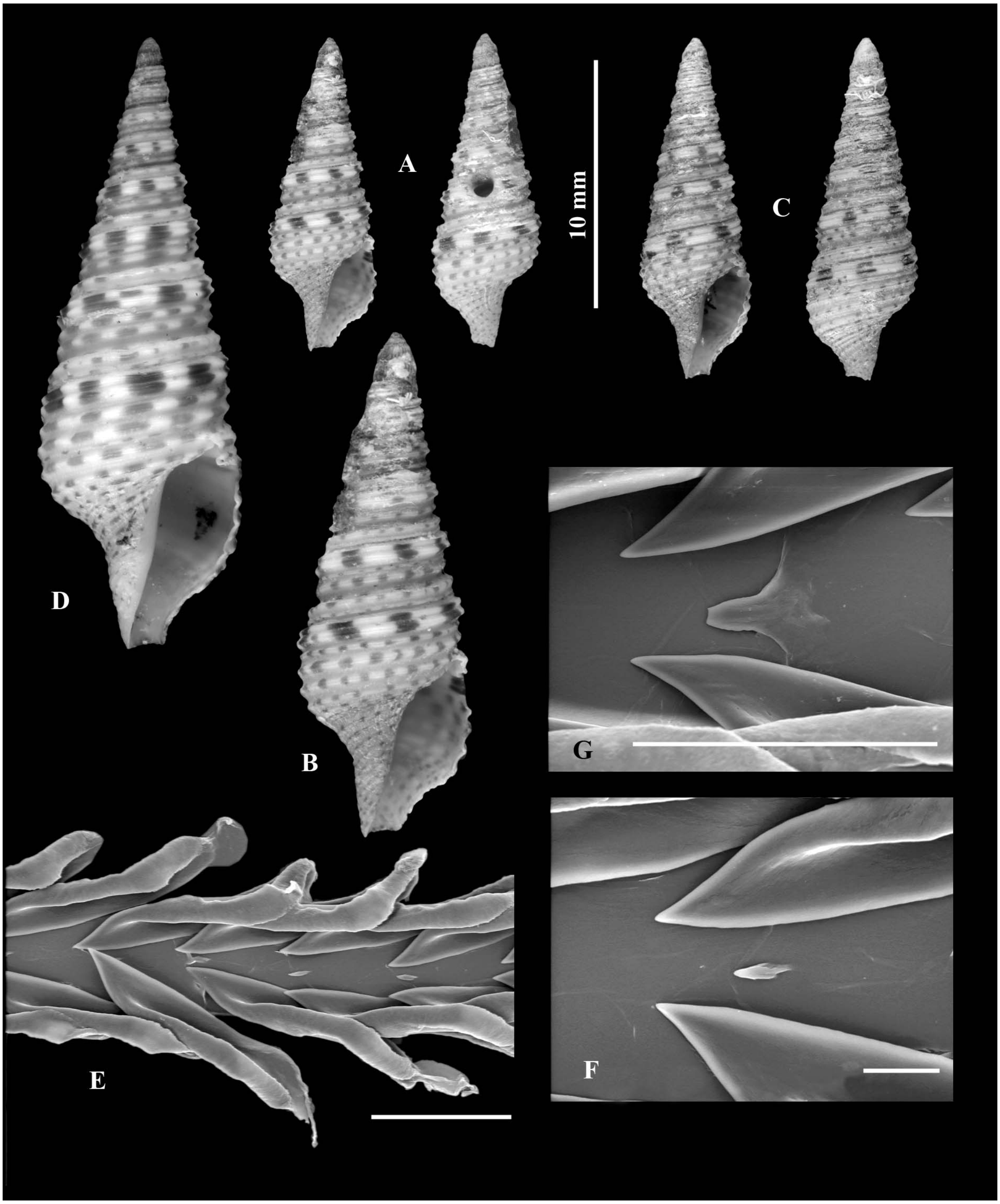

Fig. 7. *Iotyrris musivum* n. sp. **(A, B)** Holotype (B, enlarged), MNHN 20015, SL 12.6 mm (the hole in the back is the result of drilling to extract the radula). **(C)** Paratype, MNHN 17683, SL 13.9 mm. **(D)** Loyalty Islands, LIFOU 2000, Sta. 1421, 4 m, SL 24.5 mm. **(E, F)** Radula of holotype. **(G)** Central field of the radula of the specimen in Fig. 7D. All shells except B are at the same scale. Scale bars for E and G, 50 μm; F, 10 μm.

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, but in *X. sp.* only by a narrow, shallow groove. *Iotyrris musivum* differs from small specimens of *I. cingulifera* in having much larger color spots on the shell, brighter color spots on the shoulder cords, and coarser spiral sculpture. Another species remotely similar to *I. musivum* is *Lophiotoma olangoensis* Olivera, 2002. *Iotyrris musivum* 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. The radula of a specimen from Lifou (Loyalty Islands) that we identified as *L. olangoensis* appeared to be similar to that of *Xenuroturris legitima*, which consists of duplex marginal teeth, a very small, narrow central tooth, and vestigial laterals.

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 observation of the radulae:

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

(2) For COI, specimens of "*X. cingulifera*" with semi-enrolled teeth are more closely related to other species of *Iotyrris* than to the specimens of "*X. cingulifera*" with duplex teeth. As the species 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, *Iotyrris devoizei* and *I. musivum*, also is not in 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. *Iotyrris devoizei* and *I. musivum* are described as new species herein.

Taxonomic and nomenclatural implications

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

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

The syntypes of *Pleurotoma cingulifera* Lamarck, 1822 are badly worn specimens that render identification difficult. The only significative 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, this cord is always subdivided. Although some ambiguity remains, 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-collected 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 new monotypic 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 turrines with *Xenuroturris*-type shells and semi-enrolled radular teeth.

The 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 tooth shape. In practice, similarity in the shell together with dissimilarity in the 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 the radula. The subfamily Zonulispirinae McLean, 1971 (Turridae) was proposed mainly on the basis of the radula having semi-enrolled marginal teeth only, while in shell characters this subfamily is rather similar to 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 in the course of tooth maturation, by thickening of the tooth edges, longitudinal folding, and progressive elevation of the posterior edge of the tooth from the membrane. They illustrated this process for what they called *Xenuroturris cingulifera* with duplex teeth (=*X. legitima*) (Kantor and Taylor, 2000: Fig. 3g, h). Comparison of the process of maturation in both tooth 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, which is responsible for the long, solid anterior 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 *Xenuroturris*-type shells were examined from animals with dried softparts, and reveal further species pairs with duplex and semi-enrolled teeth. One case is *Xenuroturris 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 a 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 Fig. 2B2, 2B3, 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 *Xenuroturris cerithiformis* Powell, 1964 (with duplex teeth) (Fig. 8G), which differ so little in shell shape that Medinskaya and Sysoev (2001) initially confused them.

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

It is remarkable that within the subfamily Turrinae, semi-enrolled radular teeth are found only in this clade. This raises the question whether they originated once in the genus (in which case *Iotyrris* is indeed monophyletic, with conchologically similar species having different radular types as the result of convergence or homoplasy), or appeared several times (in which case *Iotyrris* is polyphyletic, with conchologically similar species having different radular types being 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 morphology are the result of conserved patterns rather than the result of convergence of evolved patterns.

Currently, *Xenuroturris* is considered a subgenus of *Lophiotoma* Casey, 1904 (Kilburn, 1983; Taylor et al., 1993; Higo et al., 1993), the main difference being the truncated base of *Xenuroturris*. Olivera (2002) even expressed serious doubts that *Xenuroturris* 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 thus not informative about the phylogenetic relationships between the two genera.

In conclusion, and despite these reservations, our working hypothesis is that *Lophiotoma*, *Xenuroturris*, 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 this diversity, we must be prepared that many of the currently accepted taxa are poly- or paraphyletic, at all taxonomic levels: specific, generic, and subfamilial.

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