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

3

4 NICOLAS PUIILLANDRE^{1*}, ALEXANDER E. FEDOSOV², PAUL ZAHARIAS¹,
5 LAETITIA AZNAR-CORMANO¹, YURI I. KANTOR².

6

7 ¹ Institut de Systématique, Évolution, Biodiversité ISYEB – UMR 7205 – CNRS,
8 MNHN, UPMC, EPHE, Muséum national d’Histoire naturelle, Sorbonne Universités,
9 57 rue Cuvier, CP26, F-75005, Paris, France

10 ² A.N. Severtzov Institute of Ecology and Evolution, Russian Academy of Sciences,
11 Leninski prospect 33, 119071, Moscow, Russian Federation

12

13 Corresponding author: Nicolas Puillandre; Institut de Systématique, Évolution,
14 Biodiversité ISYEB – UMR 7205 – CNRS, MNHN, UPMC, EPHE, Muséum national
15 d’Histoire naturelle, Sorbonne Universités, 57 rue Cuvier, CP26, F-75005, Paris,
16 France; +33 1 40 79 31 66; puillandre@mnhn.fr

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19 Running title: Integrative taxonomy of *Lophiotoma*

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33 **Abstract**

34

35 Integrative taxonomy, and in particular species delimitation using molecular data, often
36 lead to the discovery of new species. However, these new species are not systematically
37 turned into formally described species, because, among other reasons, linking
38 molecularly defined groups with available taxonomic names can be tricky. Here we
39 delimit species in the genus *Lophiotoma* (Gastropoda, Conoidea, Turridae) using two
40 unlinked genetic markers (the mitochondrial COI gene and the nuclear 28S gene), shell
41 and radula characters, and geographic and bathymetric distribution. Several methods of
42 species delimitation (ABGD, GMYC and PTP) resulted in several alternate species
43 partitions, discussed using an integrative approach. We ended up with 10 different
44 species, among which seven have been linked to available species names. We
45 designated neotypes for two of them (*L. acuta*, *L. jickelii*). The three remaining species
46 were described as new: *L. semfala* sp. n., *L. bratasusa* sp. n. and *L. kina* sp. n. We
47 discuss the difficulties encountered to locate type specimens and link them to molecular
48 species, in a context where the vast majority of mollusc types are empty, dried shells,
49 difficultly accessible for molecular sequencing.

50

51 **Keywords**

52 Species delimitation, ABGD, GMYC, PTP, neotype designation, species description.

53

54

55 **Introduction**

56

57 While DNA and integrative taxonomy (Dayrat, 2005; Will, Mishler, & Wheeler, 2005)
58 certainly participated in the revival of taxonomic research in the last 10 years, its impact
59 on species descriptions remains limited. Most species descriptions are still based on
60 morphological characters only (Pante, Schoelinck, & Puillandre, 2014), and descriptions
61 that include a molecular diagnosis remain scarce (Renner, 2016). In the Mollusca
62 collection of the Museum National d'Histoire Naturelle (MNHN), Paris, the first
63 holotype associated to a DNA sequence was registered in 2008; since then, 2,126
64 holotypes have been deposited in the MNHN collections, but only 65 are linked to a
65 DNA sequence. As quoted by Bouchet & Strong (2010), "80% of the new species
66 descriptions of shelled marine gastropod species published in 2006 contained a
67 description of the shell only [i.e. without any mention of DNA characters, but also
68 anatomy or radula]".

69 Why does the input of DNA characters remain so insignificant in the description of the
70 biodiversity, in spite of its growing popularity among biologists? One of the reasons lies
71 probably in the dichotomy between taxonomists (including amateurs, particularly active
72 in molluscs) and "molecularists", people who actually produce the DNA sequences.
73 Most species remained described based on morphological characters because these
74 characters still remain largely more accessible than DNA characters. Conversely, most
75 molecularists are not trained in taxonomy and nomenclature, and many of the new
76 species they discover, some of them being undetectable with morphological characters,
77 remain undescribed, and thus virtually ignored by the scientific community (Goldstein
78 & DeSalle, 2011). Nevertheless, both approaches should be actually encouraged and
79 applied synergistically: on the one hand, many species are difficult to distinguish
80 morphologically, and in these cases integrative taxonomy, including DNA characters,
81 proved its usefulness (Pante *et al.*, 2015); on the other hand, linking molecularly defined
82 species to available names, and eventually proposing new names, requires knowledge of
83 the nomenclatural rules, of the taxonomic literature and, in particular, of the type
84 specimens.

85 However, even close examination of the type material may be of little use in marine
86 molluscs, as many name-bearing types simply do not fulfill their function, being too

87 worn and badly preserved to confidently link the species name to other, more recently
88 collected, material (Bouchet & Strong, 2010). It is particularly true when several species
89 share identical teleoconchs, differentiated only by protoconchs, radulae, anatomical or
90 even DNA characters, as many of these characters are inaccessible on these types. Thus,
91 a lost name-bearing type would actually be preferable, because in this case a procedure
92 of neotype designation would be available, which would provide an ultimate solution to
93 a species identity problem. This however, requires either a proof that the name-bearing
94 types were lost, or application to the Commission of Zoological nomenclature, both
95 being time consuming procedures.

96 To illustrate the benefit of a combination of molecularists and taxonomists, we applied
97 an integrative taxonomy approach in a group of marine gastropods, *Lophiotoma*
98 (Gastropoda, Conoidea, Turridae) that cumulates many of the difficulties listed above,
99 plus some others, making it a good model to illustrate the link between species
100 delimitation and species description: (i) because of their shell variability, several
101 described species have been synonymized in the literature, and many names are
102 potentially applicable; (ii) preliminary results published in Puillandre *et al.* (2012b)
103 suggest that several MOTUs can share very similar shells; and (iii) type specimens of
104 some species has been lost and are known by a figure only, and therefore are difficult to
105 link to subsequently collected specimens. In this study, we apply the name *Lophiotoma*
106 to the clade defined in Puillandre *et al.* (2012b) that includes the type-species *L. acuta*
107 (Perry, 1811), but excluding other species sometimes referred as *Lophiotoma* (e.g. *L.*
108 *albina*, *L. indica*), but not phylogenetically related to *L. acuta*. These shallow-water
109 turrids, restricted to the Indo-Pacific, are known since the early 19th century. As most
110 other conoideans, they are characterized by a venom apparatus, producing toxins used to
111 capture their prey (most likely polychaetes). Their taxonomy has been revised by
112 Powell (1964), and although they are regularly sampled by shell collectors, only one
113 species (*L. vezzaroi* Cossignani, 2015) has been described since.

114 To delimit species in this genus, we followed the general workflow of Puillandre *et al.*
115 (2012b): species hypotheses are proposed in an integrative framework, based on a
116 unified species concept in which species are considered as definitely diverging lineages
117 (De Queiroz, 2007; Samadi & Barberousse, 2009). First, Primary Species Hypotheses
118 (PSH) were proposed using part of the mitochondrial COI gene and three of the most

119 widely used methods based on monolocus data: ABGD (Automatic Barcode Gap
120 Discovery, (Puillandre *et al.*, 2012a)), GMYC (General Mixed Yule Coalescent model,
121 (Pons *et al.*, 2006; Monaghan *et al.*, 2009)) and PTP (Poisson Tree Processes, (Zhang *et*
122 *al.*, 2013)). Second, monophyly of the PSH was tested performing Maximum
123 Likelihood and Bayesian Analyzes on both COI and nuclear 28S genes, two unlinked
124 genetic markers, to check whether each PSH corresponds to an independent lineage in
125 both gene trees. Finally, morphological variability, and geographic and bathymetric
126 distributions were integrated to turn the PSH into Secondary Species Hypotheses (SSH).
127 In the final step, and after a deep search in the literature and in museum collections,
128 available names were tentatively applied to the SSH, relying on shell characters and
129 type localities; when no available name was found, the SSH was described as a new
130 species.

131

132 **Material and Methods**

133

134 *Sampling*

135

136 The material was collected during several expeditions in the Indo-Pacific: Panglao 2004
137 and Aurora 2007 in the Philippines, Santo 2006 in Vanuatu, Inhaca 2011 in
138 Mozambique, Nha-Trang in Viet-Nam (2010 - 2016) and Papua Niugini (2012) and
139 Kavieng 2014 in Papua-New-Guinea (expeditions.mnhn.fr) (Fig. 1). All the material is
140 stored in the MNHN.

141 Until 2012, live specimens for molecular analysis were anaesthetized with an isotonic
142 solution of MgCl₂ and fixed in 96% ethanol. Specimens collected during later
143 expeditions were processed with a microwave oven (Galindo *et al.*, 2014): the living
144 molluscs in small volumes of sea water were exposed to microwaves for 7-30 seconds,
145 depending on specimen size. Bodies were immediately removed from shells and
146 dropped in 96% ethanol. Specimens are registered in the MNHN collection and
147 sequences were deposited in BOLD (Barcode of Life Datasystem) and GenBank
148 (Supplementary Material 1).

149

150 *DNA sequencing*

151

152 DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the
153 manufacturers' recommendations. A fragment of the cytochrome oxidase subunit I
154 (COI) and of the rRNA 28S genes were amplified using universal primers
155 LCO1490/HCO2198 (Folmer *et al.*, 1994) and either C1/D3 (Jovelin & Justine, 2001)
156 or C2CONO (GAAAAGAAGCTTTGAAGAGAGAGT) / D3 (Ober, 2002), respectively.
157 PCR reactions were performed in 25 µl, containing 3 ng of DNA, 1X reaction buffer,
158 2.5 mM MgCl₂, 0.26 mM dNTP, 0.3 mM of each primer, 5% DMSO, and 1.5 units of
159 Qbiogene Q-Bio Taq. For the COI fragment, amplification consisted of an initial
160 denaturation step at 94°C for 4 min, followed by 35 cycles of denaturation at 94°C for
161 30 s, annealing at 50°C for 30s, followed by extension at 72°C for 1 min. The final
162 extension was at 72°C for 5 min. The 28S PCR reactions were performed in 20 µL
163 reaction volumes, containing a final concentration of 1X SsoAdvanced Universal SYBR
164 Green Supermix, 0.3 mM of primers, and 0.5 µg/µL of BSA, plus 1 µL of DNA extract.
165 The amplification thermal profiles consisted of an initial denaturation for 3 min at 94°C,
166 followed by 40 cycles of denaturation at 94°C for 30s, annealing at 60°C for 30s,
167 extension at 72°C for 1min and a final extension at 72°C for 5min. PCR products were
168 purified and sequenced by the Eurofins sequencing facility.

169

170 *Species delimitation*

171

172 COI sequences were aligned manually; 28S sequences were aligned using Muscle
173 (Edgar, 2004) and alignments were checked by eye. Pairwise genetic distances (p-
174 distances) were calculated using MEGA 6 (Tamura *et al.*, 2013), following Srivathsan
175 & Meier (2012). ABGD, GMYC (both the single and multiple versions), PTP and the
176 phylogenetic methods were applied to the COI and 28S alignments, plus a
177 concatenation of the COI and 28S alignments (for a subset of specimens – see Results
178 section). For ABGD, the web version (<http://wwwabi.snv.jussieu.fr/public/abgd>) and the
179 default parameters were used, with a p-distance model. Bayesian trees were
180 reconstructed using BEAST v1.8.3 (Drummond *et al.*, 2012), running 100,000,000 (for
181 the 28S and COI+28S datasets) or 200,000,000 (for the COI dataset) generations with a
182 sampling frequency each 4,000 generations. Relative divergence times were estimated

183 using a relaxed lognormal clock with a coalescent prior and a constant population size,
184 following the recommendations of Monaghan *et al.* (2009). Both single and multiple
185 thresholds methods of GMYC were applied using the trees obtained with BEAST.
186 Maximum likelihood trees, using RaxML v8.2.8 (Stamatakis, 2006), with the robustness
187 of the nodes assessed using 1,000 bootstraps, and a Bayesian tree, using Mr.Bayes 3.2.6
188 (Huelsenbeck, Ronquist, & Hall, 2001), were reconstructed. For the MrBayes analyses,
189 each of the two runs consisted of six Markov chains and 20,000,000 generations, with 8
190 chains, 5 swaps at each generation, a sampling frequency of one tree each 2,000
191 generations and a chain temperature set at 0.02. For the Bayesian analyses (BEAST and
192 MrBayes), convergence of each run was evaluated using TRACER 1.6 (Rambaut &
193 Drummond, 2014) to check that all effective sample size values exceeded 200.
194 Consensus trees were calculated after omitting the first 25% trees as burn-in. All
195 phylogenetic analyses were performed on the Cipres Science Gateway
196 (<http://www.phylo.org/portal2>). In all cases, a GTR+I+G substitution model was used,
197 and the COI gene was divided in three partitions corresponding to the three codon
198 positions. For the concatenated datasets, four partitions were defined (3 codon positions
199 of the COI and 28S gene). PTP was run with defaults parameters using the RAxML
200 trees. Two specimens of closely related taxa were used as outgroups for phylogenetic
201 analyses: *Turris babylonia* and *Iotyrris musivum* (Conoidea, Turridae).

202

203 *Shell morphology and radula*

204

205 Radulae were prepared by standard methods (Kantor & Puillandre, 2012) and examined
206 by scanning electron microscope TeScan TS5130MM in the Institute of Ecology and
207 Evolution of Russian Academy of Sciences (IEE RAS). Protoconchs were measured in
208 standard position and the number of whorls counted according to Bouchet & Kantor
209 (2004).

210

211 **Results**

212

213 Based on the partition with the highest number of PSH obtained with the COI gene, we
214 build a reduced concatenated (COI+28S) dataset to limit computational time: 5

215 specimens per PSH and per geographic regions maximum were kept. All the partitions
216 obtained with ABGD, GMYC and PTP for the three datasets are shown in the Table 1.
217 For the COI and COI+28S datasets, two partitions are discussed among the partitions
218 proposed by ABGD: the partitions with the highest and lowest number of PSH (for the
219 28S dataset, only one partition was proposed by ABGD). The results of the GMYC
220 “multiple” analyses are not shown, as well as the results of the GMYC “single” analysis
221 for the 28S, because they proposed unrealistic number of PSH, not in agreement with
222 the other methods, the phylogenetic trees and the other characters (111 PSH with the
223 dataset COI for GMYC “multiple”, 27 for the COI+28S dataset for the GMYC
224 “multiple”, and 79 and 78 for the 28S dataset for the GMYC “single” and “multiple”,
225 respectively). In all cases, the GMYC “multiple” partition was not significantly better
226 than the GMYC “single” partition (p-value $\gg 0.05$). The 28S gene is much less
227 variable than the COI gene, and ABGD provided very few PSH with this gene (only
228 five): this partition will be ignored in the rest of the text. In all the other cases, the
229 number of PSH delimited varies from 8 to 16, all of them being compatible (i.e. they
230 correspond to more or less inclusive PSH). In several cases, these splits correspond to a
231 single specimen isolated from the others, in PSH including few specimens (less than
232 five).

233 By comparing the PSH obtained with the different datasets (Table 1), the results of the
234 phylogenetic analyses (Fig. 2 and 3), the morphological variation and the bathymetrical
235 and geographical distributions (Supplementary Material 1), we turned the PSH in SSH
236 and attributed available names to them or described them as new. Two PSH are found
237 with all the genes and methods, have very distinct shells and are in our material
238 restricted to a single archipelago: they were identified as *L. polytropa*, restricted to the
239 Philippines, and *L. vezzaroi*, in Vanuatu. Those two PSH also always correspond to
240 highly supported clades in the phylogenetic analyses. The PSH identified as *L.*
241 *abbreviata* and *L. brevicaudata*, again with very distinct shells, are either found as a
242 single PSH or as two different PSH (in one case – COI/PTP, *L. abbreviata* is divided in
243 three groups, each corresponding to an unsupported clade). Their association generally
244 corresponds to a highly supported clade. With the 28S gene, *L. abbreviata* is
245 monophyletic and (moderately) supported and *L. brevicaudata* is not monophyletic; it is
246 the opposite with the COI gene, and with both genes both PSH are reciprocally

247 monophyletic. Both are found in sympatry, sometimes even in the same station. It is the
248 only species pair that seems to have distinct bathymetric preferences, *L. abbreviata*
249 being found at average depth 2,9 m (+/-4 m) and *L. brevicaudata* at 14,8 m deep (+/- 9
250 m). One supported clade, found in Papua-New-Guinea and Vanuatu, is constantly
251 defined as a separate PSH (except with 28S-PTP): *L. bratasusa* sp. n. It is
252 morphologically very similar (see Taxonomy section), but distinguishable, to another
253 PSH restricted to Papua-New-Guinea, sometimes co-occurring with it: *L. picturata*. The
254 latter is sometimes separated in two PSH, morphologically undistinguishable and
255 phylogenetically less supported (or even not recognized as monophyletic) than the
256 whole PSH *L. picturata*. A similar situation is also found for a group of specimens with
257 shell preliminarily identified as *L. acuta*. The first PSH, *L. acuta*, is abundant and
258 widely distributed, and sometimes divided in two PSH. The second, *L. semfala* sp. n.,
259 contains fewer specimens, also widely distributed (Philippines, Papua-New-Guinea and
260 Vanuatu), and once again is sometimes divided in two PSH. However, as for *L. acuta*
261 and *L. picturata*, the support is lower for the subgroups. Finally, the two last PSH are
262 also morphologically similar: *L. jickelii* and *L. kina* sp. n. Once again, there were
263 sometimes separated in two PSH each, less supported than the more inclusive PSH. And
264 as for *L. picturata* and *L. bratasusa* sp. n., *L. semfala* sp. n. and *L. acuta* on one hand,
265 and *L. jickelii* and *L. kina* sp. n. on the other hand, are also found in sympatry,
266 sometimes co-occurring at the same station.

267

268 **Taxonomy**

269

270 We provided descriptions for the new or newly defined taxa (as in case of neotype
271 designation), and diagnosis for the species for which the status and scope do not change
272 (compared to the generally accepted scope of the species). In addition to the type
273 material, see the Supplementary Material 1 for the other material examined.

274

275 Abbreviations

276 BMNH: British Museum of Natural History, London, United Kingdom.

277 MMM: Mostra Mondiale Malacologia.

278 MHNG: Muséum d'Histoire naturelle, Geneva, Switzerland

279 MNHN: Muséum National d'Histoire Naturelle, Paris, France.

280 SMF: Forschungsinstitut Senckenberg, Frankfurt, Germany.

281 ZMB: Museum für Naturkunde, Humboldt-Universität, Berlin, Germany.

282

283

284 Superfamily CONOIDEA Fleming, 1822

285 Family TURRIDAE H. & A. Adams, 1853 (1838)

286 Genus *Lophiotoma* Casey, 1904

287 *Type species. Pleurotoma acuta* Perry, 1911, OD.

288 *Diagnosis.* Shell medium-sized to large, narrow to broad fusiform, with attenuated,
289 usually long and nearly straight canal. Protoconch multispiral in examined in this
290 respect species. Teleoconch whorls usually angulated at shoulder. Sculpture of sharp
291 pronounced cords, including sinus area. Anal sinus deep, with nearly parallel sides.
292 Operculum with apical nucleus.

293 Marginal radular teeth duplex. Anterior (inner) half is solid, narrow lanceolate, dorso-
294 ventrally compressed with sharp lateral cutting edges. In posterior half the major and
295 accessory limbs bifurcate at the angle about 45°, rather thin. The central formation
296 (sensu Kantor (2006)) is either absent or very weak, represented by central tooth, having
297 shape of flat poorly developed cusp.

298 *Remarks.* The genus was revised by Powell (1964) who recognized two subgenera
299 (nominative one and *Lophioturris* Powell, 1964) differing on the basis of the protoconch
300 – multispiral in the former and blunt paucispiral in the latter. Powell attributed five
301 Recent species to *Lophiotoma* s.s. As specified in the introduction, previous analyses
302 revealed that among those included species *Lophiotoma albina* (Lamarck, 1822) should
303 be excluded as it is more closely related to *Gemmula*-like species while on the contrary
304 *L. polytropa* (Helbling, 1779) attributed by Powell to *Lophioturris* is confidently
305 included in *Lophiotoma* on the basis of molecular analysis (Puillandre *et al.*, 2012b).
306 Protoconch of *L. polytropa* is unknown so far. *Lophioturris* with the type species *Turris*
307 *indica* (Röding, 1798) is constituting a clade with *Unedogemmula* MacNeil, 1960 (type
308 species *Turris unedo* Kiener, 1839-1840), not related to *Lophiotoma* as defined here,
309 and thus becomes junior subjective synonym of the latter. Among species treated as
310 *Lophiotoma* by Powell (1964) only one species, *L. ruthveniana* (Melville, 1923) is absent

311 in our material and its position remains unconfirmed. At the same time, recently
312 described *Lophiotoma vezzaroi* Cosignani, 2015 was sequenced and falls within the
313 *Lophiotoma* clade as defined here. This species was described from the Philippines and
314 found by us in Santo; it is conchologically rather similar to *L. ruthveniana*.
315
316 *Lophiotoma acuta* (Perry, 1811). (Fig. 4)
317 *Pleurotoma acuta* Perry, 1811: pl. 5, fig. 5.
318 *Pleurotoma marmorata* Lamarck, 1816: pl. 439, fig. 6. (non *Pleurotoma marmorata*
319 Link, 1807).
320 *Pleurotoma tigrina* Lamarck, 1822: 95 (nom. nov. pro *Pleurotoma marmorata*
321 Lamarck, 1816, non *Pleurotoma marmorata* Link, 1807).
322 *Pleurotoma punctata* Schubert & Wagner, 1829: 155, pl. 234, figs 4103 a, b. (no
323 locality).
324 *Lophiotoma microsticta* Casey, 1904: 130.
325 *Lophiotoma acuta* Perry, 1811 – Powell, 1964 (part.): 303-305, color plate 180, figs. 1-
326 10, 15-18 (non plate 180), fig. 14, 19, nec
327 *Type material*. Neotype of *Lophiotoma acuta* (here designated), MNHN IM-2007-
328 41179, the same specimen is designated as a neotype of *Pleurotoma punctata* (Schubert
329 & Wagner, 1829). Three syntypes of *Pleurotoma tigrina*, MHNG (MHNG-MOLL-
330 51664). *Type locality*: Indian Ocean, Madagascar coast. Syntypes of *Lophiotoma*
331 *microsticta*, ?USNM (fide Powell (1964), see below). *Type locality* Cebu, Philippines.
332 *Type material* of *Pleurotoma (Turris) peaseana* (Dunker, 1871), presumably lost (see
333 below).
334 *Type locality*. Vanuatu, E Malo Island, 15°43,4'S, 167°15'E, flat sand and dead corals,
335 6 m (Expedition SANTO 2006, st. DR84, R/V *Aldric*).
336 *Material examined*. 156 sequenced specimens (Supplementary Material 1).
337 *Description* (neotype) (Fig. 4 A-D): Shell medium thick, narrow fusiform, with high
338 spire and long narrow siphonal canal slightly inclined to the left. Protoconch (Fig. 4 D)
339 conical, of nearly 3 evenly convex whorls, first whorls smooth, posteriormost half a
340 whorl with 9 axial nearly straight riblets, more densely spaced in posterior part of
341 protoconch. Protoconch diameter 0.78 mm, height 0.85 mm. Teleoconch whorls
342 strongly angulated at shoulder, 10 in total. Suture shallow, subsutural region wide,

343 distinctly concave, subsutural cord low, triangular in profile, with 3 weak angular
344 ridges, central one strongest. Subsutural region smooth on upper teleoconch whorls,
345 with one spiral ridge appearing on 4th, 2 on 6th, 3 on 7th and seven on the last whorl.
346 Paired sinus cords strongest and form strong angulated shoulder. On upper whorls both
347 cords are similar in size and rounded on top, on penultimate and last whorls cords are
348 distinctly triangular in profile and upper much stronger than lower. Base of spire whorls
349 smooth on first whorl, with one spiral cord on 2-6th whorls, starting from 7th whorl the
350 number of cords gradually increases, and penultimate whorl with 6 narrow cords of
351 slightly different size; interspaces 3-4 times broader than cords. Base of last whorl with
352 5 major spiral cords and several riblets between them, canal with 20 cords, becoming
353 gradually broader, lower and more closely spaced anteriorly. Shell base gradually
354 narrowing towards narrow and long nearly straight siphonal canal. Aperture pear
355 shaped, outer lip concave in upper part and weakly convex below shoulder, gradually
356 passing into canal. Anal sinus deep, with nearly parallel sides, its posterior margin
357 straight, parallel to shell axis; outer lip in side-view rounded and opisthocline,
358 stromboid notch ill-defined. Growth lines indistinct, closely spaced. Shell creamy,
359 protoconch and two first teleoconch whorls light brown. Subsutural cord with regularly
360 spaced brown spots, not extending beyond cord. Sinus cords with distinct dark brown
361 regularly spaced spots occupying whole width of cord and separate on each cord, minor
362 spiral cords with dense brown flecks. Aperture creamy inside. Measurements: SL 38.8
363 mm, AL (with canal) 19.7 mm, SW 11.0 mm. Radula was examined in five specimens,
364 all from Papua New Guinea. It was very similar in all examined specimens (Fig. 5 A-
365 B). Radula membrane long, consists of 55-80 rows of teeth of which 25-30 are not fully
366 formed. Marginal teeth duplex. Anterior (inner) half is solid, narrow lanceolate, dorso-
367 ventrally compressed with sharp lateral cutting edges. In posterior half the major and
368 accessory limbs bifurcate at the angle about 45°, rather thin. The central formation is
369 absent or very weak, in the form of flat poorly developed cusp, looking like folds of the
370 membrane, but regularly positioned.

371 *Remarks.* The species is very variable in terms of coloration and shell shape. The base
372 color can be from pure white to light orange and even light brown (subsutural region,
373 shell base and canal) with lighter sinus area. With some reservation two color forms can
374 be distinguished, although the intermediate specimens can also be found. In light form

375 the brown spots are more scarce and usually confined to major cords, especially to
376 subsutural and sinus ones, while the smaller cords have separate brown speckles. In
377 dark form (Fig. 4 H) the entire shell can be light brown, with lighter band along the
378 sinus cords. The large brown spots on subsutural cord dissolve in lower part into brown
379 band, occupying entire subsutural zone. The brown spots on minor cords can be as large
380 as those on sinus cords. The canal and anterior part of aperture can be also brownish. At
381 the same time transitional specimens between forms can be found. The dark form was
382 found within entire distribution area of the species. In Vanuatu, which is most rich in
383 sequenced material 66% of specimens were represented by light form, 24 by dark form
384 and 10% can be attributed to intermediate forms (total number of checked specimens =
385 94). Rather distinct form is found in Vietnam and the Philippines (Fig. 4 J) – the shells
386 are large (can reach 51 mm in our material), relatively heavy and with less pronounced
387 sinus cord and the spots and speckles are rather fine, except those on subsutural cord. In
388 the molecular tree based on COI they are sister to the rest of the *Lophiotoma acuta*,
389 although do not form monophyletic group. The syntype of *Lophiotoma microsticta*
390 Casey, 1904 (illustrated by Powell (1964): pl. 233, figs. 4-5), with SL 59.7 mm is rather
391 similar to this form. Protoconchs were studied in eight specimens, are rather uniform,
392 consist of 2.75 whorls. Number of 9 axial riblets varies from 6 to 11, protoconch height
393 0.88-0.95, diameter 0.8-0.83 mm. The species is most similar to *L. semfala* sp. n. and
394 some specimens can hardly be distinguished, nevertheless the morphology of the sinus
395 cords seems to be rather uniform in *L. acuta* – on last whorl (in adult specimens) the
396 upper cord is much more pronounced than the lower and has distinct triangular shape
397 with sharp upper edge, while in *L. semfala* sp. n. the cords are nearly similar to each
398 other and are more obtuse and rounded on top (Fig. 6).

399 *Taxonomic remarks.* The species was treated as broadly distributed and strongly
400 variable. Powell (1964) listed a number of nominal taxa in the synonymy of this
401 species, including *Pleurotoma jickelii* Weinkauff, 1875 and *Pleurotoma picurata*
402 Weinkauff, 1876. On the basis of molecular and morphological analysis these two
403 species appeared to be valid. *Pleurotoma acuta* Perry, 1811 was described without
404 locality or shell measurements. Original shell illustration is a bit grotesque, although
405 suitable for positive identification. Few existing types described by Perry (1811) are
406 stored in the BMNH (Dance, 1986) and the type of *P. acuta* is not among them. Due to

407 complicated taxonomic situation with the *L. acuta* complex, a neotype is here
408 designated. The name *Pleurotoma marmorata* (non *Pleurotoma marmorata* Link, 1807
409 = *Turris chaldeia* Kilburn, Fedosov & Olivera, 2012) was listed by Lamarck (1816) (pl.
410 439, Fig. 6, Le Liste, p. 8). Later Lamarck (1822) (p. 95) renamed the species *P. tigrina*,
411 citing his own figure, but still proposed the name *Pleurotoma marmorata* for another
412 species, which became the homonym for the third time. Three syntypes of *Pleurotoma*
413 *tigrina* are in MHNG (MHNG-MOLL-51664) (Fig. 4 F-G herein) and it is seemingly
414 conspecific with *L. acuta* in our current understanding, being closer to the "dark" form.
415 Judging from the syntypes of *P. marmorata* Lamarck, 1822 (MHNG-MOLL-51663) the
416 species belong to the genus *Unedogemmula* MacNeil, 1961 and was listed in synonymy
417 of *Lophiotoma (Lophioturris) indica* (Röding, 1798) by (Powell (1964). The syntype of
418 *Lophiotoma microsticta* Casey, 1904 was illustrated by Powell (1964): pl. 233, figs. 4-
419 5) and claimed to be deposited in USNM. Nevertheless we were not able to find it in the
420 collections. Judging from the photo it has the same sculpture pattern as *L. acuta*, that is
421 the dominating upper sinus cord; therefore we confirm the opinion of Powell (1964),
422 that it is a synonym of *L. acuta*. Type material of *Pleurotoma punctata* was not traced
423 despite queries in the corresponding museums and the original illustration is rather
424 crude, although the general outline is similar to that of *L. acuta*. In order to fix the
425 problem and to stabilize the nomenclature we designate the neotype of *Pleurotoma*
426 *acuta* Perry, 1811 also as the neotype of *P. punctata*, thus the latter name is now a
427 junior objective synonym of *P. acuta*. *Pleurotoma peaseana* (Dunker, 1871)
428 (*Pleurotoma (Turris) peaseana* (Dunker, 1871): 154 (Indian Ocean)) is another species
429 of doubtful affinity, which was synonymized by Powell (1964) with *L. acuta*. It was
430 illustrated only in Weinkauff (1876, in (Weinkauff & Kobelt, 1875-1887): 66, pl. 2, fig.
431 10) The illustration is depicting rather stout shell with moderately elongate canal, much
432 shorter than in both *L. acuta* and *L. semfala*. The species may not be closely related to
433 *L. acuta*. We were not able to trace the type despite queering museums, where the
434 Dunker's type material can be stored. Powell (1964) synonymized the species with *L.*
435 *acuta* without providing any arguments, the opinion being followed by Oyama (1966)
436 and Higo, Callomon, & Gotō (1999). Moreover, Weinkauff (1876, in (Weinkauff &
437 Kobelt, 1875-1887)) described the protoconch of *peaseana* consisting of 3 smooth
438 semitranslucent whorls with poorly visible suture, not mentioning the characteristic

439 axial ribs in posteriormost part of protoconch. This seems more similar to protoconch of
440 *Unedogemmula* and we exclude the species from synonymy of *L. acuta*.

441 *Distribution*. Confirmed distribution of the species (based on sequenced specimens) –
442 tropical Indo-west Pacific (from Santo to Vietnam). Judging from the published data, it
443 also includes Madagascar (type locality of *tigrina*), South Africa (Kilburn, 1983), Red
444 Sea (Verbinnen & Dirks, 2007), Japan (Okutani, 2000), Fiji, Queensland (Australia)
445 (Powell, 1964), New Caledonia (uncatalogued MNHN material).

446

447 *Lophiotoma semifala* sp. n. (Fig. 7)

448 *Holotype*. MNHN IM-2007-41337.

449 *Type locality*. Vanuatu, Aoré I. Aimbuei Bay, 15°32,8'S, 167°11,6'E, white coral sand,
450 3-8 m (Expedition SANTO 2006, st. LD35, R/V *Alis* annex).

451 *Other material*. 5 sequenced specimens (Supplementary Material 1).

452 *Etymology*. *semifala* – the "same" in Bislama, the creole language, one of the official
453 languages of Vanuatu. Used as noun in apposition to reflect the similarity to *Lophiotoma*
454 *acuta*.

455 *Description* (holotype) (Fig. 7 A-D). Shell medium thick, narrow fusiform, with high
456 spire and long narrow siphonal canal slightly inclined to the left. Protoconch conical,
457 eroded, rendering exact whorl count and sculpture examination doubtful, of about 3
458 evenly convex whorls. Protoconch diameter 0.73 mm, height 0.85 mm. Teleoconch
459 whorls angulated at shoulder, 10 in total. Suture very shallow, indistinct, subsutural
460 region wide, distinctly concave, subsutural cord low, triangular in profile, with 3
461 angular ridges on last whorl, central one strongest. On upper teleoconch whorls only
462 central ridge persists. Subsutural region smooth on upper teleoconch whorls, with one
463 spiral ridge appearing on 4th, 2 on 6th, 3 on 7th and five on the last whorl. Paired sinus
464 cords strongest and form angulated shoulder. On upper whorls both cords are nearly
465 similar in size, obtusely triangular, on penultimate and last whorls cords are more
466 angulate, although still rounded on top, only on last whorl the upper cord is distinctly
467 stronger than lower. Base of spire whorls smooth on first four whorl, with one spiral
468 cord on 5-6th whorls, starting from 7th whorl the number of cords gradually increases,
469 and penultimate whorl with 7 narrow cords of slightly different size, median much
470 stronger; interspaces 3-4 times broader than cords. Base of last whorl with 3 major

471 spiral cords and several riblets between them, canal with 20 cords, becoming gradually
472 broader, lower and more closely spaced anteriorly. Shell base gradually narrowing
473 towards narrow and long nearly straight siphonal canal. Aperture pear shaped, outer lip
474 concave in upper part and weakly convex below shoulder, gradually passing into canal.
475 Anal sinus deep, with nearly parallel sides, its posterior margin straight, parallel to shell
476 axis; outer lip in side-view rounded and opisthocline, stromboid notch well defined.
477 Growth lines indistinct, closely spaced. Shell creamy, protoconch and three first
478 teleoconch whorls very light brown. Subsutural cord with regularly spaced brown spots,
479 not extending beyond cord, broader on last three whorls. Sinus cords with distinct dark
480 brown regularly spaced spots occupying whole width of cord and separate on each cord,
481 minor spiral cords with dense brown flecks. Aperture creamy inside. Measurements: SL
482 41.8 mm, AL (with canal) 20.9 mm, SW 10.6 mm. Radula was examined in three
483 specimens, two from Papua New Guinea and one from the Philippines. It was very
484 similar in all examined specimens (Fig. 6). Radula membrane medium long, consists of
485 33-50 rows of teeth of which 9-16 are not fully formed. Marginal teeth duplex. Anterior
486 (inner) half is solid, narrow lanceolate, dorso-ventrally compressed with sharp lateral
487 cutting edges. In posterior half the major and accessory limbs bifurcate at the angle
488 about 45°, rather thin. The central formation absent.

489 *Remarks.* The new species is represented only by 6 specimens, including the holotype
490 and despite the limited material, two rather distinct forms can be recognized. The "light"
491 form that includes the holotype has less brown spots and the base color is uniformly
492 creamy. The brown spots on subsutural cord are in most specimens confined to cord
493 itself and do not extend beyond, but in holotype on some whorls there are brownish
494 blurred extensions of the spots to subsutural region. Available specimens other than
495 holotype are smaller and less speckled. The "dark" form is represented by two
496 specimens only, one being juvenile (Fig. 7 F-G). It has slightly darker base color, with
497 light brown shell base and canal and with subsutural region below subsutural cord is
498 uniformly brown. There was not correlation between geographic distributions, since one
499 specimen of dark form was collected in the Philippines, while another in Papua New
500 Guinea at similar depths. The sinus cords of the adult specimen of the dark form are
501 also sharper on top on the last whorl. On most part of teleoconch whorls the sinus cords
502 are either similar in size, or the lower even slightly more pronounced, than the upper,

503 only on the last whorl the situation changes to opposite. Intact protoconch persists only
504 in the juvenile of the dark form (Fig. 7 G), it consists of 2.75 whorls, diameter 0.68 mm,
505 height 0.73, that is significantly smaller than in holotype, although the existing material
506 is insufficient for estimates of the variation. The species is extremely similar to
507 *Lophiotoma acuta*, which also has dark and light forms. It can be distinguished in most
508 cases by less pronounced and more rounded on top sinus cords, providing less angulated
509 appearance to the shell shoulder, as well as more similar in size cords (Fig. 6, compare
510 A-B with C-D), and domination of the lower cord over the higher one on teleoconch
511 whorls. Protoconch of *Lophiotoma acuta* is slightly larger (Fig. 8), while the radula is
512 longer (consists of 55-80 rows of teeth *versus* 33-50 rows in *L. semifala*).
513 *Distribution*. The species was found in the Philippines, Papua New Guinea and Santo.
514 In all this localities it is sympatric with *L. acuta*. Judging from available material (only
515 6 sequenced specimens), it is much more rare than *L. acuta*, for which we had more
516 than 160 specimens sequenced. Although we did not sequence any specimens from New
517 Caledonia, judging from the shell characters the species is also found in New Caledonia
518 (uncataloged MNHN material).

519

520 *Lophiotoma polytropa* (Helbling, 1779) (Fig. 9E)

521 *Murex (Fusus) polytropus* Helbling, 1779: 119, pl.2, figs 24, 25.

522 *Pleurotoma fascialis* Lamarck, 1822: 93; Kiener, 1840: 27, pl. 4, fig. 2.

523 *Lophiotoma (Lophioturris) polytropa*. – Powell, 1964: 313-314, pl. 244.

524 *Lophiotoma polytropa*. – Poppe, 2008: 770, pl. 680, fig. 4.

525 *Lophioturris polytropa*. – Lozouet & Plaziat, 2008: 134, pl. 31, figs 5-9.

526 *Type material*. Whereabouts unknown.

527 *Type locality*. Not stated.

528 *Material examined*. 6 sequenced specimens (Supplementary Material 1).

529 *Diagnosis*. Shell medium-sized, exceeding 50 mm, thick, turritiform, with thick brown
530 periostracum, shell dark-purplish brown. Sculpture of strong spiral elements, with
531 rounded or angulate subsutural cord followed by notably elevated paired and broadly
532 spaced sinus cords. Shell periphery and base with dense elevated cords, similar in size
533 to sinus cords and with intermediate finer ridges. Siphonal canal medium long, nearly
534 straight; aperture rather wide, purplish to greyish inside. Radula (Fig. 5 C) with duplex

535 marginal teeth. Anterior (inner) half is solid, lanceolate, slightly asymmetrical, with
536 nearly straight anterior margin and convex posterior margin, dorso-ventrally
537 compressed with sharp lateral cutting edges. In posterior half the major and accessory
538 limbs bifurcate at the angle about 45°, rather thin. Accessory limb is narrowing
539 interiorly, where it fuses with major limb. The central formation absent.

540 *Remarks.* The species is rather distinct from all other congeners in having strong, tightly
541 adhered periostracum and uniformly colored dark shell.

542 *Taxonomic remarks.* *Pleurotoma fascialis* (Lamarck, 1822), considered as a synonym of
543 *L. polytropa* by Powell (1964), is morphologically different, and we exclude the species
544 from synonymy of *L. polytropa*. Because the recognition of this species is not an issue,
545 and even if we were not able to locate the types, we do not designate a neotype for *L.*
546 *polytropa*.

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

553

554 *Lophiotoma abbreviata* (Reeve, 1843) (Fig. 9 C-D)

555 *Pleurotoma abbreviata* Reeve, 1843 (in 1843-1846): pl.10, fig. 86.

556 *Lophiotoma abbreviata.* – Powell, 1964: 309, pl. 237, 238, figs 1-2; Poppe (2008): pl.
557 683, fig. 5.

558 *Type material.* Lectotype (designated by Powell (1964) and 3 paralectotypes in
559 BMNH.

560 *Type locality.* Masbate Island, Philippines, reefs at low tide.

561 *Material examined.* 13 sequenced specimens (Supplementary Material 1).

562 *Diagnosis.* Shell small, turritiform, with contrasting black spots on white background
563 colour, and short siphonal canal, giving shell stout appearance. Sculpture of strong
564 spiral elements, with rounded or angulate subsutural cord followed by notably elevated
565 bisected sinus cord, and one fainter ridge on spire whorls. Shell base with dense
566 elevated cords, sometimes interchanged by fine ridges. Microsculpture of dense very

567 fine spiral treads throughout shell surface. Siphonal canal short and rather robust;
568 aperture rather wide with moderately deep anal sinus. Inside of outer lip with distinct
569 lirae.

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

586 *Distribution.* Confirmed distribution of the species (based on sequenced specimens) is
587 Papua New Guinea, New Caledonia and Santo. According to published data also found
588 in the Philippines (Springsteen & Leobrero, 1986) eastward to Fiji (Cernohorsky, 1972).
589

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

591 *Pleurotoma brevicaudata* Reeve, 1843 (in 1843-1846): pl.15, fig. 126.

592 *Lophiotoma brevicaudata.* – Powell, 1964: 406.

593 *Type material.* Lectotype and two paralectotypes in the BMNH (designated by Powell
594 (1964)) (not illustrated).

595 *Type locality.* Ticao Island, Philippines, H. Cuming collection.

596 *Material examined.* 24 sequenced specimens (Supplementary Material 1).

597 *Diagnosis:* Shell small, turritiform, with prominent spiral sculpture; spire coloured light-
598 brown or tan, siphonal canal dark-brown. Whorl outline indistinctly convex, as

599 subsutural cord separated from succeeding cords by wide and deep depression. Sinus
600 cord wide, composed of two ridges with rather shallow interspace, followed by two
601 cords on whorl's base. Interspaces between cords sculptured by fine treads. Shell base
602 convex, constricted to rather slender siphonal canal, sculptured with dense spiral to
603 oblique cords. Aperture elongate, anal sinus moderately deep, wide, angulated at its tip.
604 Outer aperture lip with white callus, distinctly lirate within.

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

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

620

621 *Lophiotoma picturata* (Wienkauff, 1876) (Fig. 10)

622 *Pleurotoma picturata* Weinkauff, 1876 in (Weinkauff & Kobelt, 1875-1887): 66, pl. 2,
623 fig. 10.

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

626 *Type locality.* Philippines (originally Indischer Ocean).

627 *Material examined.* 8 sequenced specimens (Supplementary Material 1).

628 *Diagnosis.* Shell solid, narrow turritiform, with high spire and moderately long siphonal
629 canal. Protoconch of 3.75-4 slightly convex whorls; early 3 whorls smooth and glossy,
630 latest whorl sculptured with 14-17 axial riblets (Fig. 10 E). Protoconch diameter 0.93-

631 1.12 mm, height 1.13-1.25 mm. Teleoconch whorls distinctly angulated; adapical whorl
632 portion between subsutural cord and sinus cord distinctly concave, sculptured with fine
633 threads. Base of last adult whorl cylindrical, sculptured with 3-5 spiral threads. Shell
634 base shortly constricted to slender siphonal canal. Shell base with 8-9 fine threads
635 interchanging with sharp narrow spiral ridges, siphonal with 13-15 threads. Aperture
636 elongate. Anal sinus wide and rather deep, quadrangular in its apex. Inside of aperture
637 with 9-12 distinct lirae. Background colour cream, with distinct dark-brown spots on
638 subsutural and sinus cords. Brown spots on subsutural cords surrounded by somehow
639 nebulous lighter brown or reddish blotches. Shell base with indistinct light-brown band.
640 Spiral threads with regular light-brown dots, protoconch light-brown; inside of aperture
641 cream. Radula was examined in one sequenced specimen from New Ireland (MNHN
642 IM-2013-53422, Fig. 5 E). Radula membrane long, of about 50 rows of teeth, of which
643 20 are not fully formed. Radula is very similar to other congeners, with duplex marginal
644 teeth. Anterior (inner) half is solid, narrow lanceolate, dorso-ventrally compressed with
645 sharp lateral cutting edges. In posterior half the major and accessory limbs bifurcate at
646 the angle about 45°, rather thin. The central formation indistinct.

647 *Remarks.* The species is represented in our material by eight specimens from North
648 Papua and New Ireland, ranging in height from 24.5 to 32.1 mm, showing modest
649 variation in conchological characters. The only feature, which is found to vary notably,
650 is the shape of anal sinus. It is moderately deep and wide with angulated outline in the
651 specimen MNHN IM-2013-53422, and is even wider in the Wienkauff's type, collected
652 from the Philippines. The sinus is U-shaped, and very deep in some other sequenced
653 specimens. Despite no specimens of *L. picturata* from the Philippines were sequenced
654 in the present study, we confidently apply the name to this clade of our molecular tree,
655 based on conchological features that are shared by the studied type specimen from ZMB
656 and sequenced specimens. No other specimens of *L. picturata*, mentioned by Wienkauff
657 were studied. Since a morphologically close to *L. picturata* species *L. bratasusa* sp. n.
658 was recognized in our analysis, in order to fix the identity of *Lophiotoma picturata*, we
659 here designate the studied syntype ZMB Moll 112610 as a lectotype, therefore
660 restricting the type locality as Philippines. Morphologically *L. picturata* is very close to
661 the *L. bratasusa*; however, there are some minor, but rather stable characters, that allow
662 unmistakable differentiation of the two species. Firstly, the two species differ in the

663 number of protoconch whorls – the former species has a protoconch of 3.75-4 whorls,
664 while the latter – with 3.25 whorls only. Correspondingly the diameter and height of the
665 protoconchs are slightly larger in *L. picturata* (Fig. 8). Moreover, the inside of the
666 aperture is lirate in all studied specimens of the *L. picturata*, and it is smooth in *L.*
667 *bratasusa*. Shell proportions and colouration also offer some minute differences. The *L.*
668 *picturata*, is more turriform in outline (due to comparatively shorter siphonal canal),
669 and the black or dark brown spots on the subsutural region are surrounded by less
670 contrasting light-brown or reddish blotches. On the contrary, *L. bratasusa* has a more
671 fusiform outline, and the dark spots on the subsutural region are more contrasting in
672 appearance. Weinkauff (1876) (in (Weinkauff & Kobelt, 1875-1887)), when describing
673 the species, cited *Pleurotoma variegata* sensu Reeve (1843), non Kiener (1840). The
674 illustration of Reeve (1843): pl. 1 species 2) depicts the shell from the dorsal side which
675 has a vague resemblance to *P. picturata*, although positive identification is hardly
676 possible. Powell (1964) synonymized *Pleurotoma picturata* with *Lophiotoma acuta* and
677 this viewpoint was accepted by subsequent authors.

678 Distribution. Confirmed distribution of the species (based on sequenced specimens) is
679 Papua New Guinea. The species was described from the "Indian Ocean", so its range
680 should be broader, but this needs confirmation.

681

682 *Lophiotoma bratasusa* sp. n. (Fig. 10)

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

685 *Type locality.* Papua New Guinea, Kavieng Lagoon, E of Kulinus I., Silver Sound,
686 02°42,3'S, 150°39,1'E, 7-10 m, coarse sand, coral patches (Expedition KAVIENG 2014,
687 st. KR54).

688 *Other material.* 19 sequenced specimens (Supplementary Material 1).

689 *Etymology.* *bratasusa* [pidgin] – sibling, refers to the revealed sister relationship
690 between the new species and morphologically similar *L. picturata*.

691 *Description* (holotype). Shell solid, narrow fusiform with high spire and rather long
692 siphonal canal. Protoconch of 3.25 slightly convex whorls. Earlier 2.75 whorls smooth
693 and glossy; latest 0.5 whorl sculptured with fine arcuate riblets, widely set at earlier
694 portion and more dense at transition to teleoconch. Protoconch diameter 0.89 mm,

695 height 1,13 mm. Teleoconch of 9 angulated whorls, suture shallow and inconspicuous.
696 Subsutural region distinctly concave; suture immediately bordered by fine thread,
697 followed by typically low subsutural cord, and 3-7 regularly set spiral threads. Sinus
698 cord bifurcated, formed by two subequal ridges on early whorls, whereas adapical ridge
699 is notably stronger on penultimate and last teleoconch whorls. Abapical whorls portion
700 (= whorls base) sculptured with four fine threads, fourth slightly stronger than
701 preceding. Shell base shortly constricted to slender siphonal canal, sculpture of shell
702 base of 11 fine threads, 4th and 6th elevated to form sharp spiral ridges. Siphonal canal
703 sculptured with 15 threads, spirally oriented and widely set adapically and dense,
704 weakly delineated from one-another and oblique towards canal's tip. Aperture elongate;
705 outer aperture lip convex adapically, rounded in side view. Anal sinus typically deep
706 and rather narrow with rounded apex. Inside of aperture typically smooth. Background
707 colour cream, with distinct contrast dark-brown spots on subsutural and smaller dots on
708 sinus cords. Spiral threads with regular light-brown dots, giving them appearance of
709 dashed lines. Protoconch orange; inside of aperture cream. Radula (holotype) (Fig. 5 F)
710 long, of about 55 rows of teeth, of which 25 are not fully formed. Radula is very similar
711 to other congeners, with duplex marginal teeth. Anterior (inner) half is solid, narrow
712 lanceolate, dorso-ventrally compressed with sharp lateral cutting edges. In posterior half
713 the major and accessory limbs bifurcate at the angle about 45°, rather thin. The central
714 formation absent.

715 *Remarks.* *Lophiotoma bratasusa* sp. n. shows a notable variation in shell shape,
716 sculpture pattern and coloration. The two ridges of bisected sinus cord, may be equally
717 strong, subequal, or differ notably, to the extent that the lower ridge is not stronger than
718 succeeding spiral threads. Dark spots on the subsutural cord, typically well developed,
719 may be lacking entirely, in light form (Fig. 10 L), or on the contrary the light brown
720 band on the shell base may be pronounced, and tip of siphon canal colored dark-brown
721 (Figs 10 J). The species is undoubtedly closest to the *L. picturata*, although some
722 differences between the two exist (see remarks under *L. picturata*), of which key are the
723 number of protoconch whorls (4 in *L. picturata* 1 versus 3.25 in *L. bratasusa*) the color
724 pattern on the subsutural cord (with extended lighter blotches in *L. picturata* 1 or
725 without in *L. bratasusa*), and inside of the aperture (lirate in *L. picturata* VS smooth in
726 *L. bratasusa*).

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

729

730 *Lophiotoma jickelii* (Weinkauff, 1875) (Fig. 11)

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

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

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

735 *Type locality.* Papua New Guinea, Tab Island, inner slope, 05°10,2'S, 145°50,3'E
736 (Expedition PAPUA NIUGINI, st. PR42).

737 *Material examined.* 33 sequenced specimens (Supplementary Material 1).

738 *Description* (neotype). Shell thin, fusiform (Fig. 11 A-C), with high spire and long
739 narrow siphonal canal very slightly inclined to the left. Protoconch conical (Fig. 11 D),
740 of about 3.75 evenly convex whorls, posteriormost 0.75 off a whorl before transition to
741 teleoconch with 10 distinct arcuate, more closely spaced towards the transition to
742 teleoconch. Protoconch diameter 1.0 mm, height 1.22 mm. Teleoconch whorls weakly
743 angulated at shoulder, 10.5 in total. Suture moderately deep, distinct, subsutural region
744 wide, distinctly concave, subsutural cord distinct, on upper 4 teleoconch whorls narrow,
745 rounded on top, on 5th and lower whorls with two additional angular ridges appear in
746 upper part of the cord, which becomes progressively stronger and on last whorl cord
747 consists of three distinct sharp triangular in profile ridges, middle one most elevated.
748 Subsutural region smooth on upper teleoconch whorls, with one spiral ridge appearing
749 on 3rd whorl, two on the 4th, 3 on 5th, up to six on the last whorl. Paired sinus cords
750 strongest, separated by interspace four times wider than cords, broadly obtuse triangular
751 in profile and of the same strength on last whorl. On upper whorls both cords are similar
752 in size, very closely spaced on upper four whorls and then become progressively
753 broader spaced. Base of spire whorls smooth on upper two whorls, with one spiral cord
754 on the 3-4th whorl, two on the 5th, and then fast enlarging in number up to 11, strongly
755 different in size cords on penultimate whorl. Base of last whorl with 15 cords, 5 of
756 which are much more prominent than the rest, canal with 34 cords, becoming gradually
757 lower anteriorly. Cords are slightly nodulose on intersecting with growth lines. Shell
758 base sharply narrowing towards narrow and long nearly straight siphonal canal.

759 Aperture pear shaped, strongly constricted posteriorly, with parietal callus producing
760 distinct tooth, outer lip concave in upper part and strongly convex below shoulder,
761 gradually passing into canal. Anal sinus deep, narrow, with nearly parallel sides, its
762 posterior margin nearly straight, parallel to shell axis; outer lip in side-view rounded
763 and opisthocline, stromboid notch well-defined. Shell light brown, protoconch and two
764 first teleoconch slightly darker. Subsutural cord(s) with light brown irregularly shaped
765 spots. Sinus cords with narrow and irregularly spaced brown spots, well as minor spiral
766 cords with spots sometimes having chevron shape and smaller flecks. Aperture light
767 creamy, lirated deep inside. Measurements (neotype largest of our specimens): SL 39.4
768 mm, AL (with canal) 19.8 mm, SW 10.7 mm. Radula (neotype) (Fig. 5 G) long, of
769 about 65 rows of teeth, of which 25 are not fully formed. Radula is similar to other
770 congeners, with duplex somewhat stout marginal teeth. Anterior (inner) half is solid,
771 lanceolate, dorso-ventrally compressed with sharp lateral cutting edges. In posterior half
772 the major and accessory limbs bifurcate at the angle about 45°, rather thin. The central
773 formation distinct, of small sharp narrow cusp.

774 *Remarks.* The species is rather variable in terms of sculpture and coloration. All
775 intermediate specimens can be found from very light, hardly speckled specimens from
776 Vietnam (Fig. 11 K) to very dark ones from Mozambique, similar to the dark form of *L.*
777 *acuta* (Fig. 11 J). Interesting that the dark form was found only in Mozambique and the
778 only two studied specimens from this region were dark. The degree of development of
779 spiral cords (other than subsutural and sinus cords) can also be rather different – from
780 fewer and similar in size 4 on subsutural zone to 6 strongly unequal in the neotype.
781 What is similar in all studied specimens is that subsutural cord is distinctly "composite"
782 consisting of 2 or even sometimes 3 lesser cords, that is clearly distinguish the species
783 from any even very similarly colored specimens of *L. acuta*, in which the subsutural
784 cord is distinctly single, while two much smaller additional ridges can run on it. There
785 seems to be geographically determined shell variability (only dark forms in
786 Mozambique and very light one in Vietnam), but very limited material from these
787 mentioned localities does not allow us to draw final conclusions. The species was for
788 long time considered as a synonym of *L. acuta* (eg. Powell (1964): p. 305 and many
789 others), or as a Red Sea subspecies of the former. The name was used as a valid one
790 recently for the specimens from Philippines (Heralde *et al.*, 2007; Fedosov *et al.*, 2011),

791 but its validity was never addressed from the viewpoint of taxonomy. The types of
792 *Pleurotoma jickelii* Weinkauff, 1875 originated from C. Jickeli collection, which is now
793 partially stored in the Humboldt Museum, Berlin
794 (<http://www.conchology.be/?t=9001&id=21727>). Nevertheless, the types were not
795 found in the Berlin Museum, nor in SMF, where the material of some other Weinkauff
796 is kept. Therefore we consider them as presumably lost. The species was described from
797 Massawa (presently Eritrea) based on beach collected specimen. The illustration of
798 Weinkauff & Kobelt (1875-1887): pl. 4, figs. 2, 3) is a bit ambiguous and depicts the
799 large shell (SL 53 mm) with poorly pronounced sinus cords and nearly straight sided
800 bases of spire whorls, similar to those in our specimens. Powell (1964): pl. 180, fig. 19)
801 illustrated the specimen of "form *jickelii*" from the Red Sea, very similar to ours and
802 provided adequate and accurate description of *Lophiotoma acuta* form *jickelii*. Finally,
803 Verbinnen & Dirx (2007) discussed the presence of *Lophiotoma acuta* and in Red Sea
804 and the status of *L. acuta jickelii* (Weinkauff, 1875). They illustrated the shell of *acuta*
805 (Fig. 21) as well as two shells, which represent *L. jickelii* (21a, 21b). We were able to
806 examine one shell, collected in Egypt (Fig. 88 O) and it, as well as mentioned illustrated
807 specimens, falls within intraspecific variability of a single species as defined herein by
808 molecular data. In the absence of sequenced material from the Red Sea and due to
809 confusing situation with the taxonomy of the species, we designate herein as the
810 neotype of *Lophiotoma jickelii*, the specimen collected in Tab Island, Papua New
811 Guinea, Madang Lagoon (Fig. 11 A-C). The species is most similar to *Lophiotoma kina*
812 sp. n., found in Vanuatu and Papua New Guinea. For differences see the remarks for
813 *Lophiotoma kina* sp. n. The species can be readily distinguished from *L. acuta* in less
814 pronounced subequal sinus cords rounded on top, while the upper sinus cord in *L. acuta*
815 is much more pronounced, that the lower and both sinus cords has sharp upper edge.
816 From both *L. acuta* and *L. acuta* *L. jickelii* also differs in subsutural cord that is
817 subdivided in several cords on last and penultimate whorls, while in the former it is
818 uniform with sharp upper edge and very weak additional ridges. The studied radula of
819 *L. jickelii* has broader anterior solid part of marginal teeth and more pronounced cusp of
820 the central formation.

821 *Distribution.* Confirmed distribution of the species (based on sequenced specimens) –
822 tropical Indo-west Pacific from Mozambique to Vietnam, Philippines, Papua New
823 Guinea and Vanuatu. Basing on published data also the Red Sea.

824

825 *Lophiotoma kina* sp. n. (Fig. 12)

826 *Type material.* holotype MNHN IM-2013-16307, paratype MNHN IM-2013-13278.

827 *Type locality.* Papua New Guinea, Madang Lagoon, W Tab Island, inner slope,

828 05°10,1'S, 145°50,2'E, 3-6 m (Expedition PAPUA NIUGINI, st. PR237).

829 *Other material.* 3 sequenced specimens (Supplementary Material 1).

830 *Etymology.* kina – the shell in Pidgin English, one of the official languages of Papua
831 New Guinea. Used as noun in aposition.

832 *Description* (holotype). Shell medium thick, fusiform, with high spire and long narrow
833 siphonal canal very slightly inclined to the left (Fig. 12 A-C). Protoconch (intact in the
834 specimen MNHN IM-2013-12950) conical, eroded of about 2.75 evenly convex whorls,
835 posteriormost half a whorl before transition to teleoconch with 9 axial riblets (Fig. 12
836 H). Protoconch diameter 0.88 mm, height 0.93 mm. Teleoconch whorls weakly
837 angulated at shoulder, 9.5 in total. Suture shallow, subsutural region wide, distinctly
838 concave, subsutural cord low, on upper teleoconch whorls on upper 5 whorls narrow,
839 rounded on top, on 6th whorl additional angular ridge appear in upper part of the cord,
840 which becomes progressively stronger and on last whorl cord consists of two distinct
841 ridges, upper one being twice lower than the lower ridge. Subsutural region smooth on
842 upper teleoconch whorls, with one spiral ridge appearing on 4th, 3 on 5th, 4 on 6th and
843 eight on the last whorl. Paired sinus cords strongest, separated by interspace three times
844 wider than cords, obtuse triangular in profile and nearly of the same strength on last
845 whorl. On upper whorls both cords are similar in size, with upper one being more
846 pronounced on last and penultimate whorls. Base of spire whorls smooth on upper three
847 whorls, with one spiral cord on the 4th whorl, two on the 5th, 3 on the 6th and 7 on
848 penultimate. Base of last whorl with 3 major spiral cords and one two smaller ones
849 between them, canal with 22 subequal cords, becoming gradually lower anteriorly. Shell
850 base sharply narrowing towards narrow and long nearly straight siphonal canal.
851 Aperture pear shaped, strongly constricted posteriorly with parietal callus producing
852 distinct tooth, outer lip concave in upper part and weakly convex below shoulder,

853 gradually passing into canal. Anal sinus deep, V-shaped, its posterior margin nearly
854 straight, parallel to shell axis; outer lip in side-view rounded and opisthocline,
855 stromboid notch well-defined. Growth lines indistinct, closely spaced. Shell light
856 creamy, protoconch and three first teleoconch slightly darker. Subsutural cord(s) with
857 light brown irregularly shaped spots. Sinus cords with very weak light brown regularly
858 spaced flecks, as well as minor spiral cords and spots occupying whole width of cord
859 and separate on each cord, minor spiral cords. Aperture light creamy, lirate deep
860 inside. Measurements (holotype largest specimen): SL 31.0 mm, AL (with canal) 15.7
861 mm, SW 9.3 mm. Radula (Fig. 5 I) is similar to other congeners, with duplex marginal
862 teeth. Anterior (inner) half is solid, narrow lanceolate, dorso-ventrally compressed with
863 sharp lateral cutting edges. In posterior half the major and accessory limbs bifurcate at
864 the angle about 45°, rather thin. The central formation was not examined due to radula
865 preparation.

866 *Remarks.* The species is most similar to *L. jickelii* and can be distinguished in more
867 pronounced sinus cords and correspondingly more angulated whorls, generally less
868 intensively colored shell, with only very weak brown flecks on the sinus cords and other
869 spiral elements. It has also smaller protoconch (although protoconch was available only
870 for 3 specimens), consisting of 2.75-3 whorls in *kina* versus 3.5-4.0 in *jickelii* (3.75 in
871 most specimens) (Fig. 8).

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

874

875 *Lophiotoma vezzaroi* Cossignani, 2015 (Fig. 9 F-G)

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

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

878 *Lophiotoma vezzaroi* Cossignani, 2015: 30-31, text figs.

879 *Type material.* Holotype MMM - Cupra Marittima.

880 *Type locality.* New Place Birat Samal Island, Philippines. Tangle net at 100-200 m.

881 *Additional material examined:* 1 spm, Tinina Balut Island, Philippines, tangle net at
882 100-200 m.

883 *Material examined.* 3 sequenced specimens (Supplementary Material 1).

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

894 *Remarks.* The species was confused previously with *Lophiotoma ruthveniana*. (Okutani,
895 2000) illustrated very similar specimen as *Lophiotoma abbreviata*. Although described
896 from the Philippines our material and record of Okutani suggest its distribution from
897 Japan to Papua New Guinea from 10-15 to more than 100 m.

898 *Distribution.* Vanuatu (sequenced specimens), Japan, Philippines and Papua New
899 Guinea.

900

901 **Discussion**

902

903 Following an integrative taxonomy approach, we applied several criteria and methods of
904 species delimitation to identify species boundaries within *Lophiotoma*. The three
905 exploratory methods used (ABGD, GMYC and PTP) do not always agree on the species
906 delimitation, but the use of other criteria and characters allowed choosing among the
907 alternative species partitions the most robustly supported: the 10 SSH retained are
908 recognized as genetically (based on both distances and phylogenetic relationships) and
909 morphologically distinct. The GMYC multiple method tends to oversplit, as was found
910 e.g. by Kekkonen & Hebert (2014). On the contrary, genes less variable than COI, such
911 as the 28S, tend to cluster some species.

912 Among the ten delimited species, species in three pairs (*L. acuta* - *L. semfala*, *L.*
913 *picturata* - *L. bratasusa*, and *L. jickelii* - *L. kina*) are hardly distinguishable
914 morphologically: without molecular evidence they would hardly be suspected to be
915 separate species. Moreover, the intraspecific morphological variability exceeds

916 interspecific one, particularly in the shell coloration, with the presence of "light" and
917 "dark" forms within each species of the pairs *L. acuta* – *L. semifala* and *L. jickelii* – *L.*
918 *kina*. The radular characters that sometimes can be useful for species delimitation
919 (Kantor *et al.*, 2008) were of no help in the case of *Lophiotoma*. All examined species
920 had extremely similar radular morphology and only in one species, *L. jickelii*, the radula
921 had the central formation in the shape of a weak but distinct cusp, while in all others it
922 was either absent, or indistinct. However, we confidently recognize them as distinct
923 species, because (i) both genes recognized them as distinct clades, (ii) only in two cases
924 (with the COI gene for *L. picturata* and *L. bratasusa* and with the 28S gene for *L. acuta*
925 and *L. semifala*) they are found as sister species, and (iii) remarkably, morphologically
926 similar species always occur sympatrically, which tends to support the hypothesis that
927 they do not exchange genes.

928 The integrative taxonomy approach followed here was thus efficient to propose robust
929 species hypotheses. It represents one additional example of the value of molecular
930 characters when species can hardly be distinguished morphologically, a common
931 situation in gastropods, and in particular in conoideans (e.g. (Duda *et al.*, 2008;
932 Puillandre *et al.*, 2010; Jörger & Schrödl, 2013). However, if proposing putative species
933 using DNA sequences is now common, linking the SSH to available names, most often
934 attached to non-sequenced specimens, remains problematic. Until now, all the species of
935 *Lophiotoma* were described using conchological characters only. Moreover, locating
936 type specimens to tentatively attribute their associated names to the defined SSH, based
937 on morphological resemblance, was probably the most difficult task. Among the seven
938 species already described before the present work, the type material was located for four
939 species only (*L. abbreviata*, *L. brevicaudata*, *L. picturata* and *L. vezzaroi*). For *L.*
940 *vezzaroi*, the holotype was properly designated, and for *L. abbreviata* and *L.*
941 *brevicaudata* lectotypes (and paralectotypes) were designated in previous studies. For
942 the last one, *L. picturata*, we located the syntypes and designated one lectotype and one
943 paralectotype. For the three other species, *L. acuta*, *L. jickelii* and *L. polytropa*, we were
944 unable to locate the type material (see details in the taxonomic section). In the absence
945 of type material, we had to rely on the illustrations in the original descriptions to link
946 the SSH to these names. For *L. acuta* and *L. jickelii*, because these names are associated
947 to species complexes that include morphologically similar species, we choose one of the

948 sequenced specimens in each species as a neotype. We also examined, when possible,
949 the type material and/or the original illustrations of the species synonymized with *L.*
950 *acuta* in the literature, and concluded that none of these names can confidently be
951 attributed to one of the three remaining SSH. Consequently, we described these three
952 SSH as new species: *L. semfala* sp. n., *L. bratasusa* sp. n. and *L. kina* sp. n.

953 More generally, most species of molluscs were described before the molecular
954 revolution, and the identity of most newly described species still remain based on dry
955 material and/or non-sequenced specimens (Bouchet & Strong, 2010). When dealing
956 with species complexes, attributing names to molecular groups is thus tricky. When the
957 type specimens are lost, designating a sequenced specimens as a neotype solve the
958 problem. However, when the types are still available, morphological resemblance can
959 be used to decide to which of the molecular groups the name will be attributed. We
960 applied this strategy for the two species *Xenuroturris legitima* Iredale, 1929 and *Iotyrriis*
961 *cingulifera* (Lamarck, 1822) (Kantor *et al.*, 2008): molecular studies and radula
962 analyses revealed the presence of two very similar conchologically species. The types of
963 the two mentioned names persist, both as empty shells, badly worn in the case of the
964 Lamarck's syntypes, and shell similarity helped to attribute each name to one of the two
965 molecular groups. This solution was practical, because it allowed a stabilization of the
966 nomenclature without the designation of neotypes, which in case of persisting types
967 requires lengthy consideration by the Commission of Zoological Nomenclature. Here
968 we used the same approach for *L. picturata*: we applied the name *picturata* to the
969 species that was morphologically more similar to the lectotype.

970 Because type specimens remain the only way to unambiguously link names and genetic
971 groups, one could suggest that sequencing type-specimens, when available, is the
972 ultimate solution. Traditionally, shell-bearing molluscs types are kept dried in
973 collections, which does not ensure a correct DNA conservation. Recently developed
974 NGS techniques would clearly help to sequence fragmented DNA, but a high proportion
975 of name-bearing types are empty shells, i.e. the shell does not contain the animal inside,
976 even dried. Recently published articles (Geist, Wunderlich, & Kuehn, 2008; Andree &
977 López, 2013; Villanea, Parent, & Kemp, 2016) suggest that DNA can actually be
978 extracted from shells, but whether such techniques are applicable to specimens kept
979 dried for ten, or even hundreds, of years, and for which the periostracum is potentially

980 absent, remains to be tested. It also implies that a piece of the shell (Andree & López,
981 2013) of the holotype will be destroyed, a condition that will need to be accepted by
982 museum curators.

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

995

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997

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1022

1023

1024 **References**

1025

1026 Andree KB, López MA. 2013. Species identification from archived snail shells via
1027 genetic analysis: a method for DNA extraction from empty shells. *Molluscan Research*
1028 33: 1–5.

1029 Bouchet P, Kantor YI. 2004. New Caledonia: The major centre of biodiversity for
1030 volutomitrid molluscs (Mollusca: Neogastropoda: Volutomitridae). *Systematics and*
1031 *Biodiversity* 1: 467–502.

1032 Bouchet P, Strong E. 2010. Historical name-bearing types in marine molluscs: an
1033 impediment to biodiversity studies? In: Polaszek A, ed. *Systema Naturae 250*. London:
1034 CRC Press, 63–74.

1035 Casey TL. 1904. *Notes on the Pleurotomidae with description of some new genera and*
1036 *species*. Academy of Science of St. Louis.

1037 Cernohorsky WO. 1972. *Marine shells of the Pacific*. Pacific publications.

1038 Cossignani T. 2015. *Lophiotoma vezzaroi* sp. nov. *Malacologica MOSTRA Mondiale*.
1039 *Cupra Marittima* 88: 30–31.

1040 Dance SP. 1986. *A history of shell collecting*. Leiden: Brill and Backhuys.

1041 Dayrat B. 2005. Towards integrative taxonomy. *Biological Journal of the Linnean*
1042 *Society* 85: 407–415.

1043 De Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology* 56:
1044 879–886.

- 1045 Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with
1046 BEAUti and the BEAST 1.7. *Molecular biology and evolution* 29: 1969–1973.
- 1047 Duda TF Jr, Bolin MB, Meyer C, Kohn AJ. 2008. Hidden diversity in a hyperdiverse
1048 gastropod genus: discovery of previously unidentified members of a *Conus* species
1049 complex. *Molecular Phylogenetics and Evolution* 49: 867–876.
- 1050 Dunker W. 1871. Mollusca nova Musei Godeffroy Hamburgensis. *Malakozoologische*
1051 *Blätter* 18: 150–175.
- 1052 Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high
1053 throughput. *Nucleic Acids Research* 32: 1792–1797.
- 1054 Fedosov A, Watkins M, Heralde III FM, Showers Corneli P, Concepcion GP, Olivera
1055 BM. 2011. Phylogeny of the genus *Turris*: Correlating molecular data with radular
1056 anatomy and shell morphology. *Molecular Phylogenetics and Evolution* 59: 263–270.
- 1057 Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for
1058 amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan
1059 invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- 1060 Galindo LA, Puillandre N, Strong EE, Bouchet P. 2014. Using microwaves to prepare
1061 gastropods for DNA barcoding. *Molecular Ecology Resources* 14: 700–705.
- 1062 Geist J, Wunderlich H, Kuehn R. 2008. Use of mollusc shells for DNA-based molecular
1063 analyses. *Journal of Molluscan Studies* 74: 337–343.
- 1064 Goldstein PZ, DeSalle R. 2011. Integrating DNA barcode data and taxonomic practice:
1065 Determination, discovery, and description. *Bioessays* 33: 135–147.
- 1066 Helbling S. 1779. *Beyträge zur Kenntniß neuer und seltener Konchylien. Aus einigen*
1067 *Wienerischen Sammlungen*. Gerle.
- 1068 Heralde FM, Watkins M, Ownby JP, Bandyopadhyay PK, Santos AD, Concepcion GP,
1069 Olivera BM. 2007. Molecular phylogeny of some Indo-Pacific genera in the subfamily
1070 Turrinae H. Adams and A. Adams, 1853 (1838) (Gastropoda: Neogastropoda). *Nautilus*
1071 121: 131–138.
- 1072 Higo S, Callomon P, Gotō Y. 1999. *Catalogue and bibliography of the marine shell*
1073 *bearing mollusca of Japan: gastropoda, bivalvia, polyplacophora, scaphopoda*. Elle
1074 Scientific.
- 1075 Huelsenbeck JP, Ronquist F, Hall B. 2001. MrBayes: Bayesian inference of phylogeny.
1076 *Bioinformatics* 17: 754–755.
- 1077 Jörger KM, Schrödl M. 2013. How to describe a cryptic species? Practical challenges of
1078 molecular taxonomy. *Frontiers in Zoology* 10: 59.

- 1079 Jovelin R, Justine JL. 2001. Phylogenetic relationships within the polyopisthocotylean
1080 monogeneans (Plathyhelminthes) inferred from partial 28S rDNA sequences.
1081 *International Journal for Parasitology* 31: 393–401.
- 1082 Kantor YI. 2006. On the morphology and homology of the ‘central tooth’ in the radula
1083 of Turrinae (Conoidea: Turridae). *Ruthenica* 16: 47–52.
- 1084 Kantor YI, Puillandre N. 2012. Evolution of the radular apparatus in Conoidea
1085 (Gastropoda: Neogastropoda) as inferred from a molecular phylogeny. *Malacologia* 55:
1086 55–90.
- 1087 Kantor YI, Puillandre N, Olivera BM, Bouchet P. 2008. Morphological proxies for
1088 taxonomic decision in turrids (Mollusca, Neogastropoda): a test of the value of shell and
1089 radula characters using molecular data. *Zoological Science* 25: 1156–1170.
- 1090 Kekkonen M, Hebert PDN. 2014. DNA barcode-based delineation of putative species:
1091 efficient start for taxonomic workflows. *Molecular Ecology Resources* 14: 706–715.
- 1092 Kiener L. 1840. *Species general et iconographie des Coquilles vivantes Comprenant la*
1093 *Collection du Muséum d’Histoire Naturelle de Paris, Collection Lamarck, celle du*
1094 *Prince Masséna et les Découverts Récente des Voyageurs (Genre Pleurotome)*. Paris:
1095 Rousseau.
- 1096 Kilburn RN. 1983. Turridae (Mollusca: Gastropoda) of southern Africa and
1097 Mozambique. Part 1. Subfamily Turrinae. *Annals of the Natal Museum* 25: 549–585.
- 1098 Lamarck J de. 1816. Tableau encyclopédique et méthodique des trois règnes de la
1099 nature. Vingt troisième partie. Mollusques et polypes divers.
- 1100 Lamarck JBPA. 1822. *Histoire naturelle des animaux sans vertèbres*. Editions
1101 Publibook.
- 1102 Lozouet P, Plaziat JC. 2008. Mangrove environments and molluscs. *Conchbooks*,
1103 *Hackenheim*.
- 1104 Marshall B. 1983. *A revision of the recent Triphoridae of Southern Australia (Mollusca:*
1105 *Gastropoda)*. Australian museum.
- 1106 Monaghan MT, Wild R, Elliot ., Fujisawa T, Balke M, Inward DJG, Lees DC,
1107 Ranaivosolo R, Eggleton P, Barraclough T, Vogler AP. 2009. Accelerated species
1108 inventory on Madagascar using coalescent-based models of species delineation.
1109 *Systematic Biology* 58: 298–311.
- 1110 Ober KA. 2002. Phylogenetic relationships of the carabid subfamily Harpalinae
1111 (Coleoptera) based on molecular sequence data. *Molecular Phylogenetics and Evolution*
1112 24: 228–248.
- 1113 Okutani T. 2000. *Marine mollusks in Japan*. Tokai University Press.
- 1114 Oyama K. 1966. On living Japanese Turridae (1). *Venus* 25: 1–20.

- 1115 Pante E, Puillandre N, Viricel A, Arnaud-Haond S, Aurelle D, Castelin M, Chenuil A,
1116 Destombe C, Forcioli D, Valero M, Viard F, Samadi S. 2015. Species are hypotheses:
1117 avoid connectivity assessments based on pillars of sand. *Molecular Ecology* 24: 525–
1118 544.
- 1119 Pante E, Schoelinck C, Puillandre N. 2014. From integrative taxonomy to species
1120 description: one step beyond. *Systematic Biology*: syu083.
- 1121 Perry G. 1811. *Conchology, Or the Natural History of Shells: Containing a New*
1122 *Arrangement of the Genera and Species, Illustrated by Coloured Engravings, Executed*
1123 *from the Natural Specimens, and Including the Latest Discoveries.* William Miller.
- 1124 Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S,
1125 Sumlin WD, Vogler AP. 2006. Sequence-based species delimitation for the DNA
1126 taxonomy of undescribed insects. *Systematic Biology* 55: 595–609.
- 1127 Poppe GT. 2008. *Philippine marine mollusks Volume II.* Conchbooks.
- 1128 Powell AWB. 1964. The family Turridae in the indo-pacific. Part I. The subfamily
1129 Turrinae. *Indo-Pacific Mollusca* 1: 227–411.
- 1130 Puillandre N, Lambert A, Brouillet S, Achaz G. 2012a. ABGD, Automatic Barcode Gap
1131 Discovery for primary species delimitation. *Molecular Ecology* 21: 1864–1877.
- 1132 Puillandre N, Modica MV, Zhang Y, Sirovitch L, Boisselier MC, Cruaud C, Holford M,
1133 Samadi S. 2012b. Large scale species delimitation method for hyperdiverse groups.
1134 *Molecular Ecology* 21: 2671–2691.
- 1135 Puillandre N, Sysoev A, Olivera BM, Couloux A, Bouchet P. 2010. Loss of
1136 planktotrophy and speciation: geographical fragmentation in the deep-water gastropod
1137 genus *Bathytoma* (Gastropoda, Conoidea) in the western Pacific. *Systematics and*
1138 *Biodiversity* 8: 371–394.
- 1139 Rambaut A, Drummond AJ. 2014. *Tracer v1.6.* Available from
1140 <http://beast.bio.ed.ac.uk/Tracer>.
- 1141 Reeve L. 1843. Monograph of the genus *Pleurotoma*. *Conchologia Iconica* 1.
- 1142 Renner SS. 2016. A return to Linnaeus's focus on diagnosis, not description: The use of
1143 DNA characters in the formal naming of species. *Systematic biology*: syw032.
- 1144 Samadi S, Barberousse A. 2009. Species: towards new, well-grounded practices. A
1145 response to Velasco. *Biological Journal of the Linnean Society* 96: 696–708.
- 1146 Schubert G, Wagner J. 1829. Neues systematisches Conchylien-Cabinet angefangen
1147 von Martini und Chemnitz. *Nürnberg, Bauer & Raspe* 12: 1–196.
- 1148 Springsteen FJ, Leobrera FM. 1986. *Shells of the Philippines.* Carfel Seashell Museum.

- 1149 Srivathsan A, Meier R. 2012. On the inappropriate use of Kimura-2-parameter (K2P)
1150 divergences in the DNA-barcoding literature. *Cladistics* 28: 190–194.
- 1151 Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic
1152 analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- 1153 Tamura K, Stecher G, Peterson D, Filipski A, Kumar S. 2013. MEGA6: molecular
1154 evolutionary genetics analysis version 6.0. *Molecular biology and evolution*: mst197.
- 1155 Verbinnen G, Dirx M. 2007. Red Sea Mollusca. Part 17. Class: Gastopoda. Family:
1156 Turridae. *Gloria Maris* 43: 7–27.
- 1157 Villanea FA, Parent CE, Kemp BM. 2016. Reviving Galápagos snails: ancient DNA
1158 extraction and amplification from shells of probably extinct Galápagos endemic land
1159 snails. *Journal of Molluscan Studies*: eyw011.
- 1160 Weinkauff H, Kobelt W. 1875-1887. Die Familie Pleurotomidae. Systematisches
1161 Conchylien-Cabinet von Martini und Chemnitz. Vol. 4.
- 1162 Will KP, Mishler BD, Wheeler QD. 2005. The perils of DNA Barcoding and the need
1163 for integrative taxonomy. *Systematic Biology* 54: 844–851.
- 1164 Zhang J, Kapli R, Pavlidis P, Stamatakis A. 2013. A general species delimitation
1165 method with applications to phylogenetic placements. *Bioinformatics* Advance Access.
1166

1167 **Figure legends**

1168

1169 Figure 1: Map showing the species distributions. Full squares: *L. acuta*; empty squares:
1170 *L. semfala*; stars: *L. polytropa*; diamonds: *L. abbreviata*; hexagons: *L. brevicaudata*; full
1171 circles: *L. picturata*; empty circles: *L. bratasusa*; full triangles: *L. jickelii*; empty circles:
1172 *L. kina*; crosses: *L. vezzaroii*; black symbols: confirmed presence with sequenced
1173 material; grey symbols: presence reported in the literature or in non-sequenced material.
1174 ? : “Indian Ocean”.

1175

1176 Figure 2: Bayesian trees (Mr. Bayes) for the COI (left) and 28S (right) genes. Posterior
1177 Probabilities (>0.95) and bootstraps values (>75) are shown for each node. Letters in
1178 front of each species number refer to the locality: M: Mozambique; VN: Viet-Nam; P:
1179 Philippines; PNG: Papua New Guinea; V: Vanuatu; NC: New Caledonia.

1180

1181 Figure 3: Bayesian tree of the COI and 28S genes concatenated. Posterior Probabilities
1182 (>0.95) and bootstraps values (>75) are shown for each node.

1183

1184 Figure 4: *Lophiotoma acuta* (Perry, 1811). - A-D. Neotype, MNHN IM-2007-41179, SL
1185 38.8 mm. - D. Lateral view of the protoconch. - E. Original illustration from Perry
1186 (1811). - F,G. Syntypes of *Pleurotoma tigrina* Lamarck, 1822 (MHNG-MOLL-51664).
1187 - F. SL 48.1 mm; - G. SL 56 mm. - H. Dark form, MNHN IM-2007-41007,
1188 SANTO2006, st. FR 10, SL 35.9 mm. - I. MNHN IM-2007-41025, SANTO2006, st. LD
1189 01, SL 29.7 mm. - J. MNHN IM-2009-29711, Vietnam, SL 50.9 mm. - K. MNHN IM-
1190 2013-10267, PAPUA NIUGINI, st. PR 07, SL 31.9 mm. - L. MNHN IM-2013-17040,
1191 PAPUA NIUGINI, st. PR 152, SL 32.5 mm. - M. MNHN IM-2013-46888, KAVIENG,
1192 st. KR 06, SL 38.2 mm. All shells at the same scale.

1193

1194 Figure 5: Radulae of studied *Lophiotoma*. - A,B. *Lophiotoma acuta* (Perry, 1811). - A.
1195 MNHN IM-2013-14235. - B. MNHN IM-2013-14505. - C. *Lophiotoma polytropa*
1196 (Halbling, 1779), MNHN uncataloged, PANGLAO2004, st. M 50. - D. *Lophiotoma*
1197 *brevicaudata*, MNHN IM-2007-40994, SANTO 2006. - E. *Lophiotoma picturata*
1198 (Weinkauff, 1876), MNHN IM-2013-53422, KAVIENG, st. KZ 02, SL 24.5 mm. - F.

1199 *Lophiotoma bratasusa* sp. n., holotype, MNHN IM-2013-54124. - G. *Lophiotoma*
1200 *jickelii* (Weinkauff, 1875), neotype, MNHN IM-2013-13275. - H. *Lophiotoma semfala*
1201 sp. n., MNHN IM-2013-14504. - I. *Lophiotoma kina* sp. n., holotype, MNHN IM-2013-
1202 16307. Scale bars 50 μ m.

1203

1204 Figure 6: Anal sinus and spiral sculpture of different species of *Lophiotoma*. - A.
1205 *Lophiotoma acuta* (Perry, 1811), MNHN IM-2007-41179. - B. *Lophiotoma acuta*,
1206 MNHN IM-2009-29711, SL 50-9 mm. - C. *Lophiotoma semafala* sp. n., holotype,
1207 MNHN IM-2007-41337, SL 41.8 mm. - D. *Lophiotoma semafala* sp. n., dark form,
1208 MNHN IM-2007-40830, SL 35.7 mm. - E. *Lophiotoma kina* sp. n., holotype, MNHN
1209 IM-2013-16307, SL 31.0 mm. - F. *Lophiotoma jickelii* (Weinkauff, 1875), neotype,
1210 MNHN IM-2013-13275, SL 39.4 mm. Arrows indicate diagnostic details of the
1211 sculpture.

1212

1213 Figure 7: *Lophiotoma semfala* sp. n. - A-C. Holotype, MNHN IM-2007-41337, SL 41.8
1214 mm. -D. MNHN IM-2013-14504, PAPUA NIUGINI, st. PD 41, SL 29.5 mm. - E.
1215 MNHN IM-2007-40830, Philippines, PANGLAO 2004, st. R 62, SL 35.7 mm. - F,G.
1216 Dark form, MNHN IM-2013-04019, PAPUA NIUGINI, st. PD 39, SL 12.4 mm (F – at
1217 the same scale as other shells, F' enlarged). – G. Lateral view of the protoconch. - H.
1218 MNHN IM-2013-14965, PAPUA NIUGINI, st. PD 45, SL 26.8 mm. All shells (except
1219 F') at the same scale.

1220

1221 Figure 8: Scatterplot of protoconch measurements in studied species of *Lophiotoma*. D:
1222 protoconch diameter, mm; H: exposed height, mm. - A. Diamonds: *L. semfala*; squares:
1223 *L. acuta*; triangles: *L. kina*; circles: *L. jickelii*. - B. Diamonds: *L. bratasusa*; squares: *L.*
1224 *picturata*.

1225

1226 Figure 9: Shells of examined species of *Lophiotoma*. - A,B. *Lophiotoma brevicaudata*
1227 (Reeve, 1843). - A. MNHN IM-2007-40994, SANTO 2006, st. DB12, 15°36'38.0412"S;
1228 167°10'3.558"E, 10-18 m, SL 16,7 mm. - B. MNHN IM-2013-47803 KAVIENG 2014,
1229 st. KS15 2°41'14.3988"S; 150°41'14.5608"E, 3-5 m, SL 26,0 mm. - C,D. *Lophiotoma*
1230 *abbreviata* (Reeve, 1843). - C. MNHN IM-2013-55783, New Caledonia, Nouméa,

1231 Phare Amédée, depths not documented, SL 22,4 mm. - D. MNHN IM-2007-41197,
1232 SANTO 2006, st. FB52, 15°42'42.3576"S; 167°15'5.5188"E, 7 m, SL 15,8 mm. - E.
1233 *Lophiotoma polytropa* (Helbling, 1779), MNHN IM-2007-40832, PANGLAO 2004, st.
1234 M30, 9°43'5.988"N ; 123°51'29.988"E, intertidal, SL 43,0 mm. - F,G. *Lophiotoma*
1235 *vezzaroi* Cosisgnani, 2015. - F. MNHN IM-2007-40983, SANTO 2006, st. DS04,
1236 15°31'26.2776"S; 167°14'6.7956"E, 25 m, SL 14,4 mm. – G. *radula* voucher, Tinina
1237 Balut Island, Philippines, SL 34.7 mm.
1238
1239 Figure 10: - A-F. *Lophiotoma picturata* (Wienkauff, 1876). - G-L. *Lophiotoma*
1240 *bratasusa* sp. n. - A,B. Lectotype of *Pleurotoma picturata* ZMB Moll 112610, SL 41
1241 mm. - C-E. MNHN IM-2013-53422, Papua New Guinea, SL 24.5 mm. – E. Lateral
1242 view of the protoconch. - F. MNHN IM-2013-51988, Papua New Guinea, Kavieng
1243 Lagoon, SL 30,3 mm. - G-I. *Lophiotoma bratasusa* sp. n. Holotype, MNHN IM-2013-
1244 51244, Papua New Guinea, Kavieng Lagoon, SL 26.0 mm. - J. MNHN IM-2013-15844,
1245 Papua New Guinea, Madang Lagoon, SL 30,5 mm. - K. MNHN IM-2007-41339,
1246 Vanuatu, SL 28,2 mm. L. MNHN IM-2007-41132, Vanuatu, SL 23.8 mm.
1247
1248 Figure 11: *Lophiotoma jickelii* (Weinkauff, 1875). - A-D. Neotype, MNHN IM-2013-
1249 13275. – D. Lateral view of the protoconch. - E. MNHN IM-2013-54874, Papua New
1250 Guinea, Kavieng Lagoon, SL 36.2 mm. - F. MNHN IM-2007-41003, Vanuatu, 33.8
1251 mm. - G. MNHN IM-2013-11537, Papua New Guinea, Madang Lagoon, SL 33.3 mm. -
1252 H. MNHN IM-2007-41144, Vanuatu, 35.0 mm. - I. MNHN IM-2007-41182 Vanuatu,
1253 SL 32.9 mm. - J. MNHN IM-2009-7080, Mozambique, SL 29.4 mm. - K. MNHN IM-
1254 2009-29713, Vietnam, SL 44.9 mm. - L. MNHN IM-2013-12760, Papua New Guinea,
1255 Madang Lagoon, SL 37.9 mm. - M,N. Original illustration of the species (Weinkauff,
1256 1875: pl. 4, figs 2, 3). - O. Specimen from Egypt, Brother Island, 10-35 m (collection of
1257 P. Stahlshmidt). All shells (except M-N) at the same scale.
1258
1259 Figure 12: *Lophiotoma kina* sp. n. - A-C. Holotype, MNHN IM-2013-16307, SL 31.0
1260 mm. - D. MNHN IM-2013-13278, Papua New Guinea, Madang Lagoon, SL 27.2 mm. -
1261 E. MNHN IM-2009-16927, Vanuatu, SL 23.8 mm. - F. MNHN IM-2013-51209, Papua
1262 New Guinea, Kavieng Lagoon, SL 25.4 mm. - G,H. MNHN IM-2013-12950, Papua

1263 New Guinea, Madang Lagoon, SL 20.3 mm. – H. Lateral view of the protoconch. All
1264 shells at the same scale.

Table 1: Results of the integrative species delimitation approach. 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^o 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: Viet-Nam; P: Philippines; PNG: Papua New-Guini; V: Vanuatu; NC: New Caledonia.

species	# COI	# 28S	# COI+28S	COI				28S		COI+28S				Monophyly (PP/B)						Bathymetry	Geography					
				ABGD		GMYC	PTP	ABGD	PTP	ABGD		GMYC	PTP	COI		28S		COI+28S			M	VN	P	PNG	V	NC
				lumper	splitter	simple				lumper	splitter	simple		lumper	splitter	simple	lumper	splitter	simple							
<i>polytropa</i>	6	6	5											1/92		1/92		1/95		1-3 m.			x			
<i>abbreviata</i>	13	8	5				3 groups							1/97	-/-	0,9/61	0,95/62	1/100	0,93/95	0-7 m.				x	x	x
<i>brevicaudata</i>	24	19	6												0,99/77		-/-	1/100	0,7/59	2-38 m.			x	x	x	
<i>picturata 1</i>	2	1	1												1/100	1/100	0,96/64	na	1/100	na	7-22 m.				x	
<i>picturata 2</i>	6	3	3											1/100	1/74		-/-	1/100	0,97/90	3-42 m.				x		
<i>bratasusa</i>	22	15	7											1/100			0,95/61	1/100		0-35 m.				x	x	
<i>jickelii 1</i>	28	11	9											0,95/-	-/-	-/-	1/91	0,98/80	1-22 m.	x	x	x				
<i>jickelii 2</i>	5	4	4											0,96/-	1/59	-/-	-/-	1/91	1/89	1-40 m.				x	x	
<i>acuta 1</i>	96	87	10											1/96	0,93/65	1/82	-/-	1/100	0,89/86	0-22 m.					x	
<i>acuta 2</i>	60	17	12											1/96	-/-	-/-	-/-	1/100	-/-	0-99 m.		x	x	x	x	
<i>semfala 1</i>	5	2	2											1/100	na	0,99/96	-/-	1/100	1/88	2-15 m.				x	x	
<i>semfala 2</i>	1	1	1											1/100	1/89		na	1/100	na	2-99 m.			x			
<i>vezzaroi</i>	3	2	2											1/99		1/96		1/100		15-30 m.					x	
<i>kina 1</i>	4	4	3											1/97	0,98/83	1/94	-/-	1/99	0,9/-	no data				x		
<i>kina 2</i>	1	1	1											1/97	na		na	1/99	na	3-15 m.					x	

276
277**Table 2.** List of diagnostic sites (character state – position) for both COI and 28S gene for each species

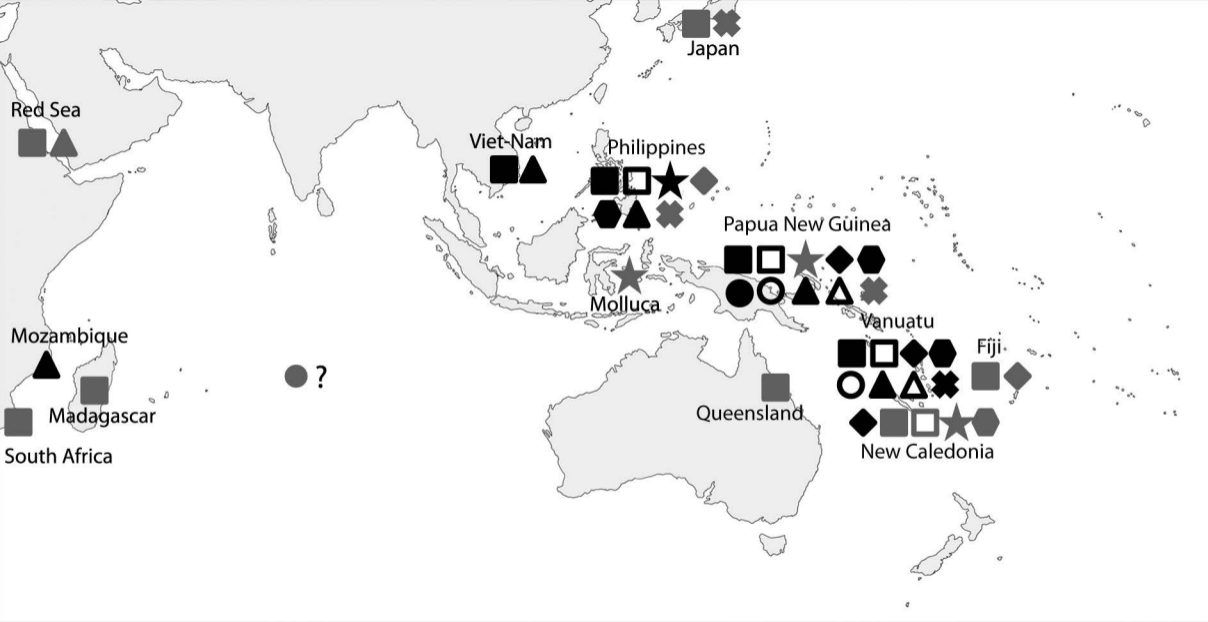
species	COI	28S
<i>L. polytropa</i>	T - 290; G - 292; C - 334; A - 376; C - 424; G - 553	A - 854; T - 860
<i>L. abbreviata</i>	G - 331	C - 396
<i>L. brevicaudata</i>	G - 535	
<i>L. jickelii</i>	C - 158; A - 313; C - 457; T - 598	
<i>L. picturata</i>	C - 100; G - 181; T - 508; C - 529; C - 538	G - 858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

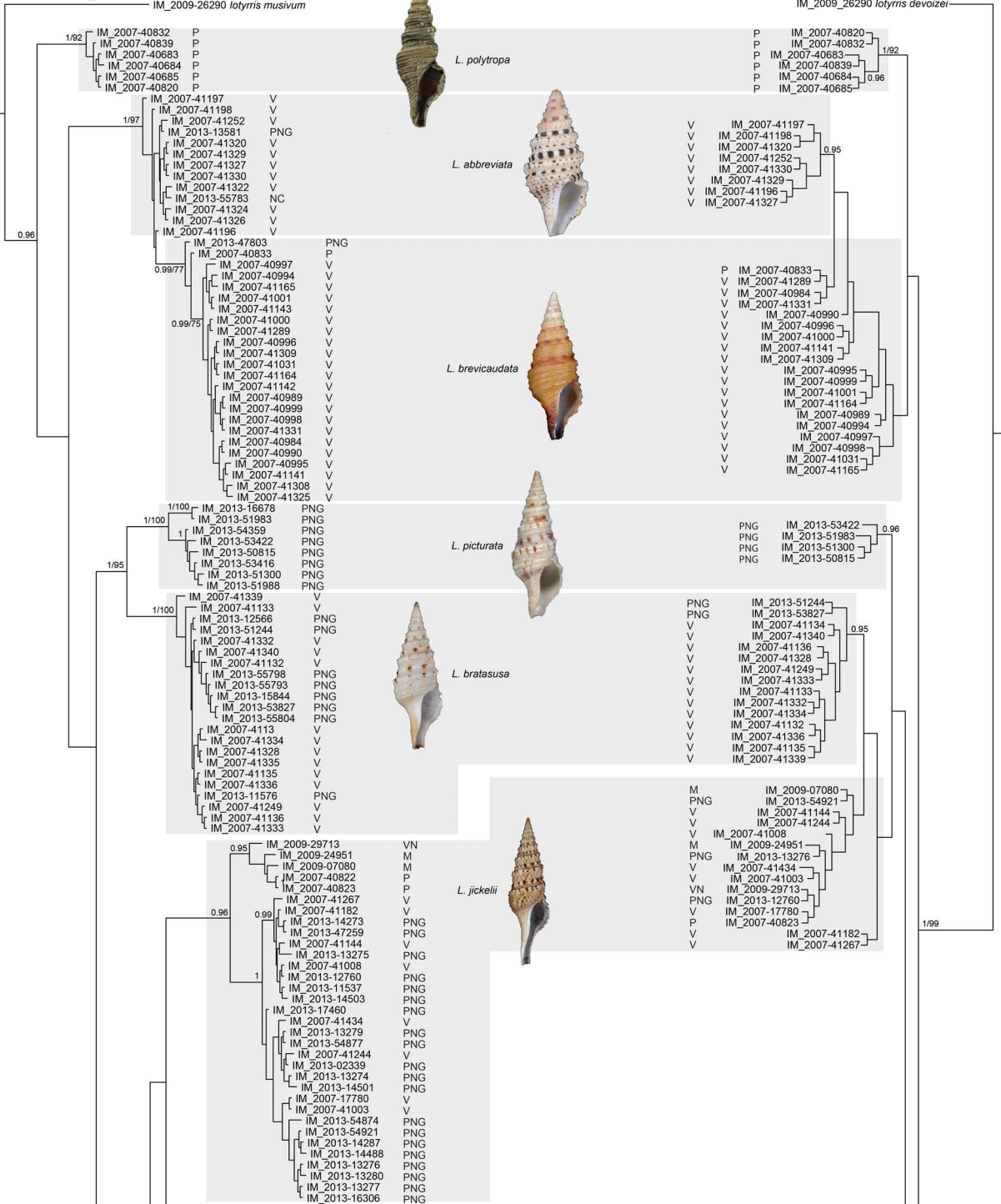
278

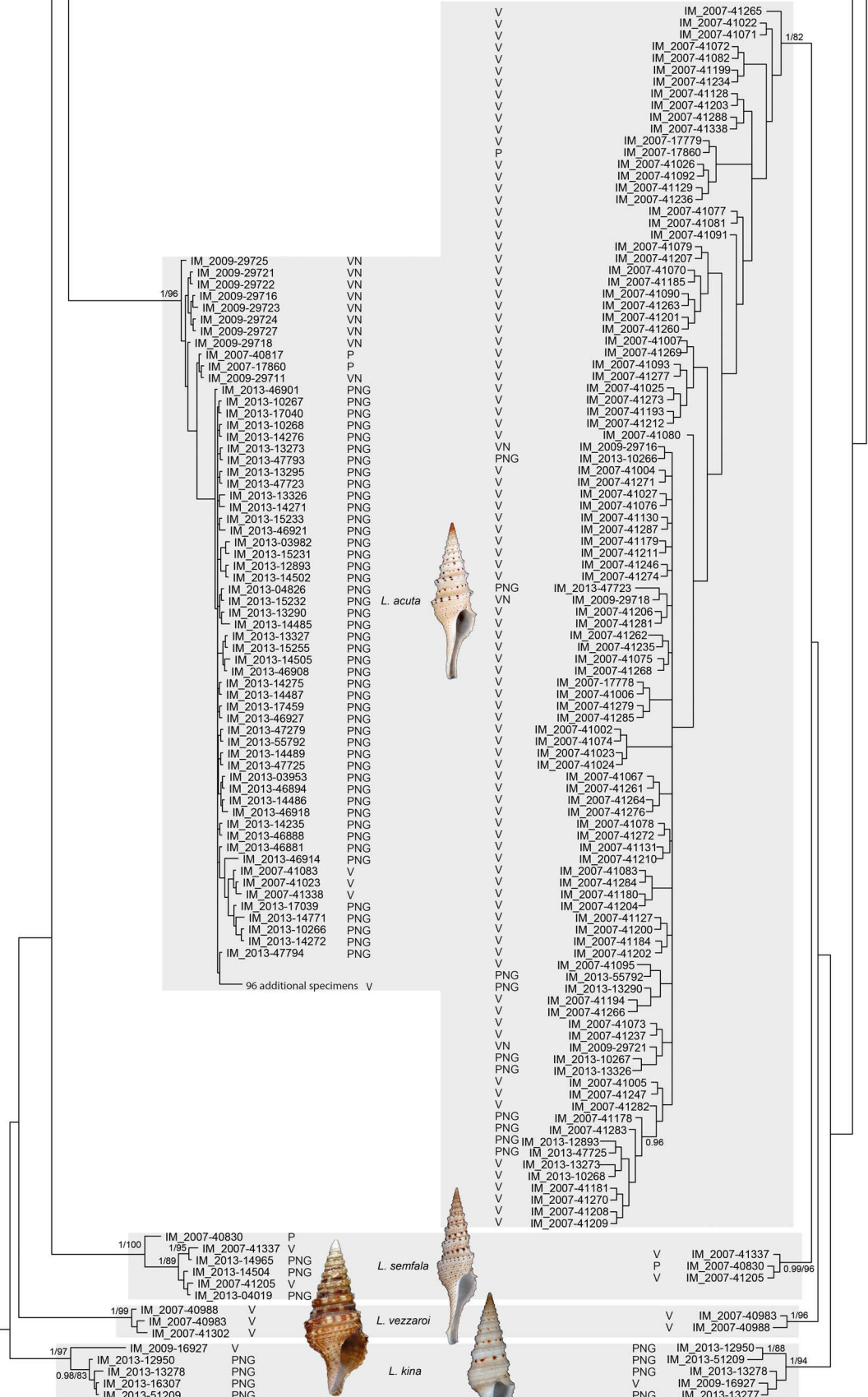
1279 **Supplementary Material**

1280

1281 Supplementary Material 1: List of specimens analyzed, with MNHN number, species
1282 name, geographic locality, depth, and BOLD and GenBank accession numbers.

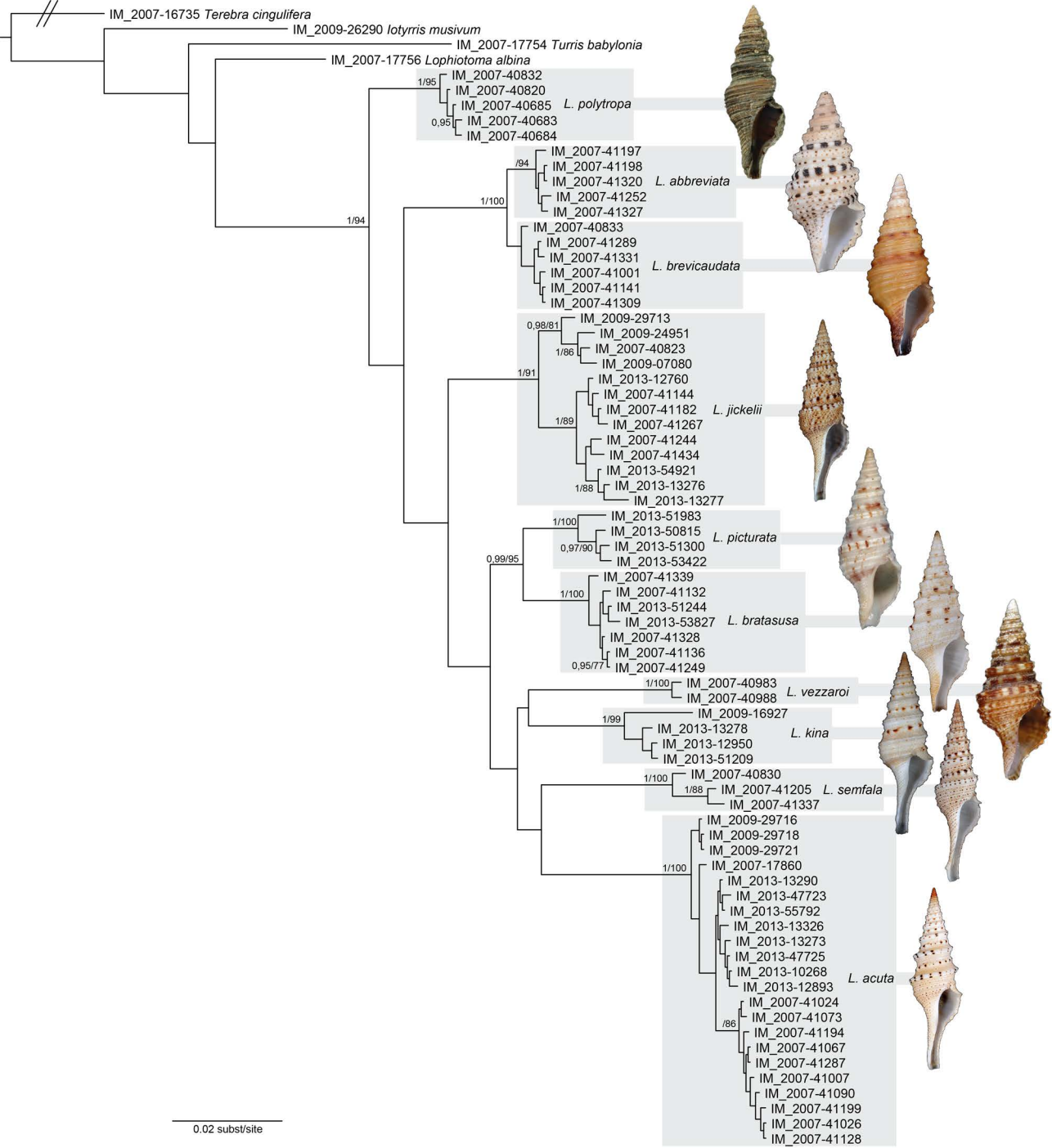


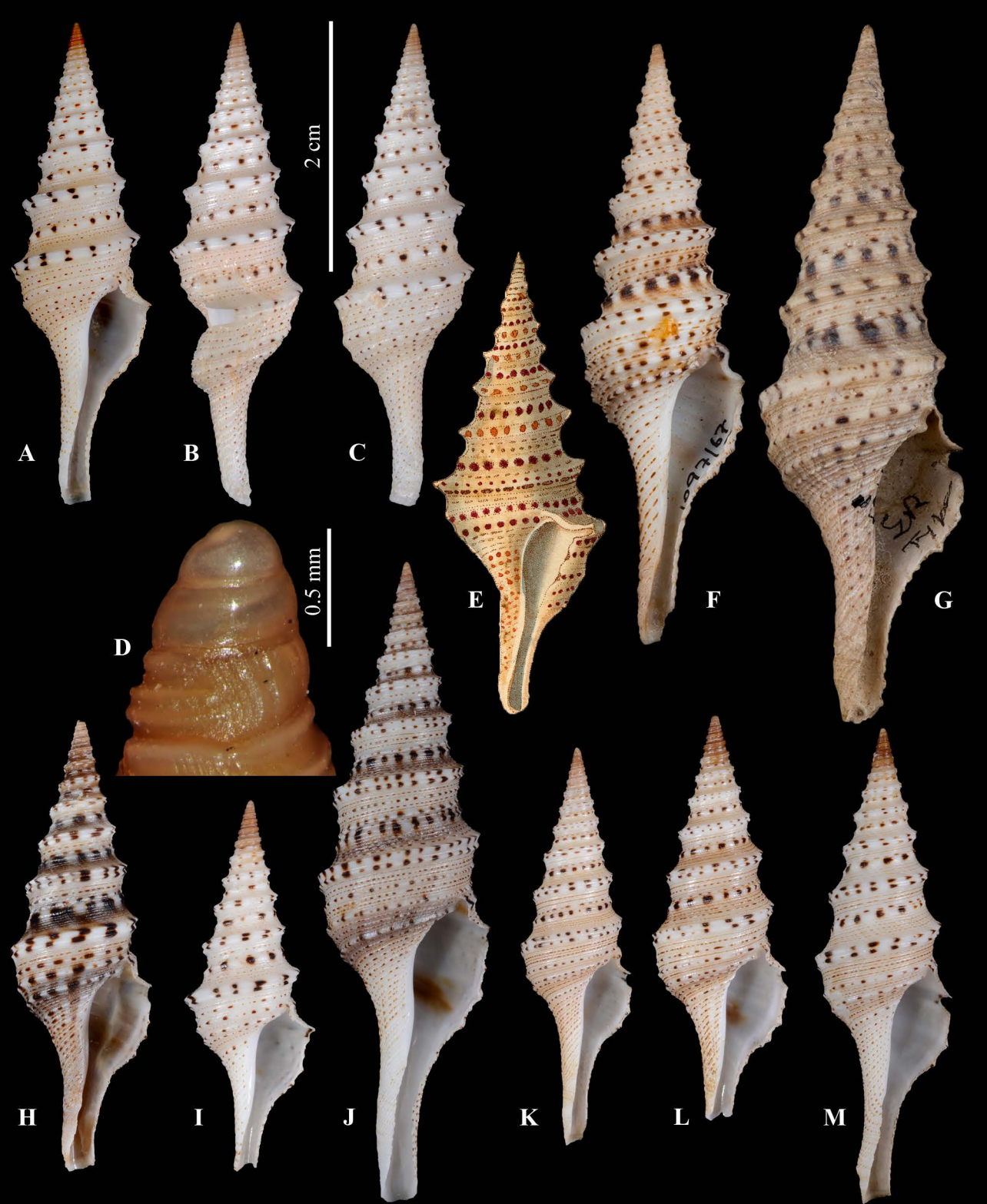


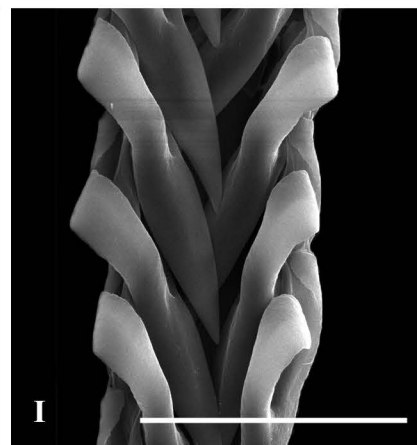
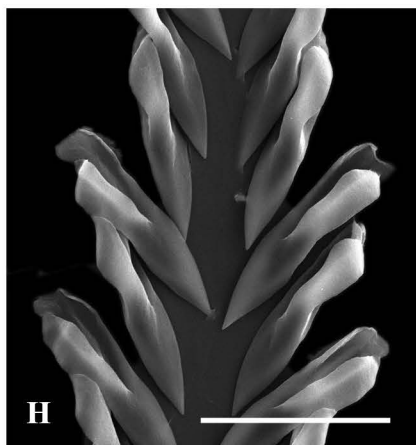
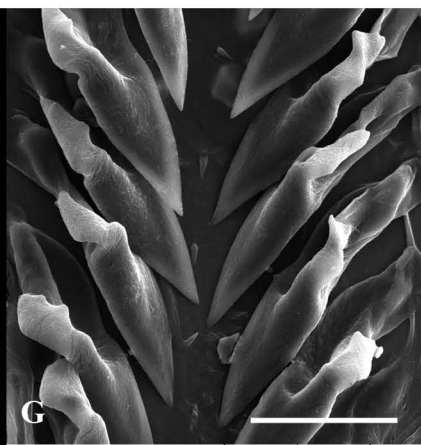
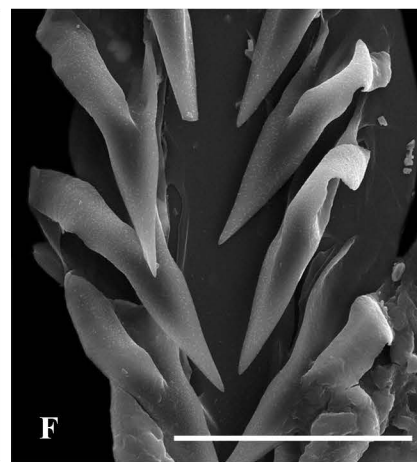
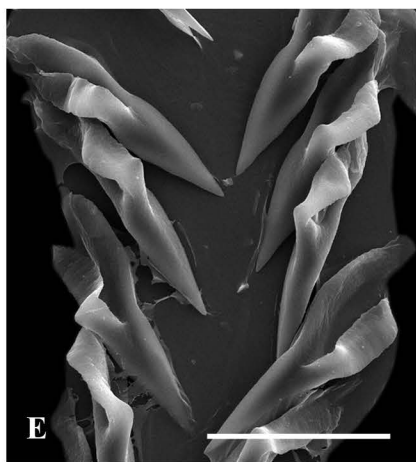
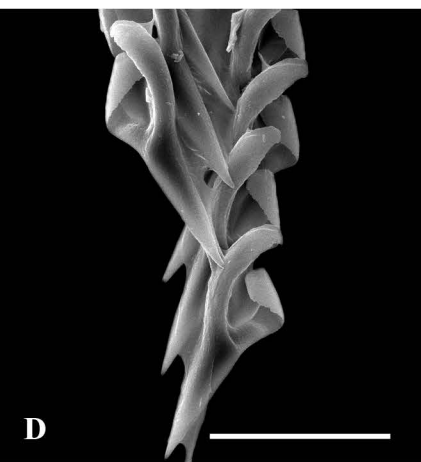
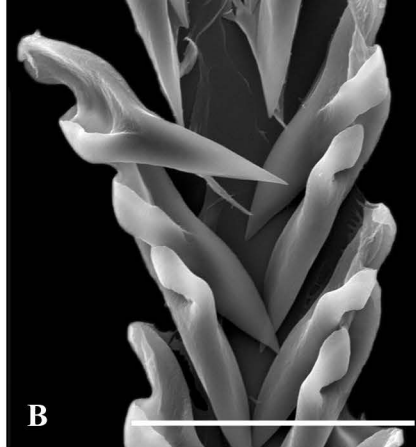
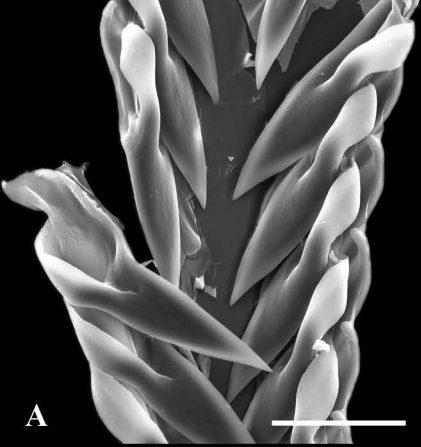


0.03 subst/site

0.003 subst/site

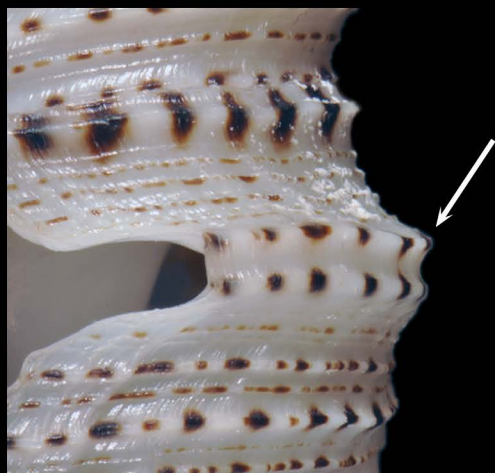






A

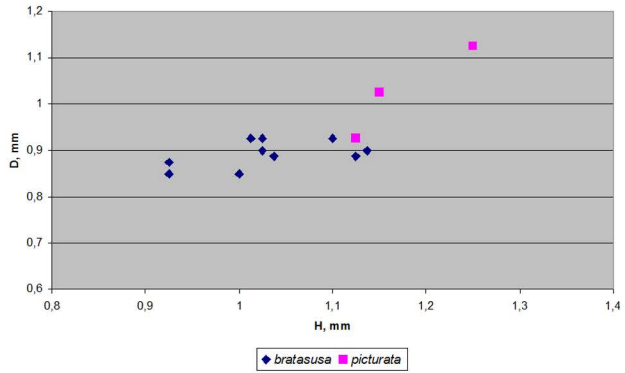
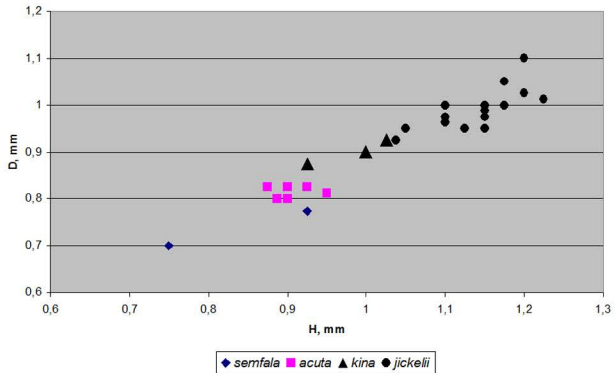
5 mm

B**C****D****E**

5 mm

F







A

B

C

D

E

F

G





