



HAL
open science

A question of rank: DNA sequences and radula characters reveal a new genus of cone snails (Gastropoda: Conidae)

Nicolas Puillandre, Manuel J Tenorio

► **To cite this version:**

Nicolas Puillandre, Manuel J Tenorio. A question of rank: DNA sequences and radula characters reveal a new genus of cone snails (Gastropoda: Conidae). *Journal of Molluscan Studies*, 2017, 83 (2), pp.200-210. <10.1093/mollus/eyx011>. <hal-02458222>

HAL Id: hal-02458222

<https://hal.science/hal-02458222v1>

Submitted on 28 Jan 2020

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

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



HAL Authorization

1 A matter of rank: DNA sequences and radula characters reveal a new genus of cone snails
2 (Gastropoda: Conidae)

3

4 Nicolas Puillandre^{1*} & Manuel J. Tenorio²

5

6

7 ¹ *Institut de Systématique, Évolution, Biodiversité ISYEB – UMR 7205 – CNRS, MNHN,*
8 *UPMC, EPHE, Muséum National d’Histoire Naturelle, Sorbonne Universités, 43 rue Cuvier,*
9 *CP26, F-75005, Paris, France.*

10 ² *Dept. CMIM y Química Inorgánica – Instituto de Biomoléculas (INBIO), Facultad de*
11 *Ciencias, Torre Norte, 1ª Planta, Universidad de Cadiz, 11510 Puerto Real, Cadiz, Spain.*

12

13 Running title: *PYGMAECONUS*, A NEW GENUS OF CONE SNAIL

14

* Corresponding author: Nicolas Puillandre, e-mail: puillandre@mnhn.fr

16 Molecular phylogenies of cone snails revealed that the c.a. 350 sequenced species are divided
17 in four main lineages, *Conus*, *Conasprella*, *Californiconus* and *Profundiconus*. In a recent
18 article, minute species (less than 8 mm) were for the first time included in a molecular
19 phylogenetic tree, and were shown to correspond to deep lineages, similar to the four
20 previously recognised, and sister-group to *Californiconus*. They were attributed to the
21 available genus names *Lilliconus* and *Pseudolilliconus*. In this article, we analyse, using
22 morphological (shell and radula) and molecular characters (cox1 gene), several species of
23 minute cone snails, and we conclude that the species considered as *Pseudolilliconus* in the
24 previous study should actually be placed in a new genus, *Pygmaeconus*. By comparing the
25 cox1 genetic distances calculated among the species of *Lilliconus*, *Pygmaeconus* and
26 *Californiconus* with the genetic distances calculated among other cone snails species included
27 in different subgenera and genera, and the estimated ages of *Lilliconus* and *Pygmaeconus* with
28 the ages of other caenogastropd genera, we conclude that *Lilliconus* and *Pygmaeconus* can be
29 considered at the genus rank.

INTRODUCTION

31

32 The linnean ranks above the species level are hardly comparable between taxa, neither in
33 terms of genetic distances, morphological divergence, species diversity or age (Johns &
34 Avise, 1998; Hedges *et al.*, 2015; Giribet *et al.*, 2016). Indeed, if the taxa are defined
35 following a clear criterion (the monophyly), deciding which clades will be named and at
36 which rank they will be placed is often arbitrary and taxonomist-dependent. Consequently,
37 some authors simply argue that ranks should be abandoned (Zachos, 2011; Lambertz & Perry,
38 2016), while others state that ranks remain important for communication, and convey
39 information (Giribet *et al.*, 2016).

40 In cone snails (Gastropoda, Conoidea), many classifications have been proposed in the past
41 two centuries, but only recently, i.e. in the last 15 years, have phylogenetic approaches been
42 used to test whether the groups defined mainly by shell characters are compatible with
43 independently evolving lineages (e.g. Espiritu *et al.*, 2001; Duda & Kohn, 2005). In fact, the
44 cladistics analyses of shell and radula characters and of the growing amount of DNA
45 sequence data have led to the conclusion that groups above the species level defined only by
46 shell morphology without regard to a phylogenetic framework are meaningless as
47 evolutionary hypotheses (Tucker & Tenorio, 2009; Puillandre *et al.*, 2014). Based on these
48 recent works, two competing classifications have been proposed (Tucker & Tenorio, 2009;
49 Puillandre *et al.*, 2015). Overall, the taxa defined in these two classifications are similar and
50 compatible, and the discrepancies mostly concern species for which the radula remains
51 unknown and/or no DNA sequences are available. However, these two classifications
52 contradict each other regarding the ranks at which the taxa are considered. Since the work of
53 Duda & Kohn (2005), living cone snails are known to consist of a few main lineages, of
54 which one in particular has radiated into several hundred species. At first, two lineages were
55 recognized (the 'large major clade' and the 'small major clade'; Duda & Kohn, 2005;

56 Williams & Duda, 2008) and subsequently the single-species lineage represented by
57 *Californiconus californicus* (Reeve, 1844) (Tucker & Tenorio, 2009; Biggs *et al.*, 2010).
58 These lineages were recognized at the level of family or subfamily (Conidae, Conilithinae and
59 Californiconinae, respectively; Tucker & Tenorio, 2009) or at the level of genus (*Conus*,
60 *Conasprella* and *Californiconus*, respectively; Puillandre *et al.*, 2015). Puillandre *et al.* (2015)
61 added a fourth lineage to the list, *Profundiconus* (previously recognized as one of the genera
62 of Conilithidae by Tucker & Tenorio, 2009). A criterion has been proposed to standardize the
63 ranks over taxa, namely temporal banding, where temporal ranges are attributed to each rank
64 (Avisé & Liu, 2011). Applying this criterion would eventually allow discriminating between
65 the two alternate cone snail classifications, by comparing the age of the main lineages of cone
66 snails to the ages of the family and genera of other conoideans. Although a family-level
67 classification of the Conoidea based on a molecular phylogeny has been proposed (Bouchet *et*
68 *al.*, 2011), only a few genera have been revised, and a large number of them are probably non-
69 monophyletic (e.g. Castelin *et al.*, 2012b; Puillandre *et al.*, 2012). Furthermore, published
70 phylogenies are not dated. Consequently, it is difficult to apply such criterion to the whole
71 cone snails. However, it can be used to tentatively attribute a rank to new lineages of cone
72 snails. In a recent article, Uribe *et al.* (2017) published a phylogeny of cone snails based on
73 full mitogenomes. The four main lineages of cone snails were recovered (*Profundiconus*,
74 *Conus*, *Californiconus* and *Conasprella*), plus two new lineages, sisters to *Californiconus*,
75 which were revealed for the first time. They correspond to minute cone snails, and were
76 tentatively attributed to two taxa placed at the genus level (thus at the same rank as the four
77 main lineages of cone snails), *Lilliconus* and *Pseudolilliconus*.

78 In the present article, we aim at testing two hypotheses. First, we will test if the two species
79 sequenced in Uribe *et al.* (2017) can be attributed to *Lilliconus* and *Pseudolilliconus*, by
80 analyzing the morphological (shell and radula) and molecular (cox1 gene) variability of

81 additional specimens and species of minute cone snails. Second, we will use two criteria to
82 determine at which rank the taxa of minute cone snails could be considered. To do so, the
83 genetic distances (calculated with the *cox1* gene) among and within the main lineages of cone
84 snails will be compared with the genetic distances among the minute cone snails and their
85 closest relative, *Californiconus*. To avoid the effect of homoplasy with the *cox1* gene,
86 important at the family level, we refrain to compare genetic distance with other families.
87 Furthermore, the estimated ages of the lineages of cone snails will be compared with ages of
88 other caenogastropod taxa obtained from the literature.

89 MATERIAL AND METHODS

90

91 *Samples*

92 Minute cone snails used for molecular analyses were collected during two expeditions of the
93 Museum national d'Histoire naturelle, Paris (MNHN; ATIMO VATAE in Madagascar in

Table 1

2010 and KAVIENG 2014 in Papua New Guinea; Table 1). During the ATIMO VATAE

95 expedition, specimens were treated with an isotonic solution of magnesium chloride until

96 relaxed (showing no response to touch) and then a tissue clip was cut; during the KAVIENG

97 2014 expedition, specimens were processed using a microwave oven (Galindo *et al.*, 2014).

98 Tissue samples were preserved in 96% ethanol and voucher shells are kept in MNHN.

99 Additional material was studied for morphological characters (shell and radula), most of it

100 previously deposited in institutional repositories.

101

102 *Shell and radula analyses*

103 We describe shell morphology using the terminology established by Röckel, Korn & Kohn

104 (1995). Descriptions are based on shells oriented in the traditional way, spire uppermost and

105 with the aperture facing the viewer. Maximum shell length (SL) was measured using a digital
106 caliper, and measurements rounded to the nearest 0.1 millimeter.

107 Specimens of shells containing the dried animal inside were digested in concentrated aqueous
108 KOH for 24 h. These included specimens MNHN-IM-2009-31328 and MNHN-IM-2013-
109 47253 which were sequenced, plus four additional specimens which were not sequenced. The
110 contents were flushed out of the shell by injecting distilled water through the aperture by
111 means of a syringe with an incurved needle. The resulting mixture was then placed in a Petri
112 dish and examined with a binocular microscope. The entire radula was removed with fine
113 tweezers and rinsed with distilled water, then mounted on a slide using Aquatex (Merck)
114 Mounting Medium and examined under an optical microscope. Photos were obtained with a
115 CCD camera attached to the microscope. Samples of individual radular teeth for scanning
116 electron microscopy (SEM) were rinsed with distilled water, allowed to dry in air and then
117 mounted on stubs covered with double-sided carbon tape. SEM studies were carried out at the
118 Museo Nacional de Ciencias Naturales-Consejo Superior de Investigaciones Científicas
119 (MNCN-CSIC) on a FEI INSPECT SEM equipped with a secondary and retro-dispersed
120 electron detector, and an analytical-INCA integrated analysis system (Oxford Instruments).

121 We used the terminology for radular teeth of Tucker & Tenorio (2009) and the abbreviations
122 of Kohn, Nishi & Pernet (1999).

123

124 *Molecular analyses*

125 DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the
126 manufacturers' recommendations. A fragment of the cytochrome oxidase subunit I (cox1) was
127 amplified using universal primers LCO1490/HCO2198 (Folmer *et al.*, 1994). PCR reactions
128 were performed in 25 μ l, containing 3 ng of DNA, 1X reaction buffer, 2.5 mM MgCl₂, 0.26
129 mM dNTP, 0.3 mM each primer, 5% DMSO and 1.5 units of Qbiogene Q-Bio Taq.

130 Amplification consisted of an initial denaturation step at 94 °C for 4 min, followed by 35
131 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C, followed by extension at 72 °C
132 for 1 min. The final extension was at 72 °C for 5 min. PCR products were purified and
133 sequenced by the Eurofins sequencing facility. Specimens and sequences were deposited in
134 BOLD and GenBank (Table 1).

135 Cox1 sequences from representative specimens of the four main deep lineages of cone snails,
136 together with four non-cone snail conoideans, chosen from closely related (Borsoniidae and
137 Conorbidae) or more distant groups (Turridae) (Puillandre *et al.*, 2011) were added to the
138 newly sequenced specimens (Table 1). Most sequences were obtained from MNHN
139 specimens, except two (*Californiconus californicus* and *Conasprella arcuata*), downloaded
140 from GenBank (Table 1). All the sequences were aligned using Muscle v. 3.8.31 (Edgar,
141 2004). The dataset was analysed using a Bayesian approach as implemented in MrBayes v.
142 3.2 (Huelsenbeck, Ronquist & Hall, 2001), with two runs consisting of four Markov chains of
143 20,000,000 generations each with a sampling frequency of one tree each 1000 generations.
144 Each codon position of the cox1 gene was treated as an unlinked partition, each following a
145 GTR model, with a gamma-distributed rate variation across sites approximated in four
146 discrete categories and a proportion of invariable sites. Convergence of each analysis was
147 evaluated using Tracer v. 1.6 (Rambaut & Drummond, 2014) and analyses were terminated
148 when ESS values were all > 200. A consensus tree was then calculated after omitting the first
149 25% trees as burn-in. Statistical support was evaluated as Bayesian posterior probability (PP).

150

151 *Comparison of genetic distances*

152 We compile a dataset of cox1 genetic distances (the most commonly sequenced gene in cone
153 snails), combining all the sequenced available in GenBank with unpublished cox1 sequenced
154 obtained from specimens preserved in the MNHN collections. Only one sequence per species

155 was retained, ending up with a total of 349 sequences. All the sequences were trimmed to the
156 “barcode” fragment (defined by the Folmer primers - Folmer *et al.*, 1994) and aligned using
157 Muscle v. 3.8.31 (Edgar, 2004). Tamura-Nei genetic distances were computed using MEGA 6
158 (Tamura *et al.*, 2013) and the pairwise distributions of the inter-generic, intra-generic/inter-
159 subgeneric and intra-subgeneric distances (following the classification of Puillandre *et al.*,
160 2015) were visualized separately.

161

162 *Comparison of clade ages*

163 A review of the literature was performed to identify articles including dated phylogenies of
164 groups within caenogastropods. For each dated tree, the stem ages of the genera were
165 estimated using the scale of the published phylogenetic trees. Only monophyletic groups (thus
166 including at least two representatives) were taken into account. These ages were then
167 compared with the stem ages of the six main lineages of cone snails, as estimated in Uribe *et*
168 *al.* (2017).

169

170 *Abbreviations of museums and institutions*

171 AMS, Australian Museum, Sydney

172 CSIC, Consejo Superior de Investigaciones Científicas, Spain

173 INHS, Illinois Natural History Survey, Illinois

174 MJT, Manuel J. Tenorio reference collection, Jerez, Spain

175 MNCN, Museo Nacional de Ciencias Naturales, Madrid

176 MNHN, Muséum National d’Histoire Naturelle, Paris

177 NBC, Naturalis Biodiversity Center, Leiden

178 NHMUK, Natural History Museum of the United Kingdom, London

179 SMNS, Staatliches Museum für Naturkunde, Stuttgart

180 WAM, Western Australian Museum, Perth

181 ZMA, Zoological Museum, Amsterdam (collection now in NBC)

182

183 RESULTS

184

185 *Phylogenetic analyses and comparison of genetic distances and clade ages*

186 Our *cox1*-based phylogenetic tree including several specimens for each sequenced species of
Fig 1 7 minute cone snails (Fig. 1) is mostly congruent with the results obtained by Uribe *et al.*

188 (2017), using only one specimen per species but full mitogenomes. All cone snail form a
189 monophyletic group, although without statistical support (PP = 0.37). Three main lineages of
190 cone snails previously reported in the literature (*Profundiconus*, *Conasprella* and *Conus*) each
191 corresponds to a highly supported clade (PP > 0.98), with shorter within-clade branches and
192 longer between-clade branches. *Conus* and *Conasprella* are sister groups (PP = 0.99), in
193 contradiction with the tree based on full mitogenomes, in which *Conasprella* is more closely
194 related to *Californiconus* and relatives (see below). *Californiconus californicus* is an
195 independent lineage, sister to the two lineages of minute cone snails revealed by Uribe *et al.*

196 (2017) (PP = 1), each characterized by relatively long branches. One of them includes two

Fig 2 97 specimens identified as *Lilliconus sagei* (Korn & Raybaudi Massilia, 1993) (Fig. 2D, E). The
198 other lineage includes eight individuals of a species that had been tentatively placed in genus
199 *Pseudolilliconus* by Tucker & Tenorio (2009), an opinion followed by Uribe *et al.* (2017),
200 namely *P. traillii* (Adams, 1855) (Fig. 2I-L). As discussed below, morphological comparison
201 suggests that *traillii* and *boschorum* (Fig. 2G; type species of *Pseudolilliconus*) do not belong
202 to the same genus or subgenus and therefore, we introduce a new taxon, *Pygmaeconus*, to
203 include *traillii* and other related species.

204 The distribution of the genetic distances calculated among genera, within genera but among
205 subgenera and within subgenera (following the classification of Puillandre *et al.*, 2015) are
206 distinct, but largely overlapping (Fig 3). In comparison, the genetic distance calculated
207 between specimens of *Californiconus*, *Lilliconus* and *Pygmaeonus* are between 0.24 and
208 0.26: it is clearly out of the within subgenera range of genetic distances for the cone snails, in
209 the right part of the within genera/among subgenera range (corresponding to the highest
210 10%), and in the middle of the among genera range.

211 The stem ages of *Lilliconus* and *Pygmaeonus* are clearly younger than the stem ages of the
212 four other main lineages of cone snails (30MYA vs 38-56 MYA – Fig 4). Compared to other
213 ages of genera of Muricidae, Bursidae and Littorinidae (Castelin *et al.*, 2012a; Reid *et al.*,
214 2012; Claremont *et al.*, 2013), the stem ages of *Lilliconus* and *Pygmaeonus* would be among
215 the youngest genera, with four genera of Rapaninae (Muricidae) that would be actually
216 younger.

217 Based on these results, we conclude that *Pygmaeonus* and *Lilliconus* (and potentially
218 *Pseudolilliconus*) are at least two different subgenera. Considering them as two different
219 genera is also compatible with the distribution of genetic distances among the four main
220 lineages of cone snails, considered here as different genera, and with the estimated ages for
221 Muricidae genera.

222

223

224

SYSTEMATIC DESCRIPTION

225

Family Conidae Fleming, 1822

226

Genus *Pygmaeonus* n. gen.

227

(Figs 2, 5)

Fig 5

228

Type species: Pygmaeonus traillii (Adams, 1855) **n. comb.** (Fig. 2I-L).

229 *ZooBank registration:*

230 *Etymology:* The name combines *Conus* and *Pygmaeus*, pertaining to a pygmy or dwarf, in
231 reference to the very small size of the species in this genus.

232

233 *Material examined:* More than 50 specimens of lots of *Pygmaeconus* species from
234 Philippines, Papua New Guinea and Indonesia in the MNHN collections and in the second
235 author reference collection were examined.

236

237 *Diagnosis:* Shell very small, squat and rounded with a high spire; protoconch paucispiral;
238 sutural ramp flat or convex; surface of last whorl sculptured with variable number of equally-
239 spaced raised minute spiral cords; small operculum present; radular tooth of large relative
240 size; anterior portion much shorter than posterior portion of tooth; tooth armed with one barb,
241 three blades and one single small denticle; blunt shaft fold present; basal spur absent.

242

243 *Shell* (Fig. 2I-Q): Shell very small (SL = 3–9 mm), broadly and ventricosely conical, often
244 squat and rounded, with high spire of straight or slightly convex profile. Nodules usually
245 absent, but a few large knobs, often rounded and obsolete, may be present. Protoconch
246 paucispiral. Sutural ramp flat or convex, often smooth, occasionally with 1–2 grooves or
247 furrows; deeply incised suture. Shoulder rounded; sides of last whorl convex; surface of last
248 whorl sculptured with variable number of equally-spaced raised minute spiral cords leaving
249 flat ribbons between; these cords usually cover entire last whorl and may reach spire, but
250 often absent on shoulder region. Anal notch shallow; anterior notch absent. Operculum small.
251 Periostracum yellowish, smooth, translucent.

252

253 *Radula* (Fig. 5): Radular tooth relatively large for size of shell (shell length/tooth length =
254 17.4–19.4); anterior portion much shorter than posterior portion of tooth. Tooth with one barb
255 and three blades according to the radular terminology of Tucker & Tenorio (2009), plus one
256 single small denticle on underside of tooth in middle of adapical opening; the small apical
257 barb opposes the short, pointed blade; wrapped around the shaft is a tusk-shaped posterior
258 blade; the third blade is a pointed structure which terminates the sheet that rolls around the
259 shaft and is located at the level of the waist of the tooth; a blunt shaft fold present; basal spur
260 absent.

261 *Distribution and habitat*: The included species occur in the Western Pacific and Eastern
262 Indian Oceans (known from Australia, Papua New Guinea, Indonesia, Philippines, Malaysia
263 and Thailand). They have been collected so far in relatively shallow water, intertidally to 40
264 m depth, among seaweed and algae (live) and among fine coral rubble and shell grit (dead).

265 266 *Remarks*

267 These morphologically unusual cone snails constitute a group of species characterized by a
268 very small shell (usually less than 0.8 cm), which had been initially placed in the genus
269 *Lilliconus* Raybaudi, 1994 (type species: *Lilliconus biraghii* (Raybaudi, 1992)) (Fig. 2A-E).
270 Apart from the very small size, the shells of species in *Lilliconus* have bicolored paucispiral,
271 often sculptured protoconchs, and distinctly angulate to carinate shoulders. The radula of
272 individuals in *Lilliconus* thus defined is composed of numerous, relatively large teeth with a
273 complex armature of barbs and blades, and absence of serrations sensu stricto and basal spur
4 (Fig. 6A, B). These features are remarkably similar to those exhibited by the radular tooth of
275 *Californiconus californicus* from the Eastern Pacific (Figs 2F, 6C), a recognized generalist
276 feeder which is known to prey on worms, molluscs, fish and even shrimps (Stewart & Gilly,
277 2005; Biggs *et al.*, 2010). Two species initially placed in genus *Lilliconus*, namely *Conus*

278 *boschorum* Moolenbeek & Coomans, 1993 (Fig. 2G) and *C. (Leptoconus) korni* Raybaudi
279 Massilia, 1993 (Fig. 2H), exhibit a remarkably distinct radular morphology. The tooth of *C.*
280 *boschorum* (Fig. 7) is relatively large, and bears three apical short and flat barbs, one of them
281 wrapping around the tooth shaft. There is no waist, and the shaft has an unusually large
282 central lumen. The most striking feature of this tooth is the rounded apex with a central,
283 rugose nucleus of unknown function. The tooth of *C. korni* (Fig. 8) is narrow and elongated
284 with a conical instead of rounded apex and also has three apical barbs, one of them articulated
285 on a basal membrane giving a 'winged' aspect. These most unusual radular morphologies led
286 to the introduction of the genus *Pseudolilliconus* Tucker & Tenorio (2009) (type species:
287 *Pseudolilliconus boschorum*).

288 The species in *Pygmaeonus*, *Lilliconus* and *Californiconus* show similarities in the general
289 aspect of their radular teeth, which can be considered synapomorphies shared by the three
290 genera, i.e. the anterior portion much shorter than posterior portion of tooth, the presence of
291 barb and multiple blades on a sheet rolling around the shaft, the presence of a shaft fold, and
292 the lack of a basal spur. The main difference of the radular tooth in *Pygmaeonus* species
293 compared to the tooth of species of the other two genera is the size of the single denticle on
294 the underside of the tooth in the middle of the adapical opening. In *Pygmaeonus* this
295 structure is reduced to a small denticle, (Fig. 5), whereas in *Lilliconus* and *Californiconus*
296 (Fig. 6) is of about the same size as the blade present on the overside of the tooth.
297 Additionally, the third blade near the waist forms a pointed structure that is more developed in
298 *Lilliconus*, and even more so in *Californiconus*. There are conchological differences and
299 similarities among the species in these genera. *Lilliconus* and *Pygmaeonus* have in common
300 the very small size of their shells, but the general rounded, rotund shape of most
301 *Pygmaeonus* species (Fig. 2I-Q) resembles that of *C. californicus* (Fig. 2F). On the contrary,
302 the shell of *Lilliconus* species have scalariform spires, often nodulose, with angulate or

303 sharply angulated shoulders (Fig. 2A-E). Additionally, the tree in Fig. 1 indicates that species
304 in these three genera are highly divergent, with genetic divergence similar to those found
305 between the other main lineages. The species in genus *Pseudolilliconus* (Fig. 2G-H) have not
306 been examined molecularly, but they display evident differences in radular morphology (Figs.
307 7 and 8). Additionally, the shell of *Pseudolilliconus* species has also features very different to
308 those of species in *Pygmaeonus*. These differences are mainly the lower, stepped spire, with
309 a straight to slightly concave profile, canaliculated teleoconch whorls, and a sharply angulated
310 shoulder. The presence of a groove on the body whorl just below the shoulder seems to be

Table 2 characteristic of species in *Pseudolilliconus* (Moolenbeek & Coomans, 1993). Table 2

312 summarizes the most relevant differences in shell and radular morphology among the genera
313 *Pygmaeonus*, *Lilliconus*, *Californiconus* and *Pseudolilliconus*.

314 Congeners:

315 *Pygmaeonus molaerivus* (Dekkers, 2016) **n. comb.**

316 *Pygmaeonus wallacei* (Lorenz & Morrison, 2004) **n. comb.**

317 *Pygmaeonus visseri* (Delsaerdt, 1990) **n. comb.**

318 *Pygmaeonus micarius* (Hedley, 1912) **n. comb.**

319 *Pygmaeonus papalis* (Weinkauff, 1875) **n. comb.**

320

321 DISCUSSION

322 Based on molecular and morphological data (both of the shell and radula), we described here
323 a new taxon of cone snails, *Pygmaeonus*. We currently recognise six species in this new
324 genus. The recently described taxon *Conus (Pseudolilliconus) molaerivus* Dekkers, 2016 (Fig.
325 2M) is more correctly placed in *Pygmaeonus*, if it is indeed considered a valid species and
326 not a synonym (color form) of *Pygmaeonus traillii*. The species *P. wallacei* (Fig. 2N) and *P.*
327 *micarius* (Fig. 2O) were considered by Moolenbeek & Goud (2008) synonyms of *P. traillii*.

328 However, given the paucispiral protoconch in all *Pygmaeonus* species that indicates non-
329 planktonic larvae with limited dispersal abilities, and the observed differences in shell pattern
330 and structure we rather consider these two species as valid. The inclusion of *Conus visseri*
331 Delsaerdt, 1990 (Fig. 2P) in the genus is only provisional, and requires further confirmation.
332 This species, known from Phuket Island, Thailand, shares with *Pygmaeonus* the small size
333 and the rounded shape. However, it has a lower spire, and instead of displaying equally-
334 spaced raised minute spiral cords on the body whorl, it appears sulcated with spiral grooves
335 containing fine axial riblets. This feature has been also observed in *Lilliconus kuiperi*
336 (Moolenbeek, 2006) (Fig. 2C). The very small size of species in genus *Pygmaeonus* may
337 have caused that many species in this group are overlooked and remain undescribed. Dead
338 specimens of *P. traillii* have been often found in shell grit samples, but finding alive
339 specimens represents a dedicated task due to their small size. The unusual size and shape
340 combination displayed by species in this genus has also led to consider that certain species
341 were not conids. For instance, *Conus micarius* Hedley, 1912 has been considered a member of
342 genus *Mitromorpha*, in the conoidean family Mitromorphidae (WoRMS Editorial Board
343 2017), i.e. *Mitromorpha micaria*. However, the holotype of *Conus micarius* (Fig. 2O) shows
344 strong conchological similarities to *P. traillii*. This might indicate a close relationship of the
345 two taxa, consistent with the inclusion of *micarius* in genus *Pygmaeonus*. *Conus papalis*
346 Weinkauff, 1875 (*nomen novum* for *Conus coronatus* Reeve, 1849) (Fig. 2Q) has been also
347 treated as a member of genus *Mitromorpha* (WoRMS Editorial Board 2017), despite its
348 inclusion in genus *Lilliconus* following the designation of the lectotype for this species
349 (Raybaudi Massilia, 1994; Lorenz, 1997). The unusually high and nodulose spire resembles
350 indeed some of the features observed in species of genus *Lilliconus*. However, the
351 geographical distribution for this species (Philippines) and other conchological characters
352 such as the presence of equally-spaced raised minute spiral cords on the last whorl would fit

353 better with its placement in *Pygmaeonus*. Further studies are needed in order to clarify the
354 status of this species, which we provisionally consider a member of *Pygmaeonus* (i.e.
355 *Pygmaeonus papalis*) and not a *Mitromorpha*.

356 The food habits of the *Pygmaeonus* species remain unknown. However, the similarities with
357 the radular tooth of *C. californicus* suggest that species in *Pygmaeonus*, and possibly the
358 species in *Lilliconus* as well, might be generalist feeders, but this hypothesis requires
359 confirmation. Direct observation of such minute shells will be difficult, but recent articles
360 demonstrated the feasibility of sequencing DNA of prey contained in the gut of cone snails
361 (Duda *et al.*, 2009).

362 The recognition of *Lilliconus* and *Pygmaeonus*, both including relatively well-known
363 species, as deep lineages of cone snails, similar to the four previously recognized main
364 lineages of cone snails, would suggest that some species, currently classified as genera within
365 (sub)families (Tucker & Tenorio, 2009) or subgenera within genera (Puillandre *et al.*, 2015),
366 with unusual radula and/or shell morphology, would potentially represent additional deep
367 lineages that remain to be discovered. One good candidate is *Pseudolilliconus*, considered
368 here as a separate taxon from *Lilliconus* and *Pygmaeonus*. This hypothesis is supported by
369 morphological characters only, and whether it actually constitutes a third lineage of minute
370 cone snails or not needs to be discussed with molecular data.

371 If molecular data are now routinely used to clarify phylogenetic relationships, turning a
372 phylogeny into an operational classification remains largely arbitrary, not to identify which
373 groups will be named (the clades) and how they will be named (following the rules of the
374 International Code of Zoological Nomenclature), but to decide at which ranks they will be
375 considered. In their revision of the cone snail classification, Puillandre *et al.* (2015) referred to
376 the prevailing usage of Conidae for all the cone snails to consider them as a single family.
377 However, such criterion cannot be applied to the taxon *Lilliconus* (and, a fortiori, to

378 *Pygmaeonus*), cited only in a few publications. We thus analysed the genetic divergence
379 within cone snails, the clade ages of closely related taxa, and ultimately, the morphological
380 divergence with other minute cone snails and *Californiconus*. Given the results obtained, we
381 decided to place *Lilliconus* and *Pygmaeonus* at the genus rank, following the ranking chosen
382 for the four other main lineages of cone snails.

383 However, we also acknowledge that taxonomic ranks may need to be re-evaluated in the
384 future. First, the molecular phylogenies currently available for cone snails include at best less
385 than 40% of the known species, and inclusion of the missing species in a phylogenetic tree
386 may drastically change the inferred pattern. Second, available molecular phylogenies are all
387 based on mitochondrial markers only, and once again the inferred pattern may be different
388 with nuclear genes. Third, acceleration of evolution (i.e. mutation rates) may lead to
389 overestimate the genetic distances and the estimated ages, and thus change our conclusions
390 regarding the ranks within cone snails. Still, more complete phylogenies with many more
391 genes, and in particular nuclear genes, would smooth such heterogeneity in diversification
392 rates. Integrating the cone snail diversity within a more general framework, with estimated
393 divergence and ages for the whole Conoidea, would also clarify the situation. To conclude,
394 the available data for cone snails support our hypothesis to recognize *Lilliconus* and
395 *Pygmaeonus* as genera, but a more complete phylogeny of the cone snails and Conoidea,
396 based on more genes, and in particular nuclear markers, is mandatory, even if such decision
397 will, in any case, remain based on subjective thresholds of divergence.

398

399

ACKNOWLEDGMENTS

400 Newly sequenced material was collected during the Kavieng Lagoon Biodiversity Survey in
401 Papua New Guinea (June 2014) (Principal Investigators: Philippe Bouchet, Jeff Kinch) and
402 the ATIMO VATAE expedition in Madagascar (May 21010) (Principal Investigator: Philippe

403 Bouchet), as part of the Our Planet Reviewed expeditions organized jointly by Muséum
404 National d'Histoire Naturelle (MNHN), Pro-Natura International (PNI) and Institut de
405 Recherche pour le Développement (IRD). The organizers acknowledge supporting funding
406 from the Total Foundation, the Prince Albert II of Monaco Foundation, the Stavros Niarchos
407 Foundation, the Laboratoire d'Excellence Diversités Biologiques et Culturelles (LabEx
408 BCDiv, ANR-10-LABX-0003-BCDiv), the Programme Investissement d'Avenir (ANR-11-
409 IDEX-0004-02), the Fonds Pacifique, and CNRS' Institut Ecologie et Environnement (INEE).
410 This project was partly supported by the Service de Systématique Moléculaire (UMS 2700
411 CNRS-MNHN) and by the project CONOTAX, funded by the French ANR (Grant Number
412 ANR-13-JSV7-0013-01). The authors also thanks Virginie Héros, Barbara Buge, Julien
413 Brisset, Manuel Caballer Gutierrez and Laetitia Aznar-Cormano for their help in curating the
414 specimens; Mr. Alberto Jorge García, from the MNCN-CSIC, Madrid, for assistance with
415 SEM studies; Andreia Salvador, Harry Taylor and Kevin Web (NHMUK, London), Mandy
416 Reid (AMS, Sydney), Jeroen Goud (NBC, Leiden) and Ira Richling (SMNS, Stuttgart) for
417 supplying photos of type material hosted at their respective institutions and the permission for
418 using them in the present work; special thanks to Emilio Rolán, Gabriella Raybaudi Massilia,
419 and Roberto Ubaldi and the Associazione Malacologica Internazionale (Italy), for allowing the
420 reproduction of several figures from *Argonauta*.

421

422 REFERENCES

- 423 AVISE, J.C. 1 LIU, J.X. 2011. On the temporal inconsistencies of Linnean taxonomic ranks.
424 *Biological Journal of the Linnean Society*, **102**: 707–714.
- 425 BIGGS, J. S., WATKINS, M., PULLANDRE, N., OWNBY, J.-P., LOPEZ-VERA, E.,
426 CHRISTENSEN, S., JUAREZ MORENO, K., LICEA NAVARRO, A., SHOWERS

- 427 CORNELI, P. & OLIVERA, B. M. 2010. Evolution of *Conus* peptide toxins: Analysis of
428 *Conus californicus* Reeve, 1844. *Molecular Phylogenetics and Evolution*, **56**: 1–12.
- 429 BOUCHET, P., KANTOR, Y., SYSOEV, A. & PUILLANDRE N. 2011. A new operational
430 classification of the Conoidea (Gastropoda). *Journal of Molluscan Studies*, **77**: 273–308.
- 431 CASTELIN, M., LORION, J., BRISSET, J., CRUAUD, C., MAESTRATI, M., UTGE, J. &
432 SAMADI, S. 2012a. Speciation patterns in gastropods with long-lived larvae from deep-sea
433 seamounts. *Molecular Ecology*, **21**: 4828–53.
- 434 CASTELIN, M., PUILLANDRE, N., KANTOR, Y., MODICA, M.V., TERRYN, Y.,
435 CRUAUD, C., BOUCHET, P. & HOLFORD, M. 2012b. Macroevolution of venom
436 apparatus innovations in auger snails (Gastropoda; Conoidea; Terebridae). *Molecular*
437 *Phylogenetics and Evolution*, **64**: 21–44.
- 438 CLAREMONT, M., VERMEIJ, G.J., WILLIAMS, S.T. & REID, D.G. 2013. Global
439 phylogeny and new classification of the Rapaninae (Gastropoda: Muricidae), dominant
440 molluscan predators on tropical rocky seashores. *Molecular Phylogenetics and Evolution*,
441 **66**: 91–102.
- 442 DUDA, T. F., JR., & KOHN, A. J. 2005. Species-level phylogeography and evolutionary
443 history of the hyperdiverse marine gastropod genus *Conus*. *Molecular Phylogenetics and*
444 *Evolution*, **34**: 257–272.
- 445 DUDA, T. F., JR., CHANG, D., LEWIS, B.D. & LEE, T. 2009. Geographic variation in
446 venom allelic composition and diets of the widespread predatory marine gastropod *Conus*
447 *ebraeus*. *PLoS ONE*, **4**: e6245.
- 448 EDGAR, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high
449 throughput. *Nucleic Acids Research*, **32**: 1792–1797.

450 ESPIRITU, D. J. D., WATKINS, M., DIA-MONJE, V., CARTIER, G. E., CRUZ, L. E., &
451 OLIVERA, B. M. 2001. Venomous cone snails: molecular phylogeny and the generation of
452 toxin diversity. *Toxicon*, **39**: 1899–1916.

453 FOLMER, O., BLACK, M., HOEH, W., LUTZ, R., & VRIJENHOEK, R. 1994. DNA
454 primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse
455 metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, **3**: 294–299.

456 GALINDO, L. A., PULLANDRE, N., STRONG, E. E., & BOUCHET, P. 2014. Using
457 microwaves to prepare gastropods for DNA barcoding. *Molecular Ecology Resources*, **14**:
458 700–705.

459 GIRIBET, G., HORMIGA, G. & EDGECOMBE, G.D. 2016. The meaning of categorical
460 ranks in evolutionary biology. *Organisms Diversity & Evolution*, **16**: 427–430.

461 HEDGES, S.B., MARIN, J., SULESKI, M. PAYMER, M. & KUMAR, S. 2015. Tree of life
462 reveals clock-like speciation and diversification. *Molecular biology and evolution*, msv037.

463 HUELSENBECK, J. P., RONQUIST, F., & HALL, B. 2001. MrBayes: Bayesian inference of
464 phylogeny. *Bioinformatics*, **17**: 754–755.

465 JOHNS, G.C. & AVISE, J.C. 1998. A comparative summary of genetic distances in the
466 vertebrates from the mitochondrial cytochrome b gene. *Molecular Biology and Evolution*,
467 **15**: 1481–90.

468 KOHN, A. J., NISHI, M., & PERNET, B. 1999. Snail spears and scimitars: a character
469 analysis of *Conus* radular teeth. *Journal of Molluscan Studies*, **65**: 461–481.

470 LAMBERTZ, M. & PERRY, S.M. 2016. Again on the meaning of categorical ranks in modern
471 evolutionary biology? *Organisms Diversity & Evolution*, **16**: 723–25.

472 LORENZ, F. 1997. Notes on the genus *Lilliconus* G. Raybaudi Massilia 1994 (Gastropoda:
473 Conidae). *Schriften zur Malakozoologie*, **10**: 4–6.

- 474 MOOLENBEEK, R. G. 2006. *Conus (Lilliconus) kuiperi* spec. nov. (Gastropoda, Conidae),
475 from the Sultanate of Oman. *Basteria*, **supplement 3**: 83–85.
- 476 MOOLENBEEK, R. G. & COOMANS, H. E. 1993. New Cones from Oman and the Status of
477 *Conus boschi*. *Apex*, **8**: 19–26.
- 478 MOOLENBEEK, R. G. & GOUD, J. 2008. A note on *Conus traillii* A. Adams, 1855 and
479 *Lilliconus wallacei* Lorenz & Morrison, 2004 (Gastropoda, Conidae). *Vita Malacologica*,
480 **6**: 63–67.
- 481 PULLANDRE, N., BOUCHET, P., DUDA, T. F., KAUFERSTEIN, S., KOHN, A. J.,
482 OLIVERA, B. M., & MEYER, C. 2014. Molecular phylogeny and evolution of the cone
483 snails (Gastropoda, Conoidea). *Molecular Phylogenetics and Evolution*, **78**: 290–303.
- 484 PULLANDRE, N., DUDA, T. F., MEYER, C.P., OLIVERA, B.M. & BOUCHET, P. 2015.
485 One, four or 100 genera? A new classification of the cone snails. *Journal of Molluscan*
486 *Studies*, **81**: 1–23.
- 487 PULLANDRE, N., KANTOR, Y. I., SYSOEV, A. V., COULOUX, A., MEYER, C. P.,
488 RAWLINGS, T. A., & BOUCHET, P. 2011. The dragon tamed? A molecular phylogeny of
489 the Conoidea (Gastropoda). *Journal of Molluscan Studies*, **77**: 259–272.
- 490 PULLANDRE, N., MODICA, M.V., SIROVITCH, Z.L., BOISSELIER, M.C., CRUAUD,
491 C., HOLFORD, M. & SAMADI, S. 2012. Large scale species delimitation method for
492 hyperdiverse groups. *Molecular Ecology*, **21**: 2671–91.
- 493 RAMBAUT, A., & DRUMMOND, A. J. 2014. Tracer v1.6. Available from
494 <http://beast.bio.ed.ac.uk/Tracer>.
- 495 RAYBAUDI MASSILIA, G. 1994. Prosobranchia: Conidae: a new genus Lilliput, yet fully
496 grown, active predators. *La Conchiglia*, **26**: 13–22.
- 497 REID, D.G., DYAL, P. & WILLIAMS, S.T. 2012. A global molecular phylogeny of 147
498 periwinkle species (Gastropoda, Littorininae). *Zoologica Scripta*, **41**: 125–36.

- 499 RÖCKEL, D., KORN, W., & KOHN, A. J. 1995. Manual of the Living Conidae. Vol. I, Indo-
500 Pacific. Wiesbaden: Christa Hemmen Verlag.
- 501 ROLÁN, E. & RAYBAUDI MASSILIA, G. 1994. New investigation on the radular teeth of
502 *Conus* (Prosobranchia, Conidae). Part I. *Argonauta*, **8**: 6–59.
- 503 STEWART, J. & GILLY, W. F. 2005. Piscivorous behavior of a temperate cone snail, *Conus*
504 *californicus*. *Biological Bulletin*, **209**: 146–153.
- 505 TAMURA, K., STECHER, G., PETERSON, D., FILIPSKY, A., KUMAR, S. 2013. MEGA6:
506 molecular evolutionary genetics analysis version 6.0. *Molecular biology and evolution*,
507 mst197.
- 508 TUCKER, J. K., & TENORIO, M. J. 2009. Systematic classification of Recent and fossil
509 conoidean gastropods. Hackenheim, Germany: Conchbooks.
- 510 URIBE, J.E., PUILLANDRE, N. & ZARDOYA, R. 2017. Beyond *Conus*: Phylogenetic
511 relationships of Conidae based on complete mitochondrial genomes. *Molecular*
512 *Phylogenetics and Evolution*, **107**: 142–51.
- 513 WILLIAMS, S. D. & DUDA, T. F., JR. 2008. Did tectonic activity stimulate oligo–miocene
514 speciation in the Indo-west pacific? *Evolution*, **62**: 1618–1634.
- 515 WoRMS Editorial Board. 2017. World Register of Marine Species. Available from
516 <http://www.marinespecies.org> [accessed 15 Jan. 2017].
- 517 ZACHOS, F.E. 2011. Linnean ranks, temporal banding, and time-clipping: why not slaughter
518 the sacred cow? *Biological Journal of the Linnean Society*, **103**: 732–34.
- 519

520 FIGURE CAPTION

521 **Figure 1.**-Bayesian phylogenetic tree obtained with the cox1 gene. Posterior probabilities (if
522 > 0.95) are shown above nodes.

523

524 **Figure 2. A.** Holotype of *Leptoconus (Thoraconus) biraghii* Raybaudi, 1992 (SMNS ZI8843,
525 Objja, 600 km North of Mogadishu, Somalia), SL = 10.5 mm. **B.** Holotype of *Conus biraghii*
526 *omanensis* Moolenbeek & Coomans, 1993 (NBC ZMA Moll. 3.92.003, Masirah Island,
527 Oman), SL = 7.7 mm. **C.** Holotype of *Conus (Lilliconus) kuiperi* Moolenbeek, 2006 (NBC
528 ZMA Moll. 4.05.17, Masirah I., Oman, 10-15 m), 5.9 mm. **D.** *Lilliconus sagei* (INHS, Tegeta,
529 Tanzania, in 3 to 6 m), 7.9 mm. **E.** *Lilliconus sagei* (MNHN IM-2009-31328, Lavanono,
530 south Madagascar), 6.4 mm. **F.** Holotype of *Conus californicus* Reeve, 1844 (NHMUK,
531 California), 23.5 mm. **G.** Holotype of *Conus boschorum* Moolenbeek & Coomans, 1993
532 (NBC ZMA Moll. 3.92.001, Masirah Island, Oman), 11.0 mm. **H.** *Conus (Pseudolilliconus)*
533 *korni* (paratype, NBC, Aden Gulf, off Northern Somalia), 11.0 mm. **I.** Lectotype of *Conus*
534 *traillii* Adams, 1855 (NHMUK, Malacca, Malaysia), SL = 7.0 mm. **J.** *Pygmaeonus traillii*
535 (MNHN IM-2013-47253, Kavieng, Papua New Guinea), 6.3 mm. **K.** *Pygmaeonus traillii*
536 (MJT coll., Mactan I., Philippines), 6.4 mm. **L.** *Pygmaeonus traillii* (MJT coll., Mactan I.,
537 Philippines), 6.3 mm. **M.** Holotype of *Conus (Pseudolilliconus) molaerivus* Dekkers, 2016
538 (NBC RMNH.5004022, Mactan I., Cebu, Philippines), 4.6 mm. **N.** *Pygmaeonus wallacei*
539 (paratype, SMNS, Taka Bulango, SW Sulawesi, Indonesia), 7.4 mm. **O** Holotype of *Conus*
540 *micarius* Hedley, 1912 (AMS, Cape York, Australia), 6.2 mm. **P.** Holotype of *Conus visseri*
541 Delsaerdt, 1990 (NBC ZMA 137077, Ka Lhim Beach, Patong Bay, Phuket I., Thailand), 8.8
542 mm. **Q.** Lectotype of *Conus papalis* Weinkauff, 1875 (NHMUK, Ticao I., Philippines), 9.0
543 mm. Scale bars = 5 mm.

544

545 **Figure 3.** Pairwise distribution of the COI genetic distances within subgenera (light grey),
546 among subgenera but within genera (dark grey) and among genera (black). Black arrow:
547 genetic distances calculated between specimens of *Californiconus*, *Lilliconus* and
548 *Pygmaeconus*.

549

550 **Figure 4.** Number of genera found for each time frame in the literature review. Black arrow:
551 *Lilliconus* and *Pygmaeconus*.

552

553 **Figure 5. A-E.** Radular teeth of *Pygmaeconus trillii* with major parts labelled, optical
554 microscopy (**A**, MNHN IM-2013-47253, Kavieng, Papua New Guinea, SL = 6.3 mm; **B**, MJT
555 coll., Cebu, Philippines, SL = 6.3 mm) and SEM (**C-E**, Cebu, Philippines, MJT coll., SL 6.4
556 mm). Abbreviations: ao, adapical opening; ba, barb; bl, blade; pb, tusk-shaped posterior
557 blade; ps, pointed structure terminating sheet that rolls around shaft; sd, single small denticle;
558 sf, shaft fold.

559

560 **Figure 6. A-C.** Radular teeth. **A.** *Lilliconus biraghii omanensis* (MJT coll., Masirah I., Oman,
561 SL = 6.3 mm). **B.** *Lilliconus sagei* (MNHN IM-2009-31328, Lavanono, South Madagascar,
562 SL = 6.4 mm). **C.** *Californiconus californicus*, (ex-coll. J. Nybakken, California, USA, SL =
563 40.3 mm). Scale bars = 100 μ m.

564

565 **Figure 7.** Scanning electron photomicrographs of the radular tooth of *Conus*
566 (*Pseudolilliconus*) *boschorum* (reproduced from Rolán & Raybaudi Massilia, 1994, with
567 permission from publisher). **A.** Entire tooth. **B.** Laterodorsal view of apical part, showing two
568 prominent barbs and third lower barb, close to shaft. **C.** Opposite view, showing two lower

569 barbs. **D.** Apical view showing unusually rounded apex with central rough area. Scale bars =
570 10 μm .

571

572 **Figure 8.** Scanning electron photomicrographs of radular tooth of *Conus (Pseudolilliconus)*

573 *korni* (reproduced from Rolán & Raybaudi Massilia, 1994, with permission from publisher).

574 **A, B.** Complete tooth, two views. **C-E.** Enlarged view of apical portion showing barbs,

575 adapical opening and enrolled lower, flat barb, externally recurved.

576

577

TABLES

578

579 **Table 1.** List of specimens analyzed.

MNHN ID	BOLD ID	Expedition	Family	Genus	species	GenBank accession number
			Conidae	<i>Californiconus</i>	<i>californicus</i>	DQ885848.1
IM-2007-17914	CONO313-08	PANGLAO_2005	Conidae	<i>Conasprella</i>	<i>pagoda</i>	EU015729
IM-2007-17921	CONO296-08	PANGLAO_2005	Conidae	<i>Conasprella</i>	<i>orbignyi</i>	EU015721
IM-2007-34849	CONO1508-14	TERRASSES	Conidae	<i>Conasprella</i>	<i>alisi</i>	KJ550113
			Conidae	<i>Conasprella</i>	<i>arcuatus</i>	KJ549861
IM-2007-30639	CONO1403-14	SANTO_2006	Conidae	<i>Conus</i>	<i>striatus</i>	KJ550458
IM-2007-30646	CONO999-10	SANTO_2006	Conidae	<i>Conus</i>	<i>distans</i>	KJ550204
IM-2007-30653	CONO1004-10	SANTO_2006	Conidae	<i>Conus</i>	<i>marmoreus</i>	KJ550367
IM-2007-30860	CONO1460-14	SANTO_2006	Conidae	<i>Conus</i>	<i>chiangi</i>	KJ550172
IM-2009-31325	submitted	ATIMO_VATAE	Conidae	<i>Lilliconus</i>	<i>sagei</i>	submitted
IM-2009-31328	submitted	ATIMO_VATAE	Conidae	<i>Lilliconus</i>	<i>sagei</i>	submitted
IM-2007-30760	CONO1027-10	EBISCO	Conidae	<i>Profundiconus</i>	<i>barazeri</i>	KJ550111
IM-2009-18243	CONO1477-14	TERRASSES	Conidae	<i>Profundiconus</i>	<i>vaubani</i>	KJ550517
IM-2013-18551	CONO1807-15	PAPUA_NIUGINI	Conidae	<i>Profundiconus</i>	<i>teramachii</i>	KT874757
IM-2013-47253	submitted	KAVIENG	Conidae	<i>Pygmaeonus</i>	<i>traillii</i>	submitted
IM-2013-47254	submitted	KAVIENG	Conidae	<i>Pygmaeonus</i>	<i>traillii</i>	submitted
IM-2013-47769	submitted	KAVIENG	Conidae	<i>Pygmaeonus</i>	<i>traillii</i>	submitted
IM-2013-47770	submitted	KAVIENG	Conidae	<i>Pygmaeonus</i>	<i>traillii</i>	submitted
IM-2013-47771	submitted	KAVIENG	Conidae	<i>Pygmaeonus</i>	<i>traillii</i>	submitted
IM-2013-50753	submitted	KAVIENG	Conidae	<i>Pygmaeonus</i>	<i>traillii</i>	submitted
IM-2013-53787	submitted	KAVIENG	Conidae	<i>Pygmaeonus</i>	<i>traillii</i>	submitted

IM-2013-54883	submitted	KAVIENG	Conidae	<i>Pygmaeonus</i>	<i>traillii</i>	submitted
IM-2007-17700	CONO147-08	BOA1	Borsoniidae	<i>Bathytoma</i>	<i>carnicolor</i>	EU015643
IM-2007-17934	CONO372-08	SALOMON_2	Borsoniidae	<i>Borsonia</i>	<i>sp.</i>	EU015746
IM-2007-42331	CONO602-08	NORFOLK_2	Conorbidae	<i>Benthofascis</i>	<i>lozoueti</i>	HQ401574
IM-2007-40991	FRANZ462-08	SANTO_2006	Turridae	<i>Turris</i>	<i>condei</i>	EU820787

580

581

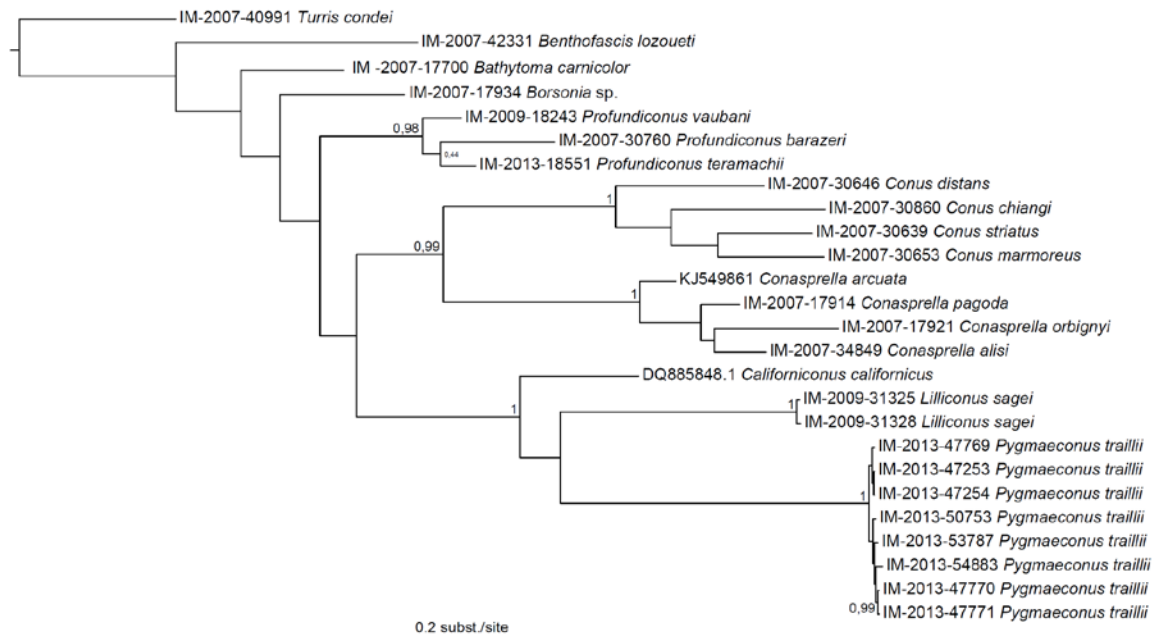
582 **Table 2.** Summary of diagnosing traits for the genera *Pygmaeconus*, *Lilliconus*, *Californiconus* and *Pseudolilliconus*.* RSH = Relative spire
 583 height = spire height (mm)/SL (mm)

Genus	SL (mm)	Shell features							Radula features			Distribution
		Protoconch	RSH*	Spire profile	Nodules	Teleoconch whorls	Shoulder	Operculum	Waist	Nº of Barb+Blades	single-serration size	
<i>Pygmaeconus</i>	3-9	Paucispiral	0.31-0.32	Straight or convex	Absent or obsolete	Convex, smooth or with one or two grooves	Rounded	Small	Present	5	Very small	Western Pacific and Eastern Indian Ocean
<i>Lilliconus</i>	6-12	Paucispiral	0.12-0.25	Straight, stepped	Present	Flat or slightly concave, with subsutural ridge	Angulated	Small	Present	5	Large	
<i>Californiconus</i>	15-40	Multispiral	0.14-0.19	Convex	Absent	Flat, smooth	Rounded	Large	Present	5	Large	Eastern Pacific
<i>Pseudolilliconus</i>	9-13	Paucispiral	0.13-0.28	Concave, stepped	Absent	Concave, canaliculated	Sharply angulated	Small	Absent	3	Absent	North-West Indian Ocean

584

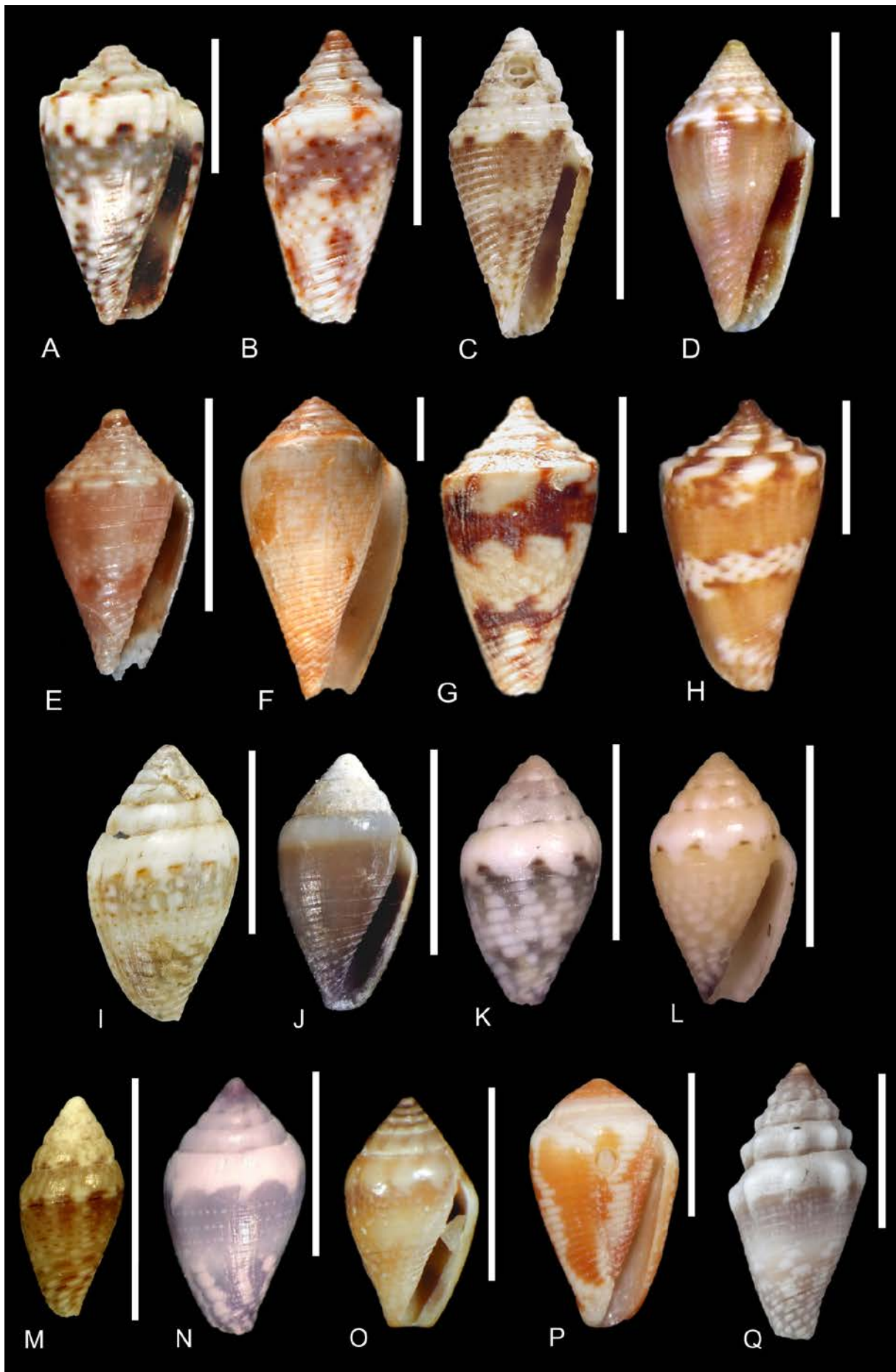
585

586 Figure 1

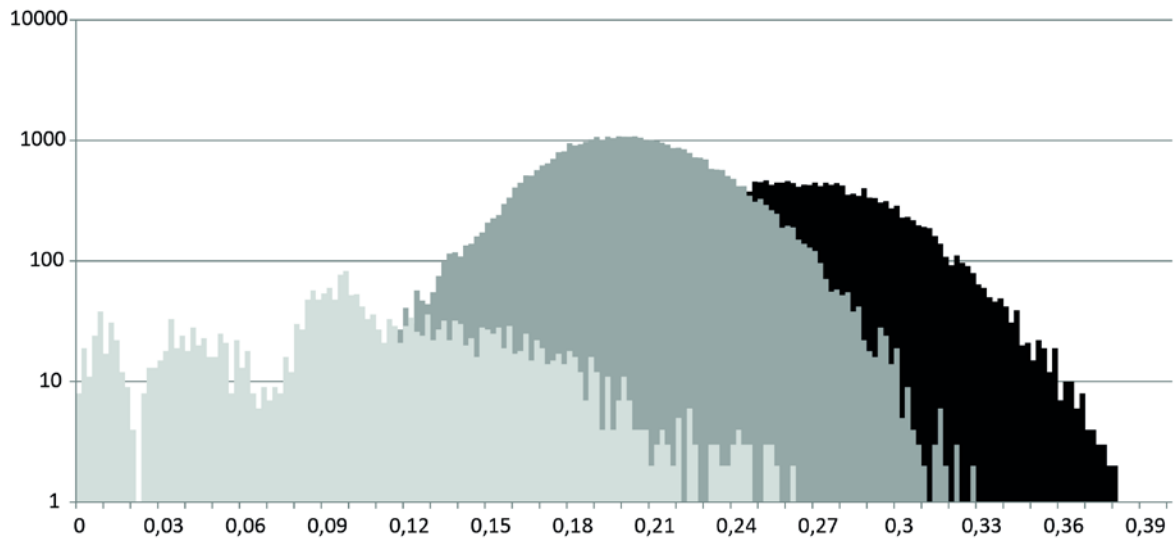


587

588



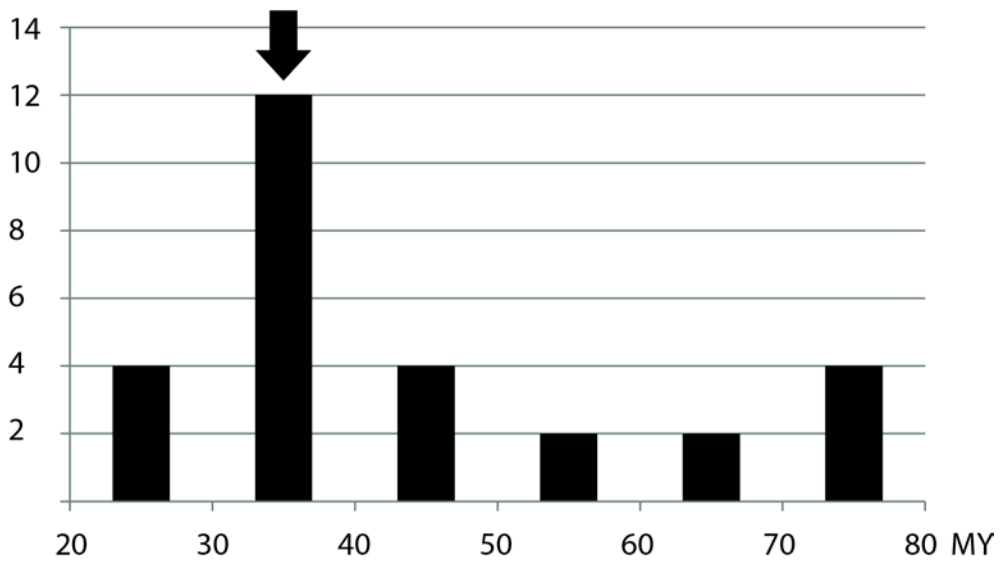
592 Figure 3



593

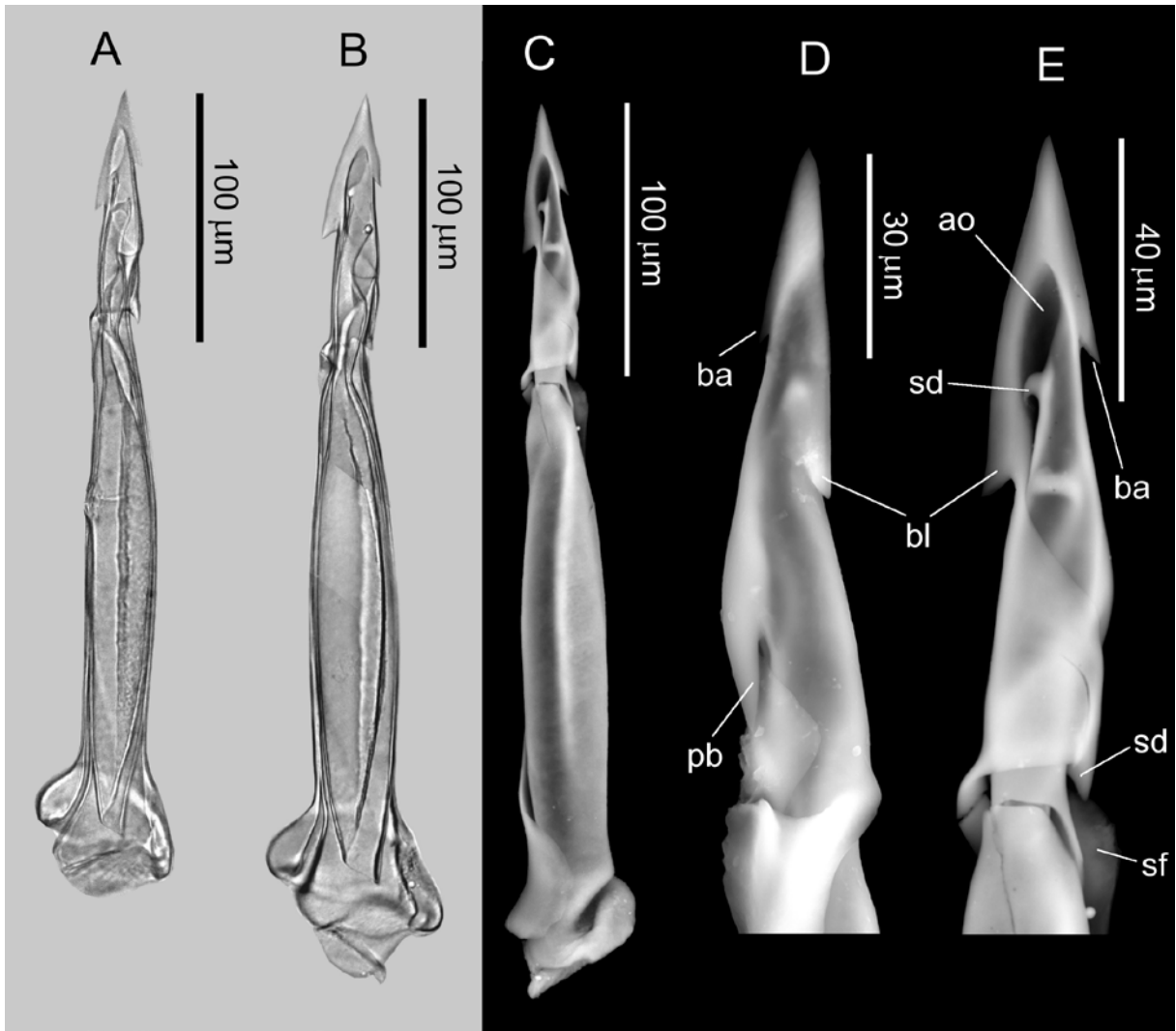
594

595 Figure 4



596

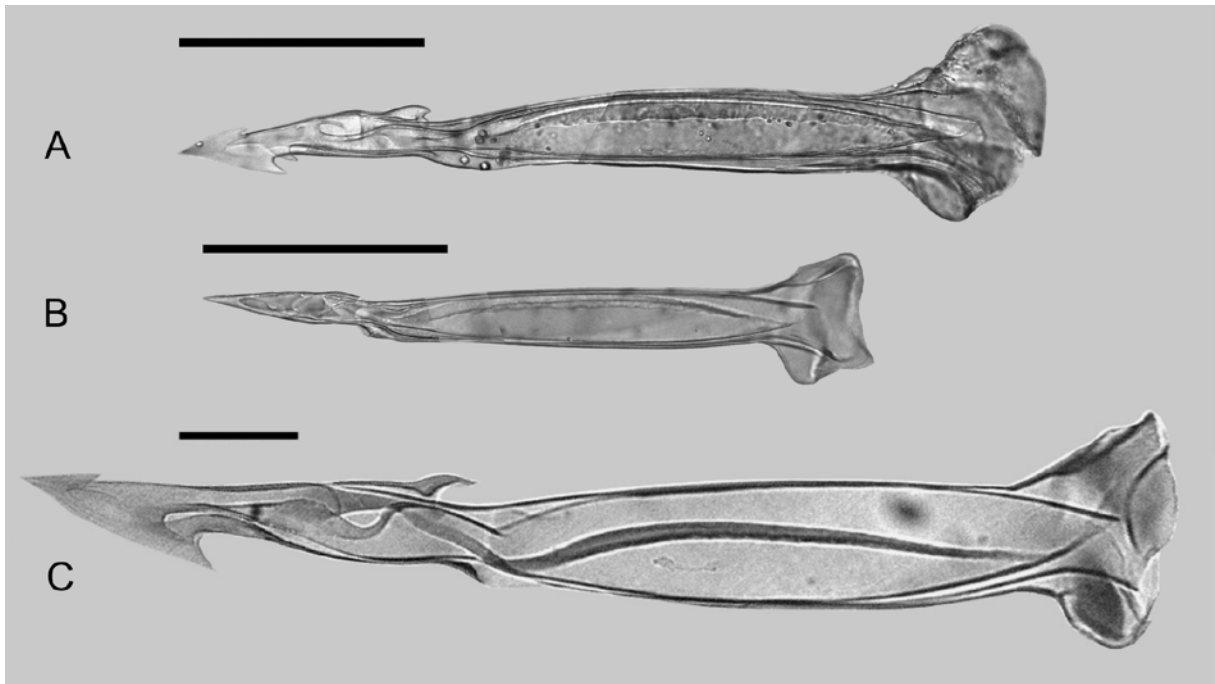
597



599

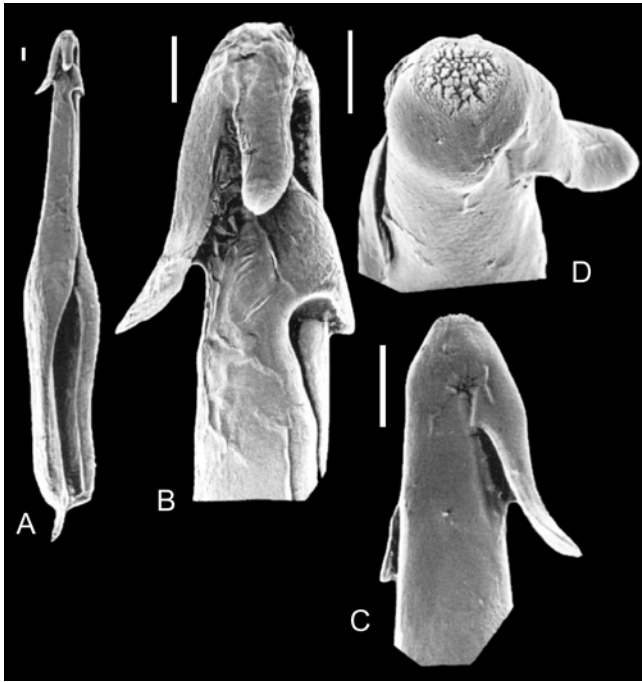
600

601 Figure 6



602

603



605

606

