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A quest for the lost types of *Lophiotoma* (Gastropoda: Conoidea: Turridae): integrative taxonomy in a nomenclatural mess

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Integrative taxonomy, and in particular species delimitation using molecular data, often leads to the discovery of new species. However, these new species are not systematically turned into formally described species, because, among other reasons, linking molecularly defined groups with available taxonomic names can be tricky. Here we delimit species in the genus *Lophiotoma* (Gastropoda, Conoidea, Turridae) using two unlinked genetic markers (the mitochondrial *COI* gene and the nuclear *28S* ribosomal RNA gene), shell and radula characters, and geographic and bathymetric distribution. Several methods of species delimitation (ABGD, GMYC and PTP) resulted in several alternate species partitions, discussed using an integrative approach. We ended up with ten different species, among which seven have been unequivocally linked to available species names. We designate neotypes for two of them (*L. acuta*, *L. jickelii*). The three remaining species are described as new: ***L. semfala* sp. nov.**, ***L. bratasusa* sp. nov.** and ***L. kina* sp. nov.** We discuss the difficulties encountered in locating type specimens and in linking them to recognized molecular species, in a context where the vast majority of mollusc types are empty, dried shells and consequently difficult to sequence.

ADDITIONAL KEYWORDS: ABGD – GMYC – neotype designation – PTP – species delimitation – species description.

INTRODUCTION

While DNA and integrative taxonomy (Dayrat, 2005; Will, Mishler & Wheeler, 2005) certainly participated in the revival of taxonomic research in the last 10 years, their impact on species descriptions remains limited. Most species descriptions are still based on morphological characters only (Pante, Schoelinck & Puillandre, 2014) and descriptions that include a molecular diagnosis remain scarce (Jörger & Schrödl, 2013; Renner, 2016). In the Mollusca collection of the Muséum National d'Histoire Naturelle (MNHN), Paris, the first holotype associated with a DNA sequence was registered in 2008; since then, 2126 holotypes have been deposited in the MNHN collection of molluscs, but only 65 are linked to a DNA sequence. As quoted by Bouchet & Strong (2010), '80% of the new species descriptions of shelled marine gastropod species published in 2006 contained a description of the shell only [i.e. not only lacking mention of DNA characters, but also anatomy or radula]'.

Why does the input of DNA characters remain so insignificant in the description of biodiversity, in spite of its growing popularity among biologists? One of the reasons lies probably in the dichotomy between taxonomists (including amateurs, particularly active in molluscs) and 'molecularists', people who actually produce the DNA sequences. Most species remain described based on morphological characters because these characters still remain largely more accessible than DNA

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characters. Conversely, most molecularists are not trained in taxonomy and nomenclature, and many of the new species they discover, some of them being undetectable with morphological characters, remain undescribed and thus virtually ignored by the scientific community (Goldstein & DeSalle, 2011). Nevertheless, both approaches should actually be encouraged and applied synergistically: on the one hand, many species are difficult to distinguish morphologically, and in these cases integrative taxonomy, including DNA characters, has proved its usefulness (Pante *et al.*, 2015); on the other hand, linking molecularly defined species to available names, and eventually proposing new names, requires knowledge of the nomenclatural rules, of the taxonomic literature and, in particular, of the type specimens.

However, even close examination of the type material may be of little use in marine molluscs, as many name-bearing types simply do not fulfil their function, being too worn and badly preserved to confidently link the species name to other, more recently collected, material (Bouchet & Strong, 2010). It is particularly true when several species share identical teleoconchs, differentiated only by protoconchs, radulae, anatomical or even DNA characters, as many of these characters are inaccessible on these types. Thus, a lost name-bearing type would actually be preferable, because in this case a neotype could be designated, which would provide an ultimate solution to a species identity problem. This, however, requires either a proof that the name-bearing types were lost or application to the Commission of Zoological nomenclature, both of which are time-consuming procedures.

To illustrate the benefit of a combination of molecularists and taxonomists, we applied an integrative taxonomic approach in a group of marine gastropods, *Lophiotoma* (Gastropoda, Conoidea, Turridae), which cumulates many of the difficulties listed above, plus some others, making it a good model to illustrate the link between species delimitation and species description: (1) preliminary results published in Puillandre *et al.* (2012b) suggest that several MOTUs can share very similar shells; (2) because of their shell variability, several described species have been synonymized in the literature, and many names are potentially applicable; and (3) type specimens of some species have been lost and are known by figures only and therefore are difficult to link to subsequently collected specimens. In this study, we apply the name *Lophiotoma* to the clade defined in Puillandre *et al.* (2012b) that includes the type species *L. acuta* (Perry, 1811), but exclude other species referred to as *Lophiotoma* [e.g. *L. albina* (Lamarck, 1822) or *L. natalensis* Bozzetti, 2016], or sometimes as 'larger *Lophiotoma*' (Olivera, 2004), but which are not phylogenetically related to *L. acuta*. These shallow-water turrids, restricted to the Indo-Pacific, have been known since the early 19th century. Like most other conoideans, they are characterized by a venom apparatus, producing toxins used to capture their prey (most likely polychaetes). Their taxonomy was revised by Powell (1964), and although they are regularly sampled by shell collectors, only one additional species (*L. vezzaroi* Cossignani, 2015) referable to the *Lophiotoma* group, as circumscribed here, has been described since.

To delimit species in this genus, we followed the general workflow of Puillandre *et al.* (2012b): species hypotheses are proposed in an integrative framework, based on a unified species concept in which species are considered as definitely diverging lineages (De Queiroz, 2007; Samadi & Barberousse, 2009). First, primary species hypotheses (PSH) were proposed using part of the mitochondrial *COI* gene and three of the most widely used methods based on monolocus data: ABGD (automatic barcode gap discovery; Puillandre *et al.*, 2012a), GMYC (general mixed Yule coalescent model; Pons *et al.*, 2006; Monaghan *et al.*, 2009) and PTP (Poisson tree processes; Zhang *et al.*, 2013). Second, monophyly of the PSH was tested performing maximum likelihood and Bayesian inference analyses on both *COI* and nuclear *28S* genes, two unlinked genetic markers, to check whether each PSH corresponds to an independent lineage in both gene trees. Finally, morphological variability and geographic and bathymetric distributions were integrated to turn the PSH into secondary species hypotheses (SSH). In the final step, and after a deep search of the literature and in museum collections, available names were tentatively applied to the SSH, relying on shell characters and type localities; when no available name was found, the SSH was described as a new species.

MATERIAL AND METHODS

Sampling

The material was collected during several expeditions to the Indo-Pacific: PANGLAO 2004 and AURORA 2007 in the Philippines, SANTO 2006 in Vanuatu, INHACA 2011 in Mozambique, Nha-Trang in Vietnam (2010–2016) and PAPUA NIUGINI (2012) and KAVIENG 2014 in Papua New Guinea (expeditions.mnhn.fr) (Fig. 1). All material is stored in the MNHN.

Until 2012, live specimens for molecular analysis were anaesthetized with an isotonic solution of $MgCl_2$ and fixed in 96% ethanol. Specimens collected during later expeditions were processed with a microwave oven (Galindo *et al.*, 2014): the living molluscs in small volumes of sea water were exposed to microwaves for 7–30 s, depending on specimen size. Bodies were immediately removed from shells and dropped in 96% ethanol. Specimens are registered in the MNHN collection and sequences were deposited in BOLD (Barcode of Life Datasystem) and GenBank (Table S1).

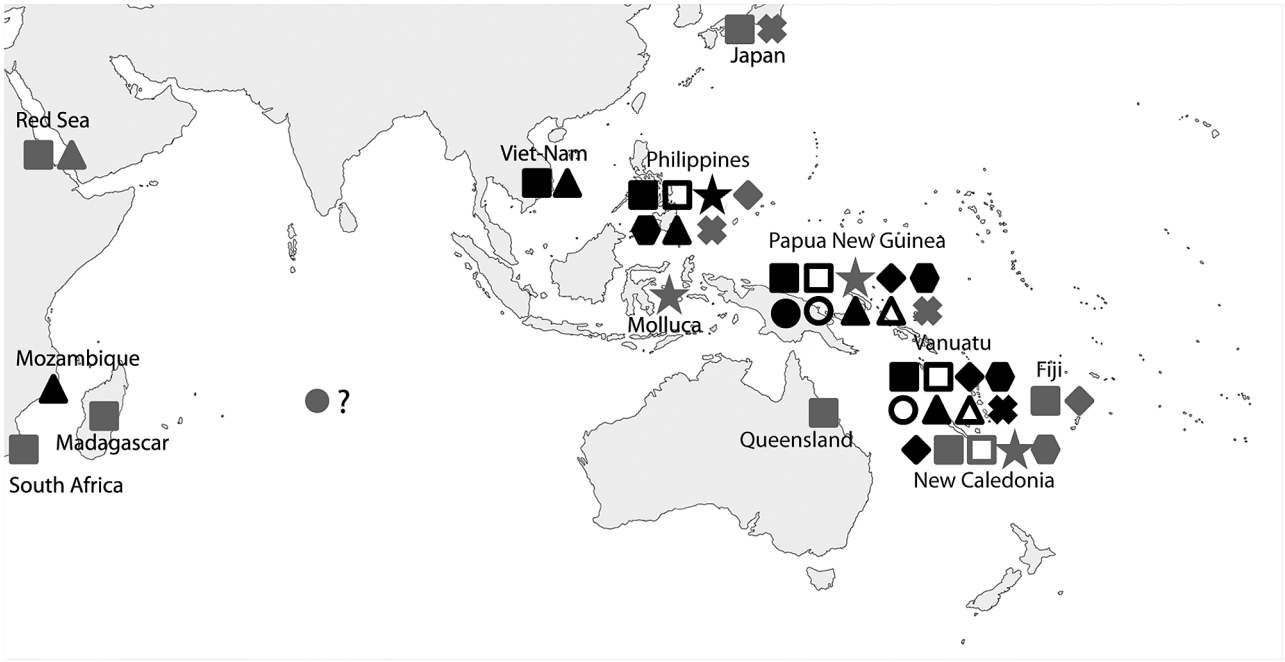

Figure 1. Map showing the species distributions. Filled squares: *L. acuta*; empty squares: ***L. semfala* sp. nov.**; stars: *L. polytropa*; diamonds: *L. abbreviate*; hexagons: *L. brevicaudata*; full circles: *L. picturata*; empty circles: ***L. bratasusa* sp. nov.**; full triangles: *L. jickelii*; empty triangles: ***L. kina* sp. nov.**; crosses: *L. vezzaroi*; black symbols: species presence confirmed with sequenced specimens; grey symbols: species presence reported in the literature or confirmed by studied (non-sequenced) specimens. ?: 'Indian Ocean'.

DNA SEQUENCING

DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the manufacturers' recommendations. A fragment of the cytochrome oxidase subunit I (*COI*) and of the *28S* rRNA genes was amplified using universal primers LCO1490/HCO2198 (Folmer *et al.*, 1994) and either C1/D3 (Jovelin & Justine, 2001) or C2CONO (GAAAAGAACTTTGAAGAGAGAGT) / D3 (Ober, 2002), respectively. PCRs were performed in 25 µL, containing 3 ng of DNA, 1X reaction buffer, 2.5 mM $MgCl_2$, 0.26 mM dNTP, 0.3 mM each primer, 5% DMSO and 1.5 units of Qbiogene Q-Bio Taq. For the *COI* fragment, amplification consisted of an initial denaturation step at 94 °C for 4 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s, followed by extension at 72 °C for 1 min. The final extension was at 72 °C for 5 min. The *28S* PCRs were performed in 20 µL reaction volumes, containing a final concentration of 1X SsoAdvanced Universal SYBR Green Supermix, 0.3 mM primers and 0.5 µg/µL of BSA and 1 µL of DNA extract. The amplification thermal profiles consisted of an initial denaturation for 3 min at 94 °C, followed by 40 cycles of denaturation at 94 °C for 30 s, annealing at 60 °C for 30 s, extension at 72 °C for 1 min and a final extension at 72 °C for 5 min. PCR products were purified and sequenced by the Eurofins sequencing facility.

SPECIES DELIMITATION

COI sequences were aligned manually; *28S* sequences were aligned using Muscle (Edgar, 2004) and alignments were checked by eye. Only 47 (over 907) nucleotides were variable in the *28S* alignment, and only a few indels (of one nucleotide each) were detected. Pairwise genetic distances (*p*-distances) were calculated using MEGA 6 (Tamura *et al.*, 2013), following Srivathsan & Meier (2012). ABGD, GMYC, PTP and the phylogenetic methods were applied to the *COI* and *28S* alignments, plus a concatenation of the *COI* and *28S* alignments (for a subset of specimens – see Results section). For ABGD, the web version (http://wwwabi.snv.jussieu.fr/public/abgd) and the default parameters were used, with a p-distance model. Bayesian trees were reconstructed using BEAST v1.8.3 (Drummond *et al.*, 2012), running 100 000 000 (for the *28S* and *COI* + *28S* datasets) or 200 000 000 (for the *COI* dataset) generations with a sampling frequency of one tree each 4000 generations. Relative divergence times were estimated using a relaxed log-normal clock with a coalescent prior and a constant population size, following the recommendations of Monaghan *et al.* (2009). Both the 'single' (one single threshold is defined for the whole tree to delimit species) and 'multiple' (multiple thresholds in the tree can be eventually defined) methods of GMYC were applied using the trees obtained

with BEAST. Maximum likelihood trees, using RaxML v8.2.8 (Stamatakis, 2006), with the robustness of the nodes assessed using 1000 bootstraps, and a Bayesian tree, using Mr.Bayes 3.2.6 (Huelsenbeck, Ronquist & Hall, 2001), were reconstructed. For the MrBayes analyses, each of the two runs consisted of eight Markov chains and 20 000 000 generations, with eight chains, five swaps at each generation, a sampling frequency of one tree each 2000 generations and a chain temperature set at 0.02. For the Bayesian analyses (BEAST and MrBayes), convergence of each run was evaluated using TRACER 1.6 (Rambaut & Drummond, 2014) to check that all effective sample size values exceeded 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. All phylogenetic analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2). In all cases, a GTR + I + G substitution model was used, and the *COI* gene was divided into three partitions corresponding to the three codon positions (as suggested using the BIC score calculated by PartitionFinder – Lanfear *et al.*, 2016). For the concatenated datasets, four partitions were defined (three codon positions of the *COI* and *28S* gene). PTP was run with defaults parameters using the RAxML trees. Two specimens of closely related taxa were used as outgroups for phylogenetic analyses: *Turris babylonia* (Linnaeus, 1758) and *Iotyrris musivum* Kantor, Puillandre, Olivera & Bouchet, 2008 (Conoidea, Turridae).

The R package SPIDER 1.4-1 (Brown *et al.*, 2012) was used to identify pure diagnostic sites in each delimited species in the *COI* and *28S* alignments.

Shell morphology and radula

Radulae were prepared by standard methods (Kantor & Puillandre, 2012) and examined by scanning electron microscope TeScan TS5130MM in the Institute of Ecology and Evolution of Russian Academy of Sciences (IEE RAS). Protoconchs were measured in standard position and the number of whorls counted according to Bouchet & Kantor (2004).

Abbreviations used in text

Abbreviations of museums and repositories

MMM: Mostra Mondiale Malacologia.
MHNG: Muséum d'Histoire Naturelle, Geneva, Switzerland.
MNHN: Muséum National d'Histoire Naturelle, Paris, France.
NHMUK: Natural History Museum of United Kingdom, London, UK.
SMF: Forschungsinstitut Senckenberg, Frankfurt, Germany.
USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.
ZMB: Museum für Naturkunde, Humboldt-Universität, Berlin, Germany.

Other abbreviations

AL: Shell aperture length;
R/V: research vessel;
SL: shell length;
SW: shell width;
st.: station.

RESULTS

Based on the partition with the highest number of PSH obtained with the *COI* gene, we built a reduced concatenated (*COI* + *28S*) dataset to limit computational time: a maximum of five specimens per PSH and per geographic region were kept. All the partitions obtained with ABGD, GMYC and PTP for the three datasets are shown in the Table 1. For the *COI* and *COI* + *28S* datasets, two partitions are discussed among the partitions proposed by ABGD: the partitions with the highest ('splitter' partition) and lowest ('lumper' partition) number of PSH (for the *28S* dataset, only one partition was proposed by ABGD). The results of the GMYC 'multiple' analyses are not shown, nor are the results of the GMYC 'single' analysis for *28S*, because they proposed an unrealistic number of PSH, that is not in agreement with either of the other methods, the phylogenetic trees or the other characters (111 PSH with the dataset *COI* for GMYC 'multiple', 27 for the *COI* + *28S* dataset for the GMYC 'multiple', and 79 and 78 for the *28S* dataset for the GMYC 'single' and 'multiple', respectively). In all cases, the GMYC 'multiple' partition was not significantly better than the GMYC 'single' partition ($P >> 0.05$). The *28S* gene is much less variable than the *COI* gene, and ABGD provided very few PSH with this gene (only five): this partition will be ignored in the rest of the text. In all the other cases, the number of PSH delimited varies from 8 to 16, all of them being compatible (i.e. they correspond to more or less inclusive PSH). In several cases (*L. picturata* 1, *L. semfala* 2 and *L. kina* 2 see Table 1 and below), these splits correspond to a single specimen isolated from the others, in PSH including few specimens (fewer than five).

By comparing the PSH obtained with the different datasets (Table 1), the results of the phylogenetic analyses (Figs 2, 3), the morphological variation and the bathymetrical and geographical distributions (Table S1), we turned the PSH into SSH and attributed available names to them or described them as new. Two PSH are found with all the genes and methods, have very distinct shells and in our material are restricted to a single archipelago: they were identified as *L. polytropa* (Helbling, 1779), restricted to the Philippines, and *L. vezzaroi*, in Vanuatu. Those two PSH also always correspond to highly supported clades in the phylogenetic analyses. The PSH identified as *L. abbreviata* (Reeve,

Table 1. Results of the integrative species delimitation approach

				COI				*28S*		*COI* + *28S*				Monophyly (PP/B)													
PSH	# *COI*	# *28S*	# *COI* + *28S*	ABGD		GMYC	PTP	ABGD	PTP	ABGD		GMYC	PTP	*COI*		*28S*		*COI*+*28S*		Bathymetry	Geography						
				Lumper	Splitter	Single				Lumper	Splitter	Single									M	VN	P	PNG	V	NC	
polytropa	6	6	5											1/92		1/92		1/95		1–3 m			x				
abbreviata	13	8	5				3 groups							1/97	–/–	0.9/61	0.95/62	1/100	0.93/95	0–7 m				x	x	x	
brevicaudata	24	19	6												0.99/77		–/–		0.7/59	2–38 m			x	x	x		
picturata 1	2	1	1											1/100	1/100	0.96/64	na	1/100	na	7–22 m				x			
picturata 2	6	3	3												1/74		–/–		0.97/90	3–42 m				x			
Bratasusa	22	15	7											1/100			0.95/61	1/100		0–35 m				x	x		
jickelii 1	28	11	9											0.96/–	0.95/–	–/–	–/–	1/91	0.98/80	1–22 m	x	x	x				
jickelii 2	5	4	4												1/59		–/–		1/89	1–40 m				x	x		
acuta 1	96	87	10											1/96	0.93/65	1/82	–/–	1/100	0.89/86	0–22 m					x		
acuta 2	60	17	12												–/–		–/–		–/–	0–99 m		x	x	x	x		
semfala 1	5	2	2											1/100	na	0.99/96	–/–	1/100	1/88	2–15 m				x	x		
semfala 2	1	1	1												1/89		na		na	2–99 m			x				
vezzaroi	3	2	2											1/99		1/96		1/100		15–30 m					x		
kina 1	4	4	3											1/97	0.98/83	1/94	–/–	1/99	0.9/–	no data				x			
kina 2	1	1	1												na		na		na	3–15 m					x		

For each group defined with at least one method, the species name as defined ultimately, the number of specimens sequenced in each dataset, the results of the three species delimitation methods (ABGD, GMYC and PTP) for the three datasets, the monophyly (with Posterior Probabilities/Bootstrap support) as assessed with each dataset, and the bathymetric and geographic distributions are provided from left to right. Na: non-applicable; M: Madagascar; VN: Vietnam; P: Philippines; PNG: Papua New Guinea; V: Vanuatu; NC: New Caledonia.

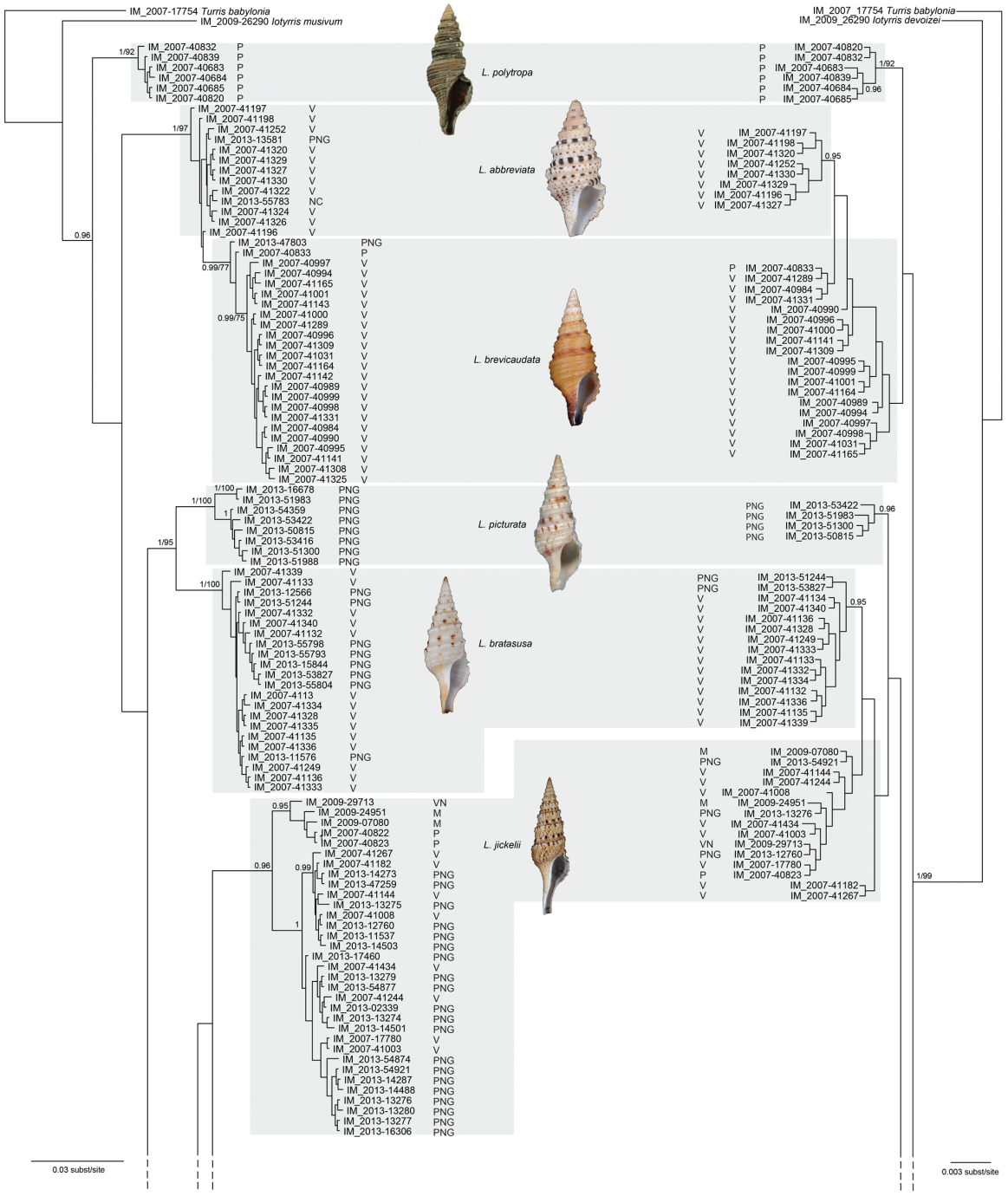

Figure 2. Bayesian trees (Mr. Bayes) for the *COI* (left) and *28S* (right) genes. Posterior probabilities (>0.95) and bootstrap values (>75) are shown for each node. Letters next to each specimen number refer to the locality: M: Mozambique; VN: Vietnam; P: Philippines; PNG: Papua New Guinea; V: Vanuatu; NC: New Caledonia.

1843) and *L. brevicaudata* (Reeve, 1843), again with very distinct shells, are either found as a single PSH or as two different PSH (in one case – *COI* – PTP, *L. abbreviata* is divided in three groups, each corresponding to an unsupported clade). Their association generally corresponds to a highly supported clade. With the *28S* gene, *L. abbreviata* is monophyletic and (moderately) supported and *L. brevicaudata* is not monophyletic; it is the opposite with the *COI* gene, and with both genes both PSH are reciprocally monophyletic. Both are found in sympatry, sometimes even at the same station. It is the only species pair that seems to have distinct bathymetric

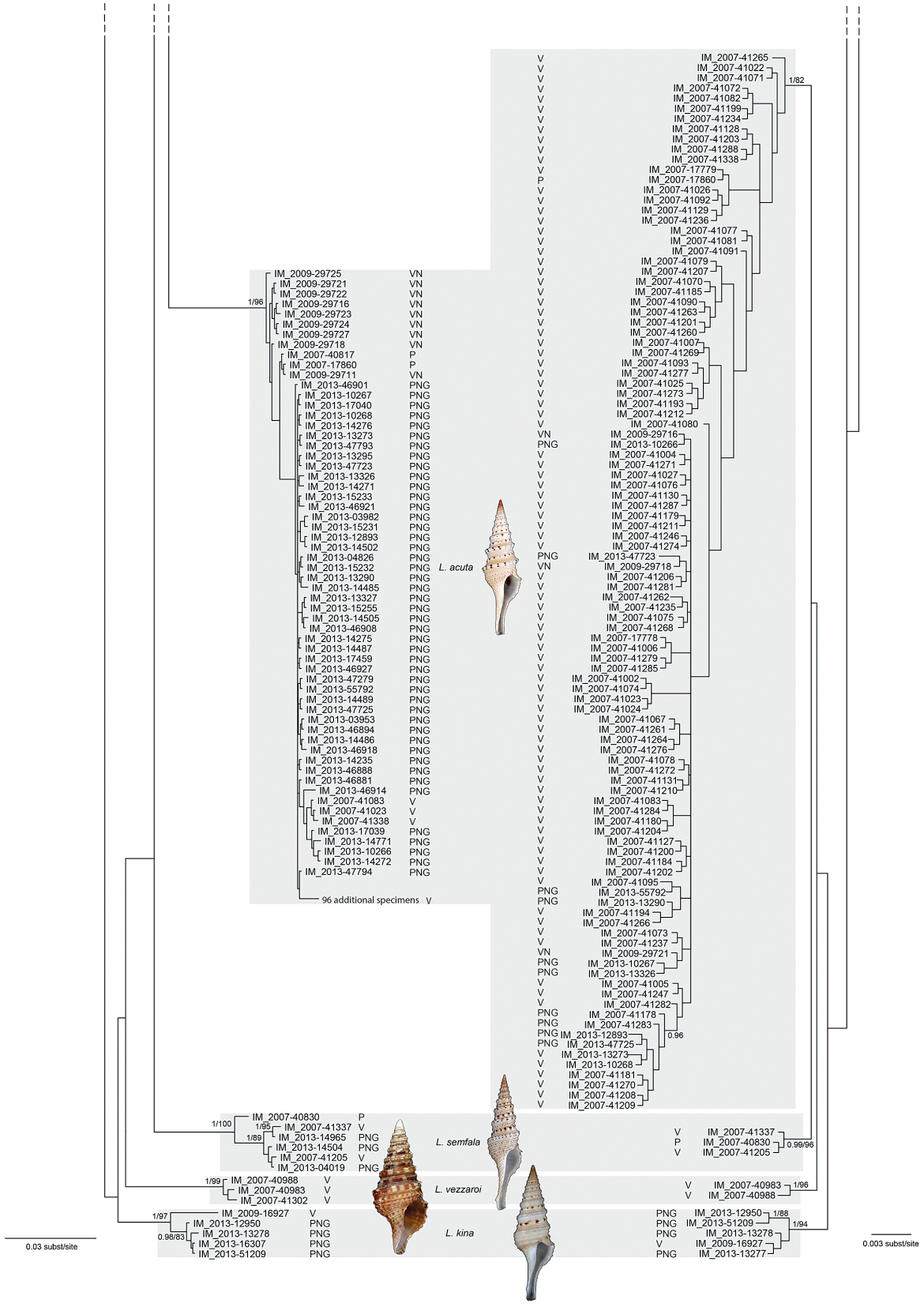

Figure 2. Continued.

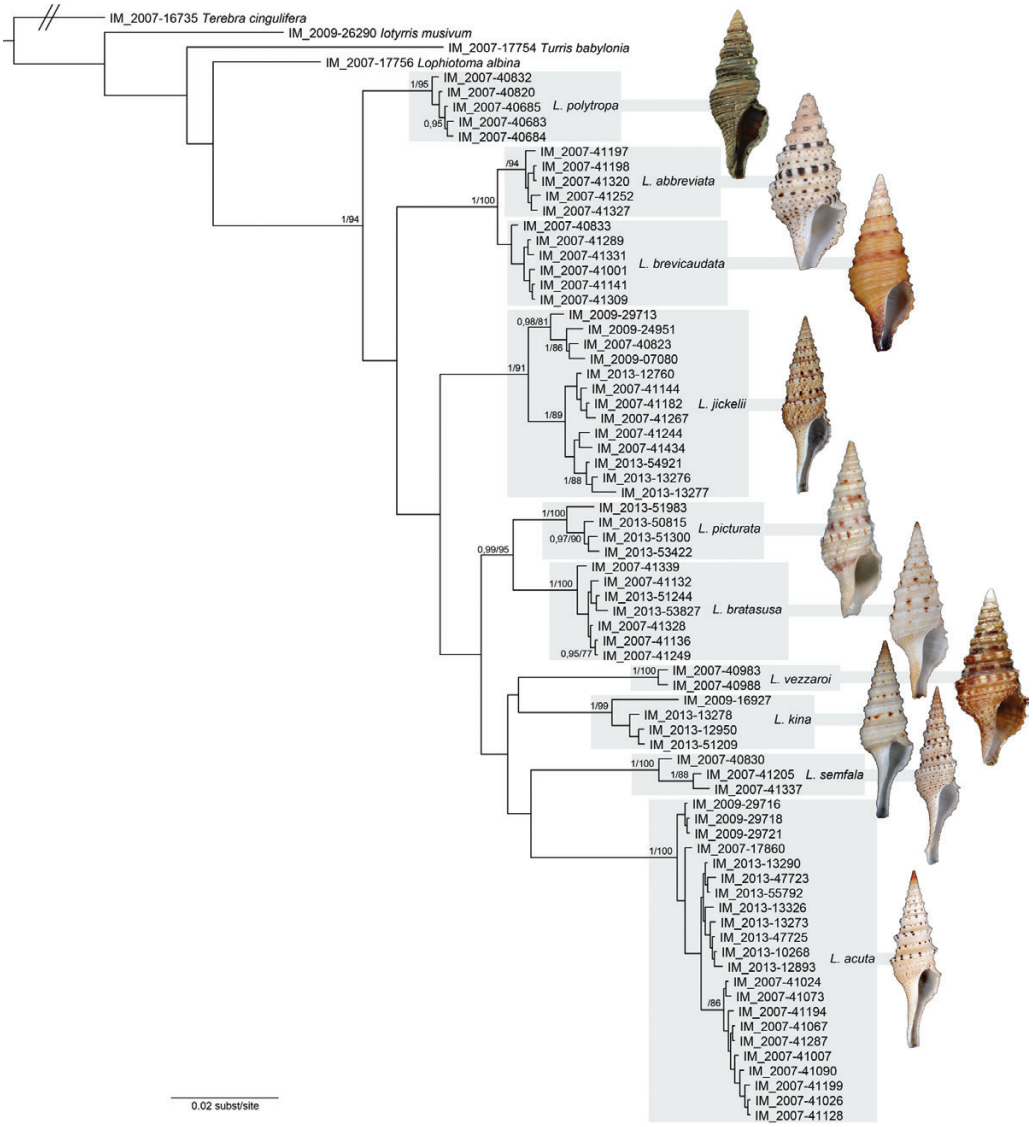

Figure 3. Bayesian tree of the *COI* and *28S* genes concatenated. Posterior probabilities (>0.95) and bootstraps values (>75) are shown for each node.

preferences, *L. abbreviata* being found at an average depth of 2.9 m down to 7 m and *L. brevicaudata* at 14.8 m (±9 m). One supported clade, found in Papua New Guinea and Vanuatu, is constantly defined as a separate PSH (except with *28S* – PTP): *L. bratasusa* sp. nov. It is morphologically very similar to (see Taxonomy section), but distinguishable from, another PSH restricted to Papua New Guinea, sometimes co-occurring with it: *L. picturata* (Weinkauff, 1876). The latter is sometimes separated into two PSH ('splitter' partition of ABGD and PTP with the *COI* gene, PTP with the *COI* + *28S* dataset), morphologically undistinguishable and phylogenetically less supported (or even not recognized as monophyletic) than the whole PSH *L. picturata*. A similar situation is also found for a group of specimens with shells preliminarily identified as *L. acuta*. The first PSH, *L. acuta*, is abundant and widely distributed and sometimes divided into two PSH ('splitter' partition of ABGD with the *COI* and *COI* + *28S* datasets). The second, *L. semfala* sp. nov., contains fewer specimens, also widely distributed (Philippines, Papua New Guinea and Vanuatu), and once again is sometimes divided into two PSH ('splitter' partition of ABGD and PTP with the *COI* gene, PTP with the *COI* + *28S* dataset). However, as for *L. acuta* and *L. picturata*, the support is lower for the subgroups. Finally, the two last PSH are also morphologically similar: *L. jickelii* (Weinkauff, 1875) and *L. kina* sp. nov. Once again, these were sometimes separated into two PSH each ('splitter' partition of ABGD and PTP with the *COI* gene, GMYC 'single' partition and PTP with the

COI + *28S* dataset for *L. kina* and 'splitter' partition of ABGD, 'single' partition of GMYC and PTP with the *COI* and *COI* + *28S* datasets for *jickelii*), less supported than the more inclusive PSH. *Lophiotoma picturata* and *L. bratasusa* sp. nov., *L. semfala* sp. nov. and *L. acuta*, on the one hand, and *L. jickelii* and *L. kina* sp. nov., on the other hand, are also found in sympatry, sometimes co-occurring at the same station.

TAXONOMY

We provide descriptions for the new or newly defined taxa (as in case of neotype designation) and diagnoses for the species for which the status and scope do not change (compared to the generally accepted scope of the species). In addition to the type material, see Table S1 for the other material examined. For each species, the list of pure diagnostic sites for both *COI* and *28S* genes is provided in Table 2.

SUPERFAMILY CONOIDEA FLEMING, 1822

FAMILY TURRIDAE H. & A. ADAMS, 1853 (1838)

GENUS *LOPHIOTOMA* CASEY, 1904

Type species: Pleurotoma acuta Perry, 1811, OD.

Diagnosis: Shell medium-sized to large, narrow to broad fusiform, with attenuated, usually long and nearly straight canal. Protoconch multispiral or paucispiral. Teleoconch whorls usually angulated at shoulder. Sculpture of sharp pronounced cords, including sinus area. Anal sinus deep, with nearly parallel sides. Operculum with apical nucleus.

Marginal radular teeth duplex. Anterior (inner) half solid, narrowly lanceolate, dorso-ventrally compressed with sharp lateral cutting edges. In posterior half major and accessory limbs bifurcate at about 45° angle, rather thin. Central formation [*sensu* Kantor (2006)] either absent or very weak, represented by central tooth in shape of flat poorly developed cusp.

Included species: Lophiotoma abbreviata (Reeve, 1843); *L. acuta* (Perry, 1811); *L. bratasusa* sp. nov.; *L. brevicaudata* (Reeve, 1843); *L. jickelii* (Weinkauff, 1875); *L. kina* sp. nov.; *L. picturata* (Weinkauff, 1876); *L. polytropa* (Helbling, 1779); *L. ruthveniana* (Melvill, 1923); *L. semfala* sp. nov.; *L. vezzaroi* Cossignani, 2015.

Remarks: The genus was revised by Powell (1964) who recognized two subgenera (nominative one and *Lophioturris* Powell, 1964) differing on the basis of the protoconch – multispiral in the former and blunt paucispiral in the latter. Powell attributed five Recent species to *Lophiotoma s.s.* As specified in the Introduction section, previous analyses revealed that among those included species *Lophiotoma albina* should be excluded as it is more closely related to *Gemmula*-like species, while on the contrary *L. polytropa* attributed by Powell to *Lophioturris* is confidently included in *Lophiotoma* on the basis of an earlier phylogenetic analysis (Puillandre *et al.*, 2012b). The protoconch of *L. polytropa* is unknown so far. *Lophioturris,* with the type species *Turris indica* (Röding, 1798), clusters in one clade with *Unedogemmula* MacNeil, 1960 (type species *Pleurotoma unedo* Kiener, 1839), not related to *Lophiotoma* as defined here, and thus becomes junior subjective synonym of the latter. Among species treated as *Lophiotoma* by Powell (1964), only one species, *L. ruthveniana* (Melvill, 1923), is absent from our material and its position remains unconfirmed. The recently described *Lophiotoma vezzaroi* Cossignani, 2015 was sequenced and falls within the *Lophiotoma*

Table 2. List of diagnostic sites (character state – position) for both *COI* and *28S* gene for each species

Species	*COI*	*28S*
L. polytropa	T – 290; G – 292; C – 334; A – 376; C – 424; G – 553	A – 854; T – 860
L. abbreviate	G – 331	C – 396
L. brevicaudata	G – 535	
L. jickelii	C – 158; A – 313; C – 457; T – 598	
L. picturata	C – 100; G – 181; T – 508; C – 529; C – 538	G – 858
***L. bratasusa* sp. nov.**	C – 151; G – 211; C – 238; C – 451	C – 833
L. vezzaroi	G – 37; C – 92; C – 259; C – 271; C – 347; T– 418; C – 533; T – 562	T – 541; A – 680; A – 696
***L. kina* sp. nov.**	A – 22; G – 232; G – 574; C – 613	
***L. semfala* sp. nov.**	C –74; A – 85; T – 127; G – 208; T – 295; C – 307; C – 319; C – 328; C – 428	C – 404; T – 855; G – 860
L. acuta	T – 169; C – 287; G – 298; C – 364; C – 407	T – 496

The positions refer to the alignments provided in Appendices 1 and 2.

clade as defined here. This species was described from the Philippines and found by us in Vanuatu; conchologically it is rather similar to *L. ruthveniana*.

Lophiotoma acuta (Perry, 1811)

(Fig. 4)

Pleurotoma acuta Perry, 1811: pl. 5, fig. 5.
Pleurotoma marmorata Lamarck, 1816: pl. 439, fig. 6 (non *Pleurotoma marmorata* Link, 1807).
Pleurotoma tigrina Lamarck, 1822: 95 (nom. nov. pro *Pleurotoma marmorata* Lamarck, 1816, non *Pleurotoma marmorata* Link, 1807).
Pleurotoma punctata Schubert & Wagner, 1829: 155, pl. 234, figs 4103 a, b (no locality).
Lophiotoma microsticta Casey, 1904: 130.
Lophiotoma acuta Perry, 1811 – Powell, 1964 (part.): 303–305, colour plate 180, figs 1–10, 15–18 (non plate 180, figs 14, 19).

Type material: Neotype of *Lophiotoma acuta* (here designated), MNHN IM-2007-41179, the same specimen is designated as a neotype of *Pleurotoma punctata* (Schubert & Wagner, 1829). Three syntypes of *Pleurotoma tigrina*, MHNG (MHNG-MOLL-51664). Syntypes of *Lophiotoma microsticta*, ?USNM [fide Powell (1964), see below]. Type locality Cebu, Philippines.

Type locality: Vanuatu, E Malo Island, 15°43.4′S, 167°15′E, flat sand and dead corals, 6 m (Expedition SANTO 2006, st. DR84, R/V *Aldric*).

Description (neotype) (Fig. 4A–D): Shell medium thick, narrow fusiform, spire high, siphonal canal long narrow, slightly inclined to left. Protoconch (Fig. 4D) conical, of nearly three evenly convex whorls, smooth first whorls, posteriormost half whorl with nine axial nearly straight riblets, more densely spaced in posterior part of protoconch. Protoconch diameter 0.78 mm, height 0.85 mm. Teleoconch whorls strongly angulated at shoulder, ten in total. Suture shallow, subsutural region wide, distinctly concave, subsutural cord low, triangular in profile, with 3 weak angular ridges, central one strongest. Subsutural region smooth on upper teleoconch whorls, with one spiral ridge appearing on fourth, two on sixth, three on seventh and seven on last whorl. Paired sinus cords strongest and form strong angulated shoulder. On upper whorls both cords similar in size and rounded on top, on penultimate and last whorls cords distinctly triangular in profile, upper much stronger. Base of spire whorls smooth on first whorl, with one spiral cord on two to sixth whorls, starting from seventh whorl number of cords gradually increases, and penultimate whorl with six slightly different in size narrow cords; interspaces three to four times broader than cords. Base of last whorl with five major spiral cords and several riblets between them, canal with 20 cords, becoming gradually broader, lower and more closely spaced anteriorly. Shell base gradually narrowing towards narrow and long nearly straight siphonal canal. Aperture pear shaped, outer lip concave in upper part and weakly convex below shoulder, gradually passing into canal. Anal sinus deep, with nearly parallel sides, with straight posterior margin parallel to shell axis; outer lip in side-view rounded and opisthocline, stromboid notch ill-defined. Growth lines indistinct, closely spaced. Shell creamy, protoconch and two first teleoconch whorls light brown. Subsutural cord with regularly spaced brown spots, not extending beyond cord. Sinus cords with distinct dark brown regularly spaced spots occupying whole width of cord and separate on each cord, minor spiral cords with dense brown flecks. Aperture creamy inside. Measurements: SL 38.8 mm, AL (with canal) 19.7 mm, SW 11.0 mm. Radula examined in five specimens, all from Papua New Guinea, very similar in all specimens (Fig. 5A, B). Radula membrane long, of 55–80 rows of teeth of which 25–30 not fully formed. Marginal teeth duplex. Anterior (inner) half solid, narrowly lanceolate, dorsoventrally compressed with sharp lateral cutting edges. In posterior half major and accessory limbs bifurcate at about 45° angle, rather thin. Central formation absent or very weak, of flat poorly developed regularly positioned cusp, looking like folds of membrane.

Remarks: The species is very variable in terms of coloration and shell shape. The base colour can be from pure white to light orange and even light brown (subsutural region, shell base and canal) with lighter sinus area. With some reservation two colour forms can be distinguished, although intermediate specimens can also be found. In the light form, the brown spots are more scarce and usually confined to major cords, especially to subsutural and sinus ones, while the smaller cords have separate brown speckles. In the dark form (Fig. 4H), the entire shell can be light brown, with a lighter band along the sinus cords. The large brown spots on the subsutural cord dissolve in the lower part into brown band, occupying the entire subsutural zone. The brown spots on minor cords can be as large as those on sinus cords. The canal and anterior part of the aperture can also be brownish. Transitional specimens between forms can be found. The dark form was found within the entire distribution area of the species. In Vanuatu, which is most rich in sequenced material, 66% of specimens were represented by the light form, 24% by the dark form and 10% were attributed to intermediate forms (total number of checked specimens 94). A rather distinct form is found in Vietnam and the Philippines (Fig. 4J) – the shells are large (reaching 51 mm in our material), relatively heavy and with a less pronounced sinus cord, and the spots and speckles are rather fine, except those

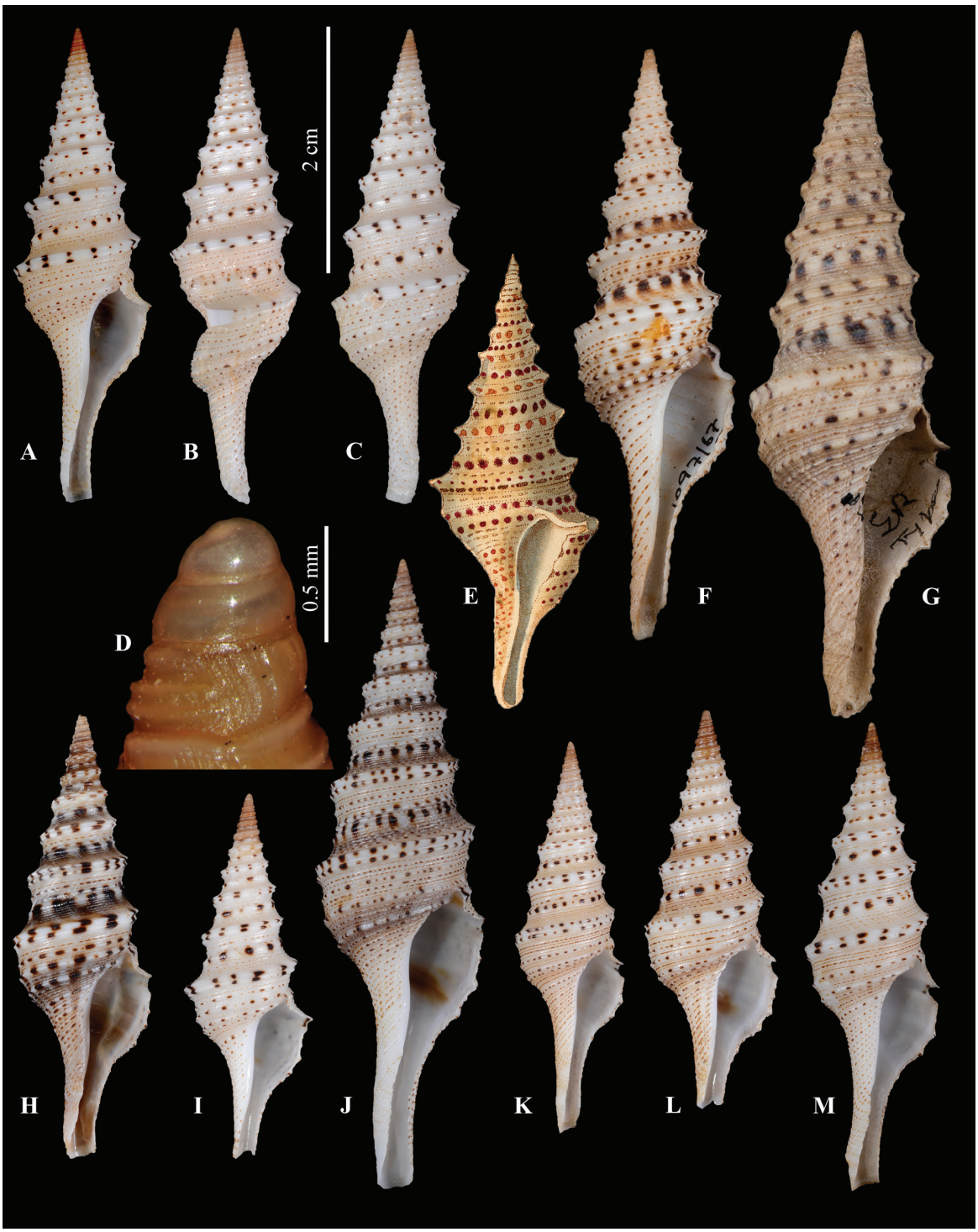

Figure 4. *Lophiotoma acuta* (Perry, 1811). (A–D) Neotype, MNHN IM-2007-41179, SANTO 2006, st. DR84, SL 38.8 mm. (D) Lateral view of the protoconch. (E) Original illustration from Perry (1811). (F–G) Syntypes of *Pleurotoma tigrina* Lamarck, 1822 (MHNG-MOLL-51664). (F) SL 48.1 mm; (G) SL 56 mm. (H) Dark form, MNHN IM-2007-41007, SANTO 2006, st. FR10, SL 35.9 mm. (I) MNHN IM-2007-41025, SANTO 2006, st. LD01, SL 29.7 mm. (J) MNHN IM-2009-29711, Vietnam, Nha Trang Bay, st. ND7, SL 50.9 mm. (K) MNHN IM-2013-10267, PAPUA NIUGINI, st. PR07, SL 31.9 mm. (L) MNHN IM-2013-17040, PAPUA NIUGINI, st. PR152, SL 32.5 mm. (M) MNHN IM-2013-46888, KAVIENG 2014, st. KR06, SL 38.2 mm. All shells at the same scale.

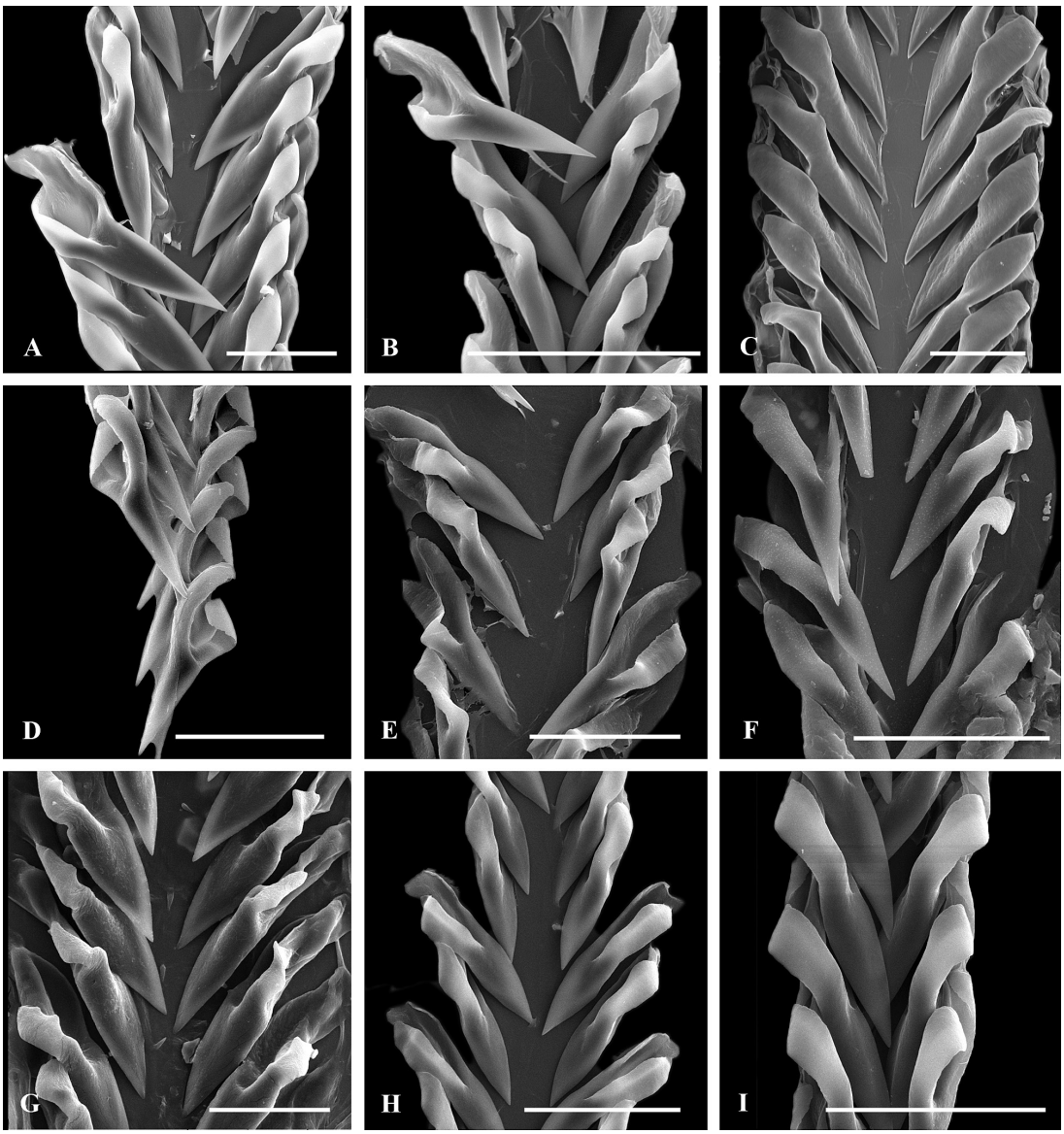

Figure 5. Radulae of studied *Lophiotoma*. (A–B) *Lophiotoma acuta* (Perry, 1811). (A) MNHN IM-2013-14235, PAPUA NIUGINI st. PD33, SL 32.1 mm. (B) MNHN IM-2013-14505, PAPUA NIUGINI st. PD41, SL 21.6. (C) *Lophiotoma polytropa* (Helbling, 1779), MNHN uncatalogued, PANGLAO 2004, st. M50. (D) *Lophiotoma brevicaudata* (Reeve, 1843), MNHN IM-2007-40994, SANTO 2006, st. DB12, SL 16.8 mm. (E) *Lophiotoma picturata* (Weinkauff, 1876), MNHN IM-2013-53422. (F) ***Lophiotoma bratasusa* sp. nov.,** holotype. (G) *Lophiotoma jickelii* (Weinkauff, 1875), neotype. (H) ***Lophiotoma semfala* sp. nov.**, MNHN IM-2013-14504. (I) ***Lophiotoma kina* sp. nov.**, holotype. Scale bars 50 μm.

on the subsutural cord. In the molecular tree based on *COI* they are sister to the rest of *Lophiotoma acuta*, but do not form a monophyletic group. The syntype of *Lophiotoma microsticta* Casey, 1904 [illustrated by Powell (1964): pl. 233, figs 4–5], with shell of 59.7 mm in length, is rather similar to this form. Protoconchs studied in eight specimens are rather uniform, consisting of 2.75 whorls. Number of axial riblets varies from 6 to 11, protoconch height 0.88–0.95, diameter 0.8–0.83 mm.

The species is most similar to *L. semfala* sp. nov. and some specimens can hardly be distinguished; nevertheless, the morphology of the sinus cords seems to be rather uniform in *L. acuta* – on the last whorl (in adult specimens) the upper cord is much more pronounced than the lower and has a distinct triangular shape with sharp upper edge, while in *L. semfala* sp. nov., the cords are nearly similar to each other and are more obtuse and rounded on top (Fig. 6).

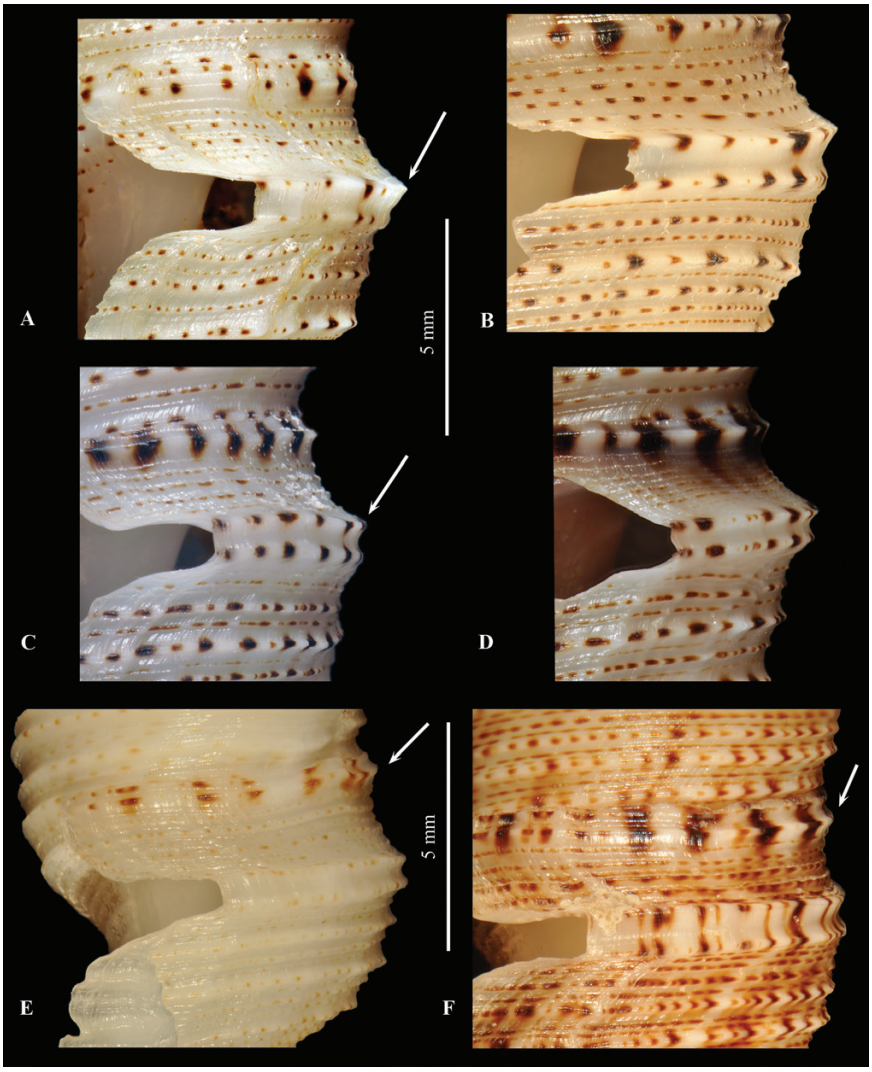

Figure 6. Anal sinus and spiral sculpture of different species of *Lophiotoma*. (A) *Lophiotoma acuta* (Perry, 1811), MNHN IM-2007-41179. (B) *Lophiotoma acuta*, MNHN IM-2009-29711, SL 50.9 mm. (C) ***Lophiotoma semfala* sp. nov.**, holotype, MNHN IM-2007-41337, SL 41.8 mm. (D) ***Lophiotoma semfala* sp. nov.**, dark form, MNHN IM-2007-40830, SL 35.7 mm. (E) ***Lophiotoma kina* sp. nov.**, holotype, MNHN IM-2013-16307, SL 31.0 mm. (F) *Lophiotoma jickelii* (Weinkauff, 1875), neotype, MNHN IM-2013-13275, SL 39.4 mm. Arrows indicate diagnostic details of the sculpture.

The species was treated as broadly distributed and strongly variable. Powell (1964) listed a number of nominal taxa in the synonymy of this species, including *Pleurotoma jickelii* Weinkauff, 1875 and *Pleurotoma picurata* Weinkauff, 1876. On the basis of molecular and morphological analysis, these two species appeared to be valid. *Pleurotoma acuta* Perry, 1811 was described without locality data or shell measurements. The original shell illustration is a bit grotesque, although suitable for positive identification. Few existing types described by Perry (1811) are stored in the NHMUK (Dance, 1986) and the type of *P. acuta* is not among them. Due to the complicated taxonomic situation with the *L. acuta* complex, a neotype is here designated. The name *Pleurotoma marmorata* (non *Pleurotoma marmorata* Link, 1807 = *Turris chaldea* Kilburn, Fedosov & Olivera, 2012) was listed by Lamarck (1816) (pl. 439, fig. 6, included in references, p. 8). Later Lamarck (1822: 95) renamed the species *P. tigrina*, citing his own figure, but still proposed the name *Pleurotoma marmorata* for another species, which became the homonym for the third time. Three syntypes of *Pleurotoma tigrina* are in MHNG (MHNG-MOLL-51664) (Fig. 4F–G herein) and it is seemingly conspecific with *L. acuta* in our current understanding, being closer to the 'dark' form. Judging from the syntypes of *P. marmorata* Lamarck, 1822 (MHNG-MOLL-51663) the species belongs to the

genus *Unedogemmula* and was listed in synonymy of *Lophiotoma* (*Lophioturris*) *indica* (Röding, 1798) by Powell (1964). The syntype of *Lophiotoma microsticta* Casey, 1904 was illustrated by Powell (1964: pl. 233, figs 4, 5) and claimed to be deposited in USNM. Nevertheless, we were not able to find it in the collections. Judging from the photo it has the same sculpture pattern as *L. acuta*, that is, the dominating upper sinus cord; therefore, we confirm the opinion of Powell (1964), that it is a synonym of *L. acuta.* The type material of *Pleurotoma punctata* was not traced despite queries in the corresponding museums and the original illustration is rather crude, although the general outline is similar to that of *L. acuta.* In order to fix the problem and to stabilize the nomenclature, we designate the neotype of *Pleurotoma acuta* Perry, 1811 as the neotype of *P. punctata* as well; thus, the latter name is now a junior objective synonym of *P. acuta.* *Pleurotoma peaseana* Dunker, 1871 [*Pleurotoma* (*Turris*) *peaseana* Dunker, 1871: 154 (Indian Ocean)] is another species of doubtful affinity, which was synonymized with *L. acuta* by Powell (1964). It was illustrated only in Weinkauff (1876, in Weinkauff & Kobelt, 1875–1887: 66, pl. 2, fig. 10). The illustration depicts a rather stout shell with moderately elongate canal, much shorter than in both *L. acuta* and *L. semfala*. The species may not be closely related to *L. acuta*. We were not able to trace the type despite querying museums where Dunker's type material might be stored. Powell (1964) synonymized the species with *L. acuta* without providing any arguments, an opinion followed by Oyama (1966) and Higo, Callomon & Gotō (1999). Moreover, Weinkauff (1876, in Weinkauff & Kobelt, 1875–1887) described the protoconch of *P. peaseana* as consisting of three smooth semitranslucent whorls with poorly visible suture, not mentioning the characteristic axial ribs in the posteriormost part of the protoconch. This seems more similar to the protoconch of *Unedogemmula* and we exclude the species from synonymy of *L. acuta.*

Distribution: Confirmed distribution of the species (based on sequenced specimens) – tropical Indo-west Pacific (from Vanuatu to Vietnam). Judging from published data, it also includes South Africa (Kilburn, 1983), Red Sea (Verbinnen & Dirkx, 2007), Japan (Okutani, 2000), Fiji, Queensland (Australia) (Powell, 1964), New Caledonia (uncatalogued MNHN material).

LOPHIOTOMA SEMFALA SP. NOV.

(FIG. 7)

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Type material: Holotype MNHN IM-2007-41337.

Type locality: Vanuatu, Aoré I. Aimbuei Bay, 15°32.8′S, 167°11.6′E, white coral sand, 3–8 m (Expedition SANTO 2006, st. LD35, R/V *Alis* annex).

Etymology: semfala – the 'same' in Bislama, the creole language, one of the official languages of Vanuatu. Used as noun in apposition to reflect the similarity to *Lophiotoma acuta*.

Description (holotype) (Fig. 7A–C): Shell medium thick, narrow fusiform, spire high, siphonal canal long narrow, slightly inclined to left. Protoconch conical, eroded, rendering exact whorl count and sculpture examination doubtful, of about three evenly convex whorls. Protoconch diameter 0.73 mm, height 0.85 mm. Teleoconch whorls angulated at shoulder, ten in total. Suture very shallow, indistinct, subsutural region wide, distinctly concave, subsutural cord low, triangular in profile, with three angular ridges on last whorl, central one strongest. On upper teleoconch whorls, only central ridge persists. Subsutural region smooth on upper teleoconch whorls, with one spiral ridge appearing on fourth, two on sixth, three on seventh and five on last whorl. Paired sinus cords strongest forming angulated shoulder. On upper whorls both cords nearly equal in size, obtusely triangular, on penultimate and last whorls cords more angulate, although still rounded on top, only on last whorl upper cord distinctly stronger than lower. Base of spire whorls smooth on first four whorl, with one spiral cord on fifth to sixth whorls, starting from seventh whorl number of cords gradually increases, and penultimate whorl with seven narrow cords of slightly different size, median much stronger; interspaces three to four times broader than cords. Base of last whorl with three major spiral cords and several riblets between them, canal with 20 cords, becoming gradually broader, lower and more closely spaced anteriorly. Shell base gradually narrowing towards narrow and long nearly straight siphonal canal. Aperture pear shaped, outer lip concave in upper part and weakly convex below shoulder, gradually passing into canal. Anal sinus deep, with nearly parallel sides, with straight posterior margin, parallel to shell axis; outer lip in side-view rounded and opisthocline, stromboid notch well defined. Growth lines indistinct, closely spaced. Shell creamy, protoconch and three first teleoconch whorls very light brown. Subsutural cord with regularly spaced brown spots, not extending beyond cord, broader on last three whorls. Sinus cords with distinct dark brown regularly spaced spots occupying whole width of cord and separate on each cord, minor spiral cords with dense brown flecks. Aperture creamy inside. Measurements: SL 41.8 mm, AL (with canal) 20.9 mm, SW 10.6 mm. Radula examined in three specimens, two from Papua

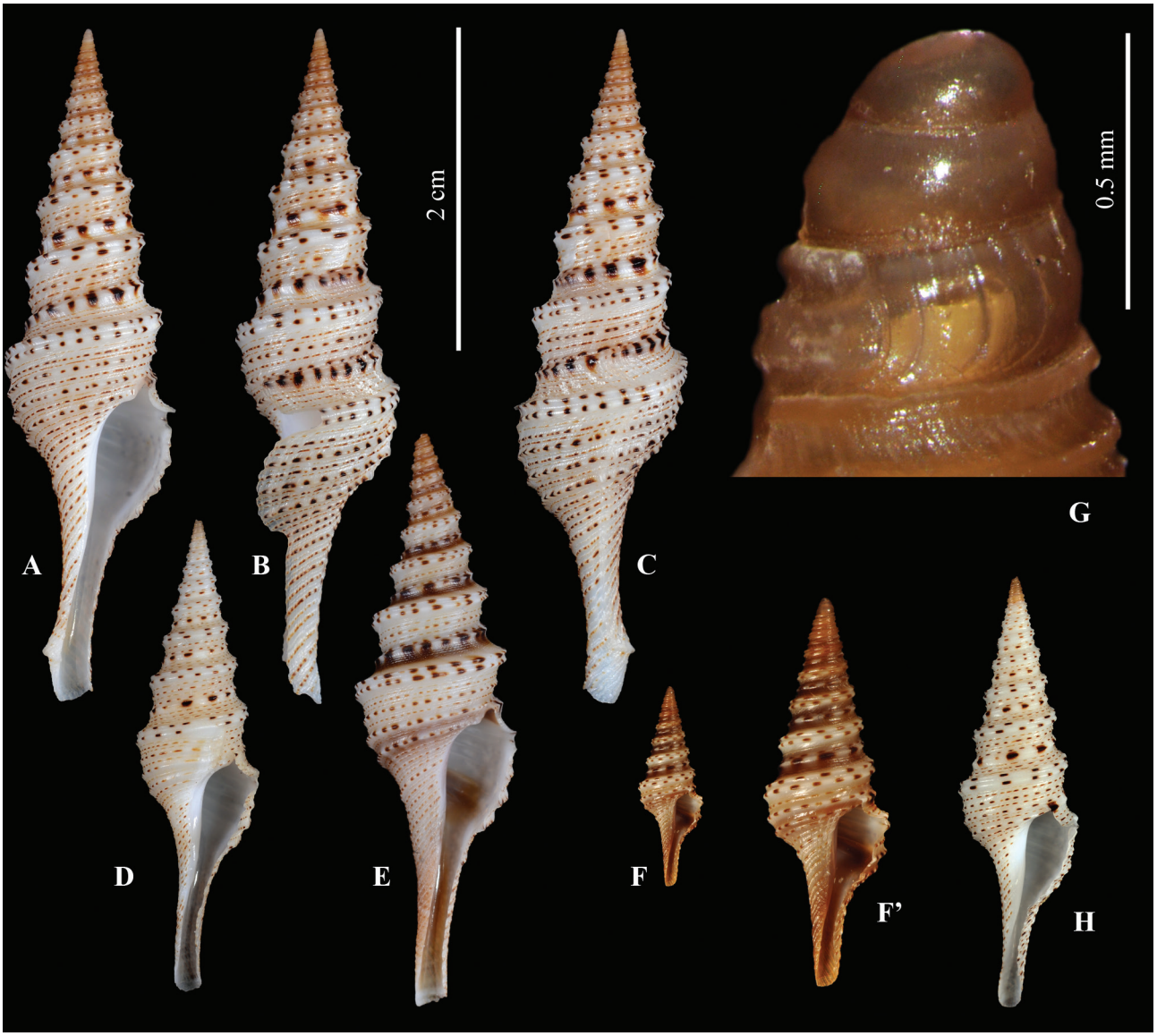

Figure 7. ***Lophiotoma semfala*** **sp. nov.** (A–C) Holotype, MNHN IM-2007-41337, SANTO 2006, st. LD35, SL 41.8 mm. (D) MNHN IM-2013-14504, PAPUA NIUGINI, st. PD41, SL 29.5 mm. (E) MNHN IM-2007-40830, Philippines, PANGLAO 2004, st. R62, SL 35.7 mm. (F–G) Dark form, MNHN IM-2013-4019, PAPUA NIUGINI, st. PD39, SL 12.4 mm (F – at the same scale as other shells, F′ enlarged). (G) Lateral view of the protoconch. (H) MNHN IM-2013-14965, PAPUA NIUGINI, st. PD45, SL 26.8 mm. All shells (except F′) at the same scale.

New Guinea and one from the Philippines, very similar in all examined specimens (Fig. 5H). Radula membrane medium long, of 33–50 rows of teeth of which 9–16 not fully formed. Marginal teeth duplex. Anterior (inner) half solid, narrowly lanceolate, dorso-ventrally compressed with sharp lateral cutting edges. In posterior half major and accessory limbs rather thin, bifurcate at about 45° angle. Central formation absent.

Remarks: The new species is represented only by six specimens, including the holotype and despite the limited material, two rather distinct forms can be recognized. The 'light' form that includes the holotype has fewer brown spots and the base colour is uniformly creamy. The brown spots on the subsutural cord are in most specimens confined to the cord itself and do not extend beyond, but in the holotype on some whorls there are brownish blurred extensions of the spots to the subsutural region. Available specimens other than the holotype are smaller and less speckled. The 'dark' form is represented by two specimens only, one being juvenile (Fig. 7F–G). It has

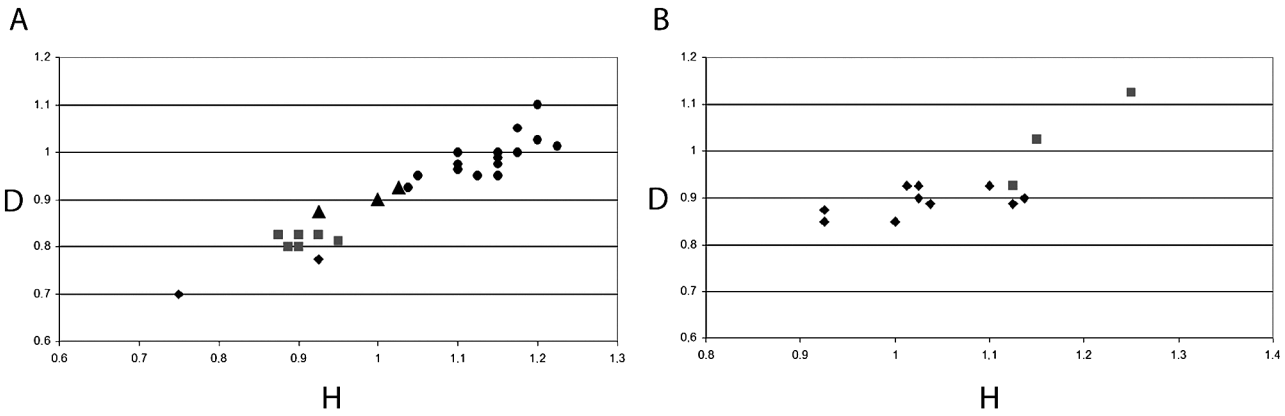

Figure 8. Scatterplot of protoconch measurements in studied species of *Lophiotoma*. D: protoconch diameter, mm; H: exposed height, mm. (A) Diamonds: ***L. semfala* sp. nov.**; squares: *L. acuta*; triangles: ***L. kina* sp. nov.**; circles: *L. jickelii*. (B) Diamonds: ***L. bratasusa* sp. nov.**; squares: *L. picturata*.

slightly darker base colour, with a light brown shell base and canal and with the subsutural region below the subsutural cord uniformly brown. There was no correlation between geographic distributions, since one specimen of the dark form was collected in the Philippines, while another in Papua New Guinea at similar depths. The sinus cords of the adult specimen of the dark form are also sharper on top on the last whorl. On most parts of the teleoconch whorls, the sinus cords are either similar in size, or the lower even slightly more pronounced, than the upper, but on the last whorl the situation is reversed. An intact protoconch persists only in the juvenile of the dark form (Fig. 7G), it consists of 2.75 whorls, diameter 0.68 mm, height 0.73, which is significantly smaller than in holotype, although the existing material is insufficient for estimates of variation. The species is extremely similar to *Lophiotoma acuta*, which also has dark and light forms. It can be distinguished in most cases by being less pronounced and more rounded on the top sinus cords, providing a less angulated appearance to the shell shoulder, as well as the cords being more similar in size (Fig. 6, compare A, B with C, D), and domination of the lower cord over the higher one on the teleoconch whorls. The protoconch of *Lophiotoma acuta* is slightly larger (Fig. 8), while the radula is longer (consists of 55–80 rows of teeth vs. 33–50 rows in *L. semfala* sp. nov.).

Distribution: The species was found in the Philippines, Papua New Guinea and Vanuatu. In all these localities, it is sympatric with *L. acuta*. Judging from available material (only six sequenced specimens), it is much more rare than *L. acuta*, for which we had sequenced more than 160 specimens. Although we did not sequence any specimens from New Caledonia, judging from the shell characters the species is also found in New Caledonia (uncatalogued MNHN material).

LOPHIOTOMA POLYTROPA (HELBLING, 1779) (FIG. 9E)

Murex (*Fusus*) *polytropus* Helbling, 1779: 119, pl. 2, figs 24, 25.
Pleurotoma fascialis Lamarck, 1822: 93; – Kiener, 1840: 27, pl. 4, fig. 2.
Lophiotoma (*Lophioturris*) *polytropa*. – Powell, 1964: 313–314, pl. 244.
Lophiotoma polytropa. – Poppe, 2008: 770, pl. 680, fig. 4.
Lophioturris polytropa. – Lozouet & Plaziat, 2008: 134, pl. 31, figs 5–9.

Type material: Murex (*Fusus*) *polytropus*, whereabouts unknown; syntypes of *Pleurotoma fascialis*, MHNG (personal communication of P. Stahlschmidt, not seen).

Type locality: Not stated.

Diagnosis: Shell medium-sized, exceeding 50 mm, thick, turriform, with thick brown periostracum, shell dark-purplish brown. Sculpture of strong spiral elements, with rounded or angulate subsutural cord followed by notably elevated paired and broadly spaced sinus cords. Shell periphery and base with dense elevated cords, similar in size to sinus cords and with intermediate finer ridges. Siphonal canal medium long, nearly straight; aperture rather wide, purplish to greyish inside. Radula (Fig. 5C) with duplex marginal teeth. Anterior (inner) half solid, lanceolate, slightly asymmetrical, with nearly straight anterior margin and convex posterior margin, dorso-ventrally compressed with

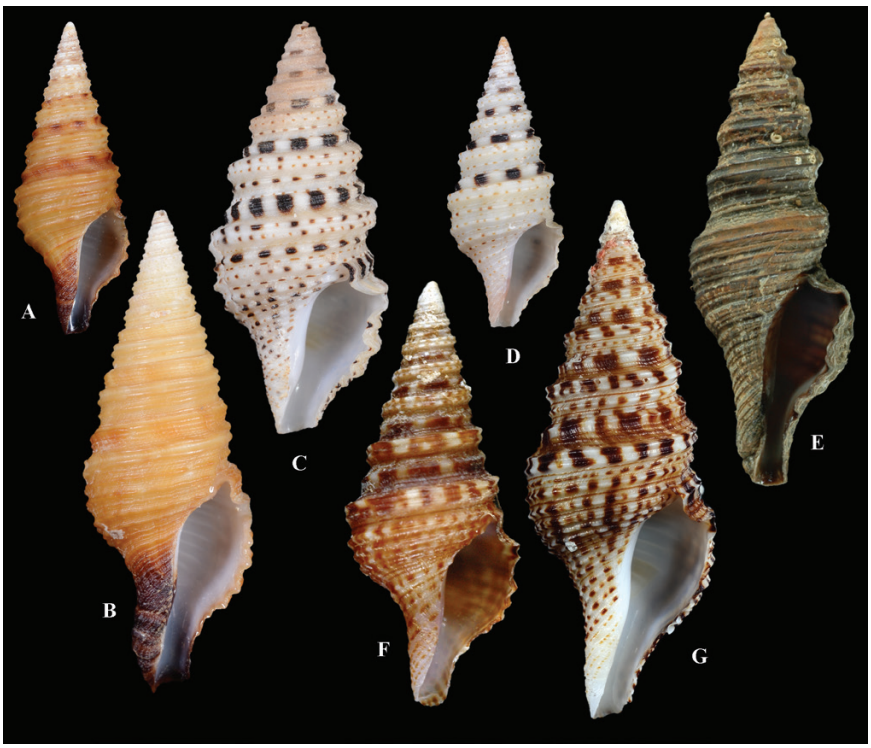

Figure 9. Shells of examined species of *Lophiotoma.* (A–B) *Lophiotoma brevicaudata* (Reeve, 1843). (A) MNHN IM-2007-40994, SANTO 2006, st. DB12, SL 16.7 mm. (B) MNHN IM-2013-47803 KAVIENG 2014, st. KS15, SL 26.0 mm. (C–D) *Lophiotoma abbreviata* (Reeve, 1843). (C) MNHN IM-2013-55783, New Caledonia, Nouméa, SL 22.4 mm. (D) MNHN IM-2007-41197, SANTO 2006, st. FB52, SL 15.8 mm. (E) *Lophiotoma polytropa* (Helbling, 1779), MNHN IM-2007-40832, PANGLAO 2004, st. M30, SL 43.0 mm. (F–G) *Lophiotoma vezzaroi* Cossignani, 2015. (F) MNHN IM-2007-40983, SANTO 2006, st. DS04, SL 14.4 mm. (G) Radula voucher, Tinina, Balut Island, Philippines, SL 34.7 mm.

sharp lateral cutting edges. In posterior half major and accessory limbs bifurcate at about 45° angle, rather thin. Accessory limb narrowing interiorly, where it fuses with major limb. Central formation absent.

Remarks: The species is rather distinct from all other congeners in having a strong, tightly adhered periostracum and uniformly coloured dark shell.

Pleurotoma fascialis Lamarck, 1822, was considered as a synonym of *L. polytropa* by Powell (1964). Although we have not seen the type material of the species, judging from the illustration of Kiener (1840: 27, pl. 4, fig. 2), the type of *Pleurotoma fascialis* is morphologically similar to the illustration of Helbling and therefore we follow Powell's opinion. Because the recognition of this species is not an issue, even though we were not able to locate the types of Helbling, we do not designate a neotype for *L. polytropa*.

Distribution: Powell (1964) recorded the species from the Philippines, Moluccas, New Britain and New Caledonia. The species is considered rare. Nevertheless, Lozouet & Plaziat (2008) found it common in the mangrove environments of the lower estuary of the Abatan River (Bohol, Philippines). All the sequenced specimens originated from this locality. The species was successfully recollected several years later in the mentioned biotope (Kantor, Fedosov, unpublished).

LOPHIOTOMA ABBREVIATA (REEVE, 1843) (FIG. 9C, D)

Pleurotoma abbreviata Reeve, 1843 (in 1843–1846): pl. 10, fig. 86.

Lophiotoma abbreviata. – Powell, 1964: 309, pls. 237–238, figs 1, 2; Poppe, (2008): pl. 683, fig. 5.

Type material: Lectotype [designated by Powell (1964)] and three paralectotypes in NHMUK.

Type locality: Masbate Island, Philippines, reefs at low tide.

Diagnosis: Shell small, turriform, with contrasting black spots on white background colour, and short siphonal canal, giving shell stout appearance. Sculpture of strong

spiral elements, with rounded or angulate subsutural cord followed by notably elevated bisected sinus cord, and one fainter ridge on spire whorls. Shell base with dense elevated cords, sometimes interchanged by fine ridges. Microsculpture of dense very fine spiral treads throughout shell surface. Siphonal canal short and rather robust; aperture rather wide with moderately deep anal sinus. Inside of outer lip with distinct lirae.

Remarks: The small and robust-looking shell of *L. abbreviata* differs from notably more elongated, with long siphonal canal *L. jickelii*, *L. vezzaroi*, *L. semfala* sp. nov. and *L. kina* sp. nov. In turn, the variegated colour pattern readily distinguishes *L. abbreviata* from tan *L. brevicaudata* and dark-brown *L. polytropa*. While being distinctive among congeners, *L. abbreviata* resembles small species of the genus *Iotyrris*, *I. devoizei* and *I. kingae*, primarily in colour pattern. However, both mentioned *Iotyrris* species have an even shorter siphonal canal and thus proportionally much higher spire. Besides, the spiral elements are denser, and the whorl profile is less angulate, because of the lower sinus cord in *Iotyrris* species. Powell recognized two subspecies in addition to the nominotypical: *L. abbreviata lifouensis* (Sowerby, 1907) known only from Lifou, Loyalty Islands; and *L. abbreviata ustulata* (Reeve, 1846) with unknown type locality. The latter subspecies differs markedly in shell from the nominotypical one and its status remains unclear, as suggested by Powell (1964). We also did not have specimens from Lifou available for sequencing and therefore the status of *L. abbreviata lifouensis* remains unresolved. Concerning the latter, Cernohorsky (1972) claimed that the shells corresponding to both nominotypical and *lifuensis* subspecies were collected sympatrically in Fiji.

Distribution: Confirmed distribution of the species (based on sequenced specimens) is Papua New Guinea, New Caledonia and Vanuatu. According to published data, it is also found in the Philippines (Springsteen & Leobrera, 1986) eastward to Fiji (Cernohorsky, 1972).

Lophiotoma brevicaudata (Reeve, 1843)
(Fig. 9 A, B)

Pleurotoma brevicaudata Reeve, 1843 (in 1843–1846): pl. 15, fig. 126.
Lophiotoma brevicaudata – Powell, 1964: 406.

Type material: Lectotype and two paralectotypes in the NHMUK [designated by Powell (1964)] (not illustrated).

Type locality: Ticao Island, Philippines, H. Cuming collection.

Diagnosis: Shell small, turriform, with prominent spiral sculpture; spire coloured light-brown or tan, siphonal canal dark-brown. Whorl outline indistinctly convex, as subsutural cord separated from succeeding cords by wide and deep depression. Sinus cord wide, composed of two ridges with rather shallow interspace, followed by two cords on whorl's base. Interspaces between cords sculptured by fine treads. Shell base convex, constricted to rather slender siphonal canal, sculptured with dense spiral to oblique cords. Aperture elongate, anal sinus moderately deep, wide, angulated at tip. Outer aperture lip with white callus, distinctly lirate within.

Remarks: Lophiotoma brevicaudata is one of the easily recognizable species, primarily because of its characteristic colour pattern with tan or light brown background colour, and dark siphonal canal. Crests of spiral ridges are sometimes dark-brown as well. In particular, rather monotonous coloration of the spire readily sets *L. brevicaudata* apart from the most closely related *L. abbreviata*. At the same time, *L. brevicaudata* is notably lighter, and in maturity smaller than *L. polytropa*. In addition to colour pattern, a rather short siphonal canal, as compared to *L. acuta*, *L. jickelii*, *L. vezzaroi*, *L. semfala* sp. nov. and *L. kina* sp. nov., allows rather straightforward identification of *L. brevicaudata* among congeners. The radula was examined in one sequenced specimen from Vanuatu (Fig. 5D). The radula is very similar to other congeners, with duplex marginal teeth. The anterior (inner) half is solid, narrowly lanceolate, dorso-ventrally compressed with sharp lateral cutting edges. In the posterior half the major and accessory limbs bifurcate at an angle of about 45°, rather thin. The central formation was not studied due to radula preparation.

Distribution: Confirmed distribution of the species (based on sequenced specimens) is from Philippines to Vanuatu. According to MNHN material, also New Caledonia.

Lophiotoma picturata (Weinkauff, 1876)
(Fig. 10A–F)

Pleurotoma picturata Weinkauff, 1876 in Weinkauff & Kobelt, 1875–1887: 66, pl. 2, fig. 10.

Type material: Lectotype (here designated) ZMB Moll 112610, ex-Paetel collection, Philippines, SL 41 mm; paralectotype ZMB Moll 112610.

Type locality: Philippines (originally Indischer Ocean).

Diagnosis: Shell solid, narrow turriform, with high spire and moderately long siphonal canal. Protoconch

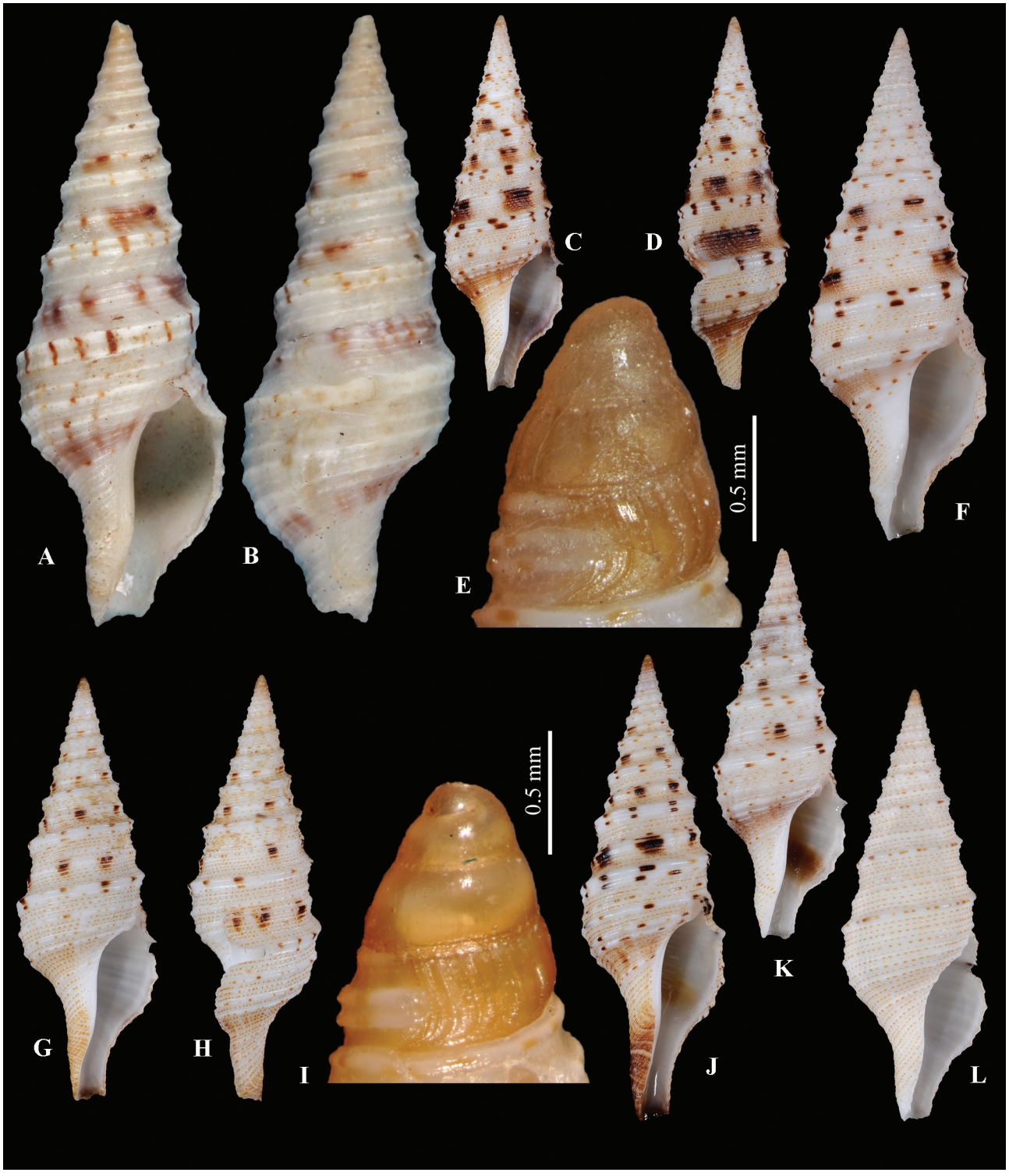

Figure 10. Shells of examined species of *Lophiotoma*. (A–F) *Lophiotoma picturata* (Weinkauff, 1876). (A, B) Lectotype of *Pleurotoma picturata* ZMB Moll 112610, SL 41 mm. (C–E) MNHN IM-2013-53422, KAVIENG 2014, st. KZ02, SL 24.5 mm. (E) Lateral view of the protoconch. (F) MNHN IM-2013-51988, KAVIENG 2014, st. KR62, SL 30.3 mm. (G–L) ***Lophiotoma bratasusa* sp. nov.** (G–I) Holotype, MNHN IM-2013-51244, KAVIENG 2014, st. KR54, SL 26.0 mm. (J) MNHN IM-2013-15844, PAPUA NIUGINI, st. PM41, SL 30.5 mm. (K) MNHN IM-2007-41339, SANTO 2006, st. DR106, SL 28.2 mm. (L) MNHN IM-2007-41132, SANTO 2006, st. LD04, SL 23.8 mm.

of 3.75–4 slightly convex whorls; early three whorls smooth and glossy, latest whorl sculptured with 14–17 axial riblets (Fig. 10E). Protoconch diameter 0.93–1.12 mm, height 1.13–1.25 mm. Teleoconch whorls distinctly angulated; spire whorls sculptured with fine subsutural cord, and strong bifurcated sinus cord, and fine threads on subsutural area and whorl base. Adapical whorl portion between subsutural cord and sinus cord distinctly concave. Shell base shortly constricted to slender siphonal canal. Shell base with eight to nine fine threads interchanging with sharp narrow spiral ridges, canal with 13–15 threads. Aperture elongate. Anal sinus wide and rather deep, quadrangular in its apex. Aperture usually with 9–12 distinct lirae inside. Background colour cream, with distinct dark-brown spots on subsutural and sinus cords. Brown spots on subsutural cords surrounded by somewhat nebulose lighter brown or reddish blotches. Shell base with indistinct light-brown band. Spiral threads with regular light-brown dots, protoconch light-brown; aperture cream inside. Radula examined in one sequenced specimen from New Ireland (MNHN IM-2013-53422, Fig. 5E). Radula membrane long, of about 50 rows of teeth, of which 20 not fully formed. Radula very similar to other congeners, with duplex marginal teeth. Anterior (inner) half solid, narrowly lanceolate, dorso-ventrally compressed with sharp lateral cutting edges. In posterior half, major and accessory limbs bifurcate at about 45° angle, rather thin. Central formation indistinct.

Remarks: The species is represented in our material by eight specimens from Bismarck Sea (Madang lagoon and New Ireland), ranging in height from 24.5 to 32.1 mm, showing modest variation in conchological characters. The only feature that is found to vary notably is the shape of the anal sinus. It is moderately deep and wide with an angulated outline in specimen MNHN IM-2013-53422 (Fig. 10C, D), and even wider in Weinkauff's type, collected from the Philippines. The sinus is U-shaped, and very deep in some other sequenced specimens. Despite the fact that no specimens of *L. picturata* from the Philippines were sequenced in the present study, we confidently apply the name to this clade of our molecular tree, based on conchological features that are shared by the studied type specimen from ZMB and sequenced specimens. No other specimens of *L. picturata*, mentioned by Weinkauff, were studied. Since a species morphologically close to *L. picturata* – *L. bratasusa* sp. nov. – was recognized in our analysis, in order to fix the identity of *Lophiotoma picturata*, we here designate the studied syntype ZMB Moll 112610 as a lectotype, thereby setting the type locality as the Philippines. Morphologically *L. picturata* is very close to *L. bratasusa* sp. nov.; however, there are some minor, but rather stable, characters that allow unmistakable differentiation of the two species. Firstly, the two species differ in the number of protoconch whorls – the former species has a protoconch of 3.75–4 whorls, while the latter – with 3.25 whorls only. Correspondingly the diameter and height of the protoconchs are slightly larger in *L. picturata* (Fig. 8). Shell proportions and coloration also offer some minute differences. *Lophiotoma picturata* is more turriform in outline (due to comparatively shorter siphonal canal), and the black or dark brown spots on the subsutural region are surrounded by less contrasting light-brown or reddish blotches. On the contrary, *L. bratasusa* has a more fusiform outline, and the dark spots on the subsutural region are more contrasting in appearance. Weinkauff (1876 in Weinkauff & Kobelt, 1875–1887), when describing the species, cited *Pleurotoma variegata sensu* Reeve (1843), non Kiener (1840). The illustration of Reeve (1843: pl. 1, species 2) depicts the shell from the dorsal side which has a vague resemblance to *P. picturata*, although positive identification is hardly possible. Powell (1964) synonymized *Pleurotoma picturata* with *Lophiotoma acuta* and this viewpoint was accepted by subsequent authors.

Distribution: Confirmed distribution of the species (based on sequenced specimens) is Papua New Guinea. The lectotype was collected in the Philippines and the original type locality was 'Indian Ocean', so its range should be broader, but this needs confirmation.

LOPHIOTOMA BRATASUSA SP. NOV.

(FIG. 10G–L)

urn:lsid:zoobank.org:act:768A32A5-678A-4F03-8FC4-270EB8DE197C

Type material: Holotype MNHN IM-2013-51244, SL 26.0 mm; paratype 1, MNHN IM-2013-12566, paratype 2, MNHN IM-2013-53827.

Type locality: Papua New Guinea, Kavieng Lagoon, E of Kulinus I., Silver Sound, 02°42.3′S, 150°39.1′E, 7–10 m, coarse sand, coral patches (Expedition KAVIENG 2014, st. KR54).

Etymology: bratasusa – sibling in Pidgin English, refers to the revealed sister relationship between the new species and morphologically similar *L. picturata*. Used as a noun in apposition.

Description (holotype): Shell solid, narrow fusiform with high spire and rather long siphonal canal. Protoconch of 3.25 slightly convex whorls. Earlier 2.75 whorls smooth and glossy; latest 0.5 whorl sculptured with fine arcuate riblets, widely set at earlier portion

and more dense at transition to teleoconch. Protoconch diameter 0.89 mm, height 1.13 mm. Teleoconch of nine angulated whorls, suture shallow and inconspicuous. Subsutural region distinctly concave; suture immediately bordered by fine thread, followed by typically low subsutural cord, and three to seven regularly set spiral threads. Sinus cord bifurcated, formed by two subequal ridges on early whorls, adapical ridge notably stronger on penultimate and last teleoconch whorls. Abapical whorls portion (=whorl's base) sculptured with four fine threads, fourth slightly stronger than preceding. Shell base shortly constricted to slender siphonal canal, sculpture of shell base of 11 fine threads, fourth and sixth elevated to form sharp spiral ridges. Siphonal canal with 15 threads, spirally oriented and widely set adapically and dense, weakly delineated from one-another and oblique towards canal's tip. Aperture elongate; outer aperture lip convex adapically, rounded in side view. Anal sinus typically deep and rather narrow with rounded apex. Aperture smooth inside, or bearing 8–9 weak lirae. Background colour cream, with distinct contrast dark-brown spots on subsutural and smaller dots on sinus cords. Spiral threads with regular light-brown dots, giving them appearance of dashed lines. Protoconch orange; inside of aperture cream. Radula (holotype) (Fig. 5F) long, of about 55 rows of teeth, of which 25 nascent. Radula very similar to other congeners, with duplex marginal teeth. Anterior (inner) half solid, narrowly lanceolate, dorso-ventrally compressed with sharp lateral cutting edges. In posterior half major and accessory limbs bifurcate at about 45° angle, rather thin. Central formation absent.

Remarks: Lophiotoma bratasusa sp. nov. varies notably in shell shape, sculpture pattern and coloration. The two ridges of bisected sinus cord may be equally strong, subequal or differ notably, to the extent that the lower ridge is not stronger than succeeding spiral threads. Dark spots on the subsutural cord, typically well developed, may be lacking entirely in the light form (Fig. 10L), or on the contrary the light brown band on the shell base may be pronounced, and the tip of the siphonal canal coloured dark-brown (Fig. 10J). The species is undoubtedly closest to *L. picturata*, although some differences between the two exist (see remarks under *L. picturata*), of which key are the number of protoconch whorls (4 in *L. picturata* v. 3.25 in *L. bratasusa* sp. nov.) and the colour pattern on the subsutural cord (with extended lighter blotches in *L. picturata* or without in *L. bratasusa* sp. nov.).

Distribution: Confirmed distribution of the species (based on sequenced specimens) is Vanuatu and Papua New Guinea.

LOPHIOTOMA JICKELII (WEINKAUFF, 1875)

(FIG. 11)

Pleurotoma jickelii Weinkauff, 1875 in Weinkauff & Kobelt, 1875–1887: 20, pl. 4, figs 2, 3 (Massaua, Red Sea).

Lophiotoma acuta form *jickelii*. – Powell, 1964: 305, pl. 180, figs 14, 19.

Type material: Neotype MNHN IM-2013-13275 (here designated).

Type locality: Papua New Guinea, Tab Island, inner slope, 05°10.2′S, 145°50.3′E (Expedition PAPUA NIUGINI, st. PR42).

Description (neotype): Shell thin, fusiform (Fig. 11A–C), with high spire and long narrow siphonal canal very slightly inclined to left. Protoconch conical (Fig. 11D), of about 3.75 evenly convex whorls, posteriormost 0.75 whorl before transition to teleoconch with ten distinct arcuate ribs, more closely spaced towards transition to teleoconch. Protoconch diameter 1.0 mm, height 1.22 mm. Teleoconch whorls weakly angulated at shoulder, 10.5 in total. Suture moderately deep, distinct, subsutural region wide, distinctly concave. Subsutural cord distinct, narrow on upper four teleoconch whorls, rounded on top, with two additional angular ridges appearing in upper part of cord on 5th and subsequent whorls. Ridges become progressively stronger and on last whorl cord of three distinct sharp triangular in profile ridges, middle one most elevated. Subsutural region smooth on upper teleoconch whorls, with one spiral ridge appearing on third whorl, two on the fourth, three on fifth, up to six on the last whorl. Paired sinus cords strongest, separated by interspace four times wider than cords, broadly obtuse triangular in profile and of same strength on last whorl. On upper whorls both cords similar in size, very closely spaced on upper four whorls progressively broader spaced on later whorls. Base of spire whorls smooth on upper two whorls, with one spiral cord on the third to fourth whorl, two on fifth, and then fast enlarging in number up to 11, strongly different in size cords on penultimate whorl. Base of last whorl with 15 cords, five of which much more prominent; canal with 34 cords, becoming gradually lower anteriorly. Cords slightly nodulose on intersections with growth lines. Shell base sharply narrowing towards narrow and long nearly straight siphonal canal. Aperture pear shaped, strongly constricted posteriorly, with parietal callus producing distinct tooth, outer lip concave in upper part and strongly convex below shoulder, gradually passing into canal. Anal sinus deep, narrow, with nearly parallel sides, and nearly straight

Figure 11. *Lophiotoma jickelii* (Weinkauff, 1875). (A–D) Neotype, MNHN IM-2013-13275, PAPUA NIUGINI, st. PR42, SL 39.4 mm. (D) Lateral view of the protoconch. (E) MNHN IM-2013-54874, KAVIENG 2014, st. KR136, SL 36.2 mm. (F) MNHN IM-2007-41003, Vanuatu, SANTO 2006, SE corner of Espiritu Santo, 33.8 mm. (G) MNHN IM-2013-11537, PAPUA NIUGINI, st. PD08, SL 33.3 mm. (H) MNHN IM-2007-41144, SANTO 2006, st. AT38, SL 35.0 mm. (I) MNHN IM-2007-41182, SANTO 2006, st. ZR11, SL 32.9 mm. (J) MNHN IM-2009-7080, Mozambique, Inhaca Island, SL 29.4 mm. (K) MNHN IM-2009-29713, Vietnam, Nha Trang Bay, st. ND7, SL 44.9 mm. (L) MNHN IM-2013-12760, PAPUA NIUGINI, st. PR33, SL 37.9 mm. (M, N) Original illustration of the species (Weinkauff, 1875: pl. 4, figs 2, 3). (O) Specimen from Egypt, Brother Island, 10–35 m (collection of P. Stahlschmidt). All shells (except M, N) at the same scale.

posterior margin, parallel to shell axis; outer lip in side view rounded and opisthocline, stromboid notch well-defined. Shell light brown, protoconch and two first teleoconch whorls slightly darker. Subsutural cord(s) with light brown irregularly shaped spots. Sinus cords with narrow and irregularly spaced brown spots, minor spiral cords with spots sometimes chevron shaped and smaller flecks. Aperture light creamy, lirated deep inside. Measurements (neotype largest of our specimens): SL 39.4 mm, AL (with canal) 19.8 mm, SW 10.7 mm. Radula (neotype) (Fig. 5G) long, of about 65 rows of teeth, of which 25 nascent. Radula similar to other congeners, with duplex somewhat stout marginal teeth. Anterior (inner) half is solid, lanceolate, dorso-ventrally compressed with sharp lateral cutting edges. In posterior half major and accessory limbs bifurcate at about 45° angle, rather thin. Central formation distinct, of small sharp narrow cusp.

Remarks: The species is rather variable in terms of sculpture and coloration. All intermediate specimens can be found from very light, hardly speckled specimens from Vietnam (Fig. 11K) to very dark ones from Mozambique, similar to the dark form of *L. acuta* (Fig. 11J). Interestingly, the dark form was found only in Mozambique and the only two studied specimens from this region were dark. The degree of development of spiral cords (other than subsutural and sinus cords) can also be rather different: there can be as few as four subequal cords on the subsutural zone, up to six strongly unequal cords in the neotype. In all studied specimens, there are two or even sometimes three closely spaced cords immediately below the suture. On the contrary, in *L. acuta* and *L. semfala* sp. nov. the subsutural cord is single, sometimes with two much weaker additional threads running along it. This allows a reliable differentiation of *L. jickelii* from both *L. acuta* and *L. semfala* sp. nov. There seems to be geographically determined shell variability, with only dark forms sampled in Mozambique, and very light ones in Vietnam; however, very limited material available from the mentioned localities does not allow us to draw final conclusions. The species was for a long time considered to be a synonym of *L. acuta* (Powell, 1964: 305 and many others), or a Red Sea subspecies of *L. acuta*. The name was used as a valid one recently for specimens from the Philippines (Heralde *et al.*, 2007; Fedosov *et al.*, 2011), but its validity was never addressed from the viewpoint of taxonomy. The type of *Pleurotoma jickelii* Weinkauff, 1875 originated from C. Jickeli's collection, which is now partially stored in the Humboldt Museum, Berlin (http://www.conchology.be/?t=9001&id=21727). Nevertheless, the types were not found in the Berlin Museum, nor in SMF, where the material of some other Weinkauff species is kept. Therefore, we consider them to be lost. The species was described from Massawa (presently Eritrea) based on a beach-collected specimen. The illustration of Weinkauff & Kobelt (1875–1887): pl. 4, figs 2, 3) is a bit ambiguous and depicts the large shell (SL 53 mm) with poorly pronounced sinus cords and nearly straight sided bases of spire whorls, similar to those in our specimens. Powell (1964: pl. 180, fig. 19) illustrated a specimen of 'form *jickelii*' from the Red Sea very similar to ours and provided an adequate and accurate description of *Lophiotoma acuta* form *jickelii*. Finally, Verbinnen & Dirkx (2007) discussed the occurrence of *Lophiotoma acuta* in the Red Sea and the status of *L. acuta jickelii* (Weinkauff, 1875). They illustrated the shell of *acuta* (fig. 21) as well as two shells which represent *L. jickelii* (21a, 21b). We were able to examine one shell, collected in Egypt (Fig. 11O) and it, as well as specimens illustrated by Verbinnen & Dirkx, falls within intraspecific variability of a single species as defined herein by molecular data. In the absence of sequenced material from the Red Sea and due to the confusing situation with the taxonomy of the species, we designate herein the specimen collected in Tab Island, Papua New Guinea, Madang Lagoon (Fig. 11A–C) as the neotype of *Lophiotoma jickelii*. The species is most similar to *Lophiotoma kina* sp. nov., found in Vanuatu and Papua New Guinea. For differences see the remarks for *Lophiotoma kina* sp. nov. The species can be readily distinguished from *L. acuta* by its less pronounced subequal sinus cords rounded on top, while in *L. acuta* the upper sinus cord is much more pronounced than the lower and both sinus cords have a sharp upper edge. *Lophiotoma jickelii* also differs from both *L. acuta* and *L. semfala* sp. nov. in that the subsutural cord is subdivided into several cords on the last and penultimate whorls in the former species while in the latter two it is uniform with a sharp upper edge and very weak additional ridges. The studied radula of *L. jickelii* has a broader anterior solid part of marginal teeth and a more pronounced cusp on the central formation.

Distribution: Confirmed distribution of the species (based on sequenced specimens) – tropical Indo-West Pacific from Mozambique to Vietnam, Philippines, Papua New Guinea, Vanuatu. Based on published data also the Red Sea.

LOPHIOTOMA KINA SP. NOV.

(FIG. 12)

urn:lsid:zoobank.org:act:BB330B09-7334-4F5D-B7FF-30F43737680A

Type material: Holotype MNHN IM-2013-16307, paratype MNHN IM-2013-13278.

Type locality: Papua New Guinea, Madang Lagoon, W Tab Island, inner slope, 05°10.1′S, 145°50.2′E, 3–6 m (Expedition PAPUA NIUGINI, st. PR237).

Etymology: kina – the shell in Pidgin English, one of the official languages of Papua New Guinea. Used as a noun in apposition.

Description (holotype): Shell medium thick, fusiform, with high spire and long narrow siphonal canal very slightly inclined to left (Fig. 12A–C). Protoconch (intact in the specimen MNHN IM-2013-12950) conical, eroded of about 2.75 evenly convex whorls, posteriormost half whorl before transition to teleoconch with nine axial riblets (Fig. 12H). Protoconch diameter

Figure 12. ***Lophiotoma kina*** **sp. nov.** (A–C) Holotype, MNHN IM-2013-16307, PAPUA NIUGINI, st. PR237, SL 31.0 mm. (D) MNHN IM-2013-13278, PAPUA NIUGINI, st. PR42, SL 27.2 mm. (E) MNHN IM-2009-16927, SANTO 2006, st. FR10, SL 23.8 mm. (F) MNHN IM-2013-51209, KAVIENG 2014, st. KD13, SL 25.4 mm. (G–H) MNHN IM-2013-12950, PAPUA NIUGINI, st. PD23, SL 20.3 mm. (H) Lateral view of the protoconch. All shells at the same scale.

0.88 mm, height 0.93 mm. Teleoconch whorls weakly angulated at shoulder, 9.5 in total. Suture shallow, subsutural region wide, distinctly concave, subsutural cord low, on upper five whorls narrow, rounded on top. On sixth whorl, additional angular ridge appearing in upper cord part, which becomes progressively

stronger and on last whorl cord consists of two distinct ridges, adapical one being twice lower than abapical ridge. Subsutural region smooth on upper teleoconch whorls, with one spiral ridge appearing on fourth, three on fifth, four on sixth and eight on last whorl. Paired sinus cords strongest, separated by interspace three times wider than cords, obtuse triangular in profile and nearly of same strength on last whorl. On early whorls both cords similar in size, with upper one being more pronounced on last and penultimate whorls. Base of spire whorls smooth on upper three whorls, with one spiral cord on fourth whorl, two on fifth, three on the sixth and seven on penultimate. Base of last whorl with three major spiral cords and two smaller ones between them, canal with 22 subequal cords, becoming gradually lower anteriorly. Shell base sharply narrowing towards narrow and long nearly straight siphonal canal. Aperture pear shaped, strongly constricted posteriorly with parietal callus producing distinct tooth, outer lip concave in upper part and weakly convex below shoulder, gradually passing into canal. Anal sinus deep, V-shaped, posterior margin nearly straight, parallel to shell axis; outer lip in side view rounded and opisthocline, stromboid notch well-defined. Growth lines indistinct, closely spaced. Shell light creamy, protoconch and three first teleoconch whorls slightly darker. Subsutural cord(s) with light brown irregularly shaped spots. Sinus cords with very weak light brown regularly spaced flecks, as well as minor spiral cords; spots occupying whole width of cord. Aperture light creamy, lirated deep inside. Measurements (holotype largest specimen): SL 31.0 mm, AL (with canal) 15.7 mm, SW 9.3 mm. Radula (Fig. 5I) is similar to other congeners, with duplex marginal teeth. Anterior (inner) half solid, narrowly lanceolate, dorso-ventrally compressed with sharp lateral cutting edges. In posterior half, major and accessory limbs bifurcate at about 45° angle, rather thin. Central formation was not examined due to radula preparation.

Remarks: The species is most similar to *L. jickelii* and can be distinguished by the more pronounced sinus cords and correspondingly more angulated whorls, generally less intensively coloured shell, with only very weak brown flecks on the sinus cords and other spiral elements. It also has a smaller protoconch (although the protoconch was available only in three specimens), consisting of 2.75–3 whorls in *L. kina* sp. nov. vs. 3.5–4.0 in *L. jickelii* (3.75 in most specimens) (Fig. 8).

Distribution: Confirmed distribution of the species (based on sequenced specimens) is Vanuatu and Papua New Guinea.

LOPHIOTOMA VEZZAROI COSSIGNANI, 2015 (FIG. 9F–G)

Lophiotoma abbreviata. – Okutani, 2000: pl. 313, fig. 54 (not of Reeve, 1843).

Lophiotoma cf. *ruthveniana* Melvill, 1923. – Poppe, 2008: pl. 683, fig. 4.

Lophiotoma vezzaroi Cossignani, 2015: 30–31, text figs.

Type material: Holotype MMM – Cupra Marittima.

Type locality: New Place Birat Samal Island, Philippines. Tangle net at 100–200 m.

Material examined: Three specimens sequenced (Table S1), one specimen Tinina Balut Island, Philippines, tangle net at 100–200 m.

Diagnosis: Shell medium sized (up to 39 mm), turriform, with prominent spiral sculpture; shell coloured with dense irregularly shaped brown to dark brown spots, siphonal canal off-white to tan. Whorl outline moderately convex, angulated at sinus. Sinus cords paired, subequal in size, with narrow interspace. Subsutural ramp and shell base sculptured with varying in width and prominence cords and finer riblets. Shell base convex, strongly constricted to rather slender siphonal canal, sculptured with dense spiral to oblique cords. Aperture elongate, anal sinus moderately deep, wide, angulated at tip. Aperture distinctly lirate inside. Radula examined in one poorly preserved specimen from Tinina, Balut Island (Fig. 9G), in all respects similar to other studied herein species of *Lophiotoma*.

Remarks: The species was confused previously with *Lophiotoma ruthveniana*. Okutani (2000) illustrated a specimen very similar to *Lophiotoma abbreviata*. Although described from the Philippines, our material and the record of Okutani suggest that its distribution extends from Japan to Papua New Guinea and Vanuatu from 10 to 15 to more than 100 m depth.

Distribution: Vanuatu (sequenced specimens), Japan, Philippines and Papua New Guinea.

DISCUSSION

Following an integrative taxonomic approach, we applied several criteria and methods of species delimitation to identify species boundaries within *Lophiotoma*. The three exploratory methods used (ABGD, GMYC and PTP) do not always agree on the species delimitation, but the use of other criteria and characters allowed the most robustly supported species partitions

to be chosen: the ten SSH retained are recognized as genetically (based on both distances and phylogenetic relationships) and morphologically distinct. The application of the GMYC 'multiple' method to our dataset resulted in notably oversplit partitions; a similar tendency was found, for example by Kekkonen & Hebert (2014). On the contrary, genes less variable than *COI*, such as *28S*, tend to cluster some partitions that are later found worthy of recognition as species.

Among the ten delimited species, species in three pairs (*L. acuta* – *L. semfala* sp. nov., *L. picturata* – *L. bratasusa* sp. nov. and *L. jickelii* – *L. kina* sp. nov.) are barely distinguishable morphologically: without molecular evidence they would hardly be suspected to be separate species. Moreover, the intraspecific morphological variability exceeds the interspecific variability, particularly in shell coloration, with the presence of 'light' and 'dark' forms within each species of the pairs *L. acuta* – *L. semfala* sp. nov. and *L. jickelii* – *L. kina* sp. nov. The radular characters that sometimes can be useful for species delimitation (Kantor *et al.*, 2008) were of no help in the case of *Lophiotoma*. All examined species had extremely similar radular morphology, and only in one species, *L. jickelii* the central formation of the radula in the shape of a weak but distinct cusp was observed, while in all others it was either absent, or indistinct. However, we confidently recognize them as distinct species, based on the following considerations: (1) both genes recognized them as six distinct clades, (2) only in two cases (with the *COI* gene for *L. picturata* and *L. bratasusa* sp. nov. and with the *28S* gene for *L. acuta* and *L. semfala* sp. nov.) are 'morphological pairs' also recovered as sister species, and (3) remarkably, morphologically similar species always occur sympatrically, which tends to support the hypothesis of genetic isolation between species in 'morphological pairs'.

The integrative taxonomic approach followed here was thus efficient to propose robust species hypotheses. It represents one additional example of the value of molecular characters when species can hardly be distinguished morphologically, a common situation in gastropods (Jörger & Schrödl, 2013) and, in particular, in conoideans (e.g. Duda *et al.*, 2008; Puillandre *et al.*, 2010). However, if proposing putative species using DNA sequences is now common, linking the SSH to available names, most often attached to nonsequenced type specimens, remains problematic. Until now, all species of *Lophiotoma* have been described using conchological characters only. Moreover, locating type specimens to tentatively attribute their associated names to the defined SSH, based on morphological resemblance, was probably the most difficult task. Among the seven species already described before the present work, the type material was located for four species only (*L. abbreviata*, *L. brevicaudata*, *L. picturata* and *L. vezzaroi*). For *L. vezzaroi*, the holotype was properly designated, and for *L. abbreviata* and *L. brevicaudata* lectotypes were designated in previous studies. For the last one, *L. picturata*, we located two syntypes and designated a lectotype. For the three other species, *L. acuta*, *L. jickelii* and *L. polytropa*, we were unable to locate the type material (see details in the taxonomic section). In the absence of type material, we had to rely on the illustrations in the original descriptions to link the SSH to these names. For *L. acuta* and *L. jickelii*, because these names are associated with species complexes that include morphologically similar species, we choose one of the sequenced specimens in each species as a neotype. We also examined, when possible, the type material and/or the original illustrations of the species synonymized with *L. acuta* in the literature, and concluded that none of these names can confidently be attributed to one of the three remaining SSH. Consequently, we described these three SSH as new species: *L. semfala* sp. nov., *L. bratasusa* sp. nov. and *L. kina* sp. nov.

More generally, most species of molluscs were described before the molecular revolution, and the identity of most newly described species still remains based on dry material and/or nonsequenced specimens (Bouchet & Strong, 2010). When dealing with species complexes, attributing names to molecular groups is thus tricky. When the type specimens are lost, designating a sequenced specimen as a neotype solves the problem. However, when the types are still available, only morphological resemblance can be used to decide to which of the molecular groups the name will be attributed. We applied this strategy earlier to unravel relationship between forms of *Xenuroturris cingulifera* (Lamarck, 1822), for which molecular analyses and studies of radula revealed presence of two species that were very similar conchologically (Kantor *et al.*, 2008). An available name *Xenuroturris legitima* Iredale, 1929 was unearthed in the synonymy of *Iotyrris cingulifera* and applied to the nontypical form of *Xenuroturris cingulifera*. This decision was enabled by the fact that the types of the two mentioned names persist, both as empty shells, badly worn in the case of the Lamark's syntypes, and shell similarity helped to attribute each name to one of the two molecular groups. This solution was practical, because it allowed a stabilization of the nomenclature without the designation of neotypes, which in case of persisting types requires lengthy consideration by the Commission of Zoological Nomenclature. Here we used the same approach for *L. picturata*: we applied the name *picturata* to the species that was morphologically more similar to the lectotype.

Because type specimens remain the only way to unambiguously link names and genetic groups, one could suggest that sequencing type specimens, when available, is the ultimate solution. Traditionally, shell-bearing mollusc types are kept dried in collections, which does not ensure a correct DNA conservation. Recently developed NGS techniques would clearly help to sequence fragmented DNA, but a high proportion of name-bearing types are empty shells, which do not contain any remains of tissue inside. Recently published articles (Geist, Wunderlich & Kuehn, 2008; Andree & López, 2013; Villanea, Parent & Kemp, 2016) suggest that DNA can actually be extracted from shells, but whether such techniques are applicable to specimens kept dried for tens, or even hundreds of years, and for which the periostractum is potentially absent, remains to be tested. It also implies that a piece of the shell (Andree & López, 2013) of the holotype will be destroyed, a condition that will need to be accepted by museum curators.

In any case, providing DNA sequences should become the gold standard in species delimitation and description in groups where morphological characters are misleading, such as in Conoidea, to avoid erroneous species hypotheses based on shell characters only and to facilitate the attribution of names to genetic sequences in the future. Even if sequencing DNA from empty shells seem conceivable, it is difficult to imagine that all types of shelled molluscs will be sequenced in the future (for technical and financial reasons), and in most cases linking these names to molecular groups will be subject to controversy. Paraphrasing Marshall (1983), who said that 'under absolutely no circumstances should further new species [of Triphoridae] be proposed unless a complete, unworn protoconch can be illustrated,' ideally, under absolutely no circumstances should further new species of turrids be proposed without any molecular data.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. List of specimens analysed, with MNHN number, species name, geographic locality, depth, and BOLD and GenBank accession numbers.

Appendix 1. *COI* alignment.

Appendix 2. *28S* alignment.