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## Starting to unravel the toxoglossan knot: Molecular phylogeny of the “turrids” (Neogastropoda: Conoidea)

N. Puillandre, S. Samadi, M.-C. Boisselier, A.V. V Sysoev, Y.I. I Kantor, C. Cruaud, A. Couloux, P. Bouchet

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1 **Starting to unravel the toxoglossan knot: Molecular phylogeny of the “turrids”**  
2 **(Neogastropoda: Conoidea)**

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4 N. Puillandre <sup>a,b,\*</sup>, S. Samadi <sup>a</sup>, M.-C. Boisselier <sup>a</sup>, A.V. Sysoev <sup>c</sup>, Y.I. Kantor <sup>d</sup>, C. Cruaud <sup>e</sup>, A.  
5 Couloux <sup>e</sup>, P. Bouchet <sup>b</sup>

6  
7 <sup>a</sup>UMR 7138, Systématique, adaptation, évolution, UPMC, IRD, MNHN, CNRS, Service de  
8 systématique moléculaire (CNRS, IFR 101), Département systématique et évolution,  
9 Muséum National d’Histoire Naturelle, CP26, 57 rue Cuvier, 75231 Paris Cedex 05, France

10  
11 <sup>b</sup>USM 602/UMS CNRS 2700, Muséum National d’Histoire Naturelle, Département  
12 Systématique et Evolution, 55 rue Buffon, 75231 Paris Cedex 05, France

13  
14 <sup>c</sup>Zoological Museum of Moscow State University, Bolshaya Nikitskaya str. 6, Moscow  
15 103009, Russia

16  
17 <sup>d</sup>A. N. Severtzov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninski  
18 prospect 33, Moscow 119071, Russia

19  
20 <sup>e</sup>GENOSCOPE, Centre National de Séquençage, 2 rue Gaston Crémieux, CP 5706, 91057  
21 Evry Cedex, France

22  
23 \*Corresponding author. Address: UMR 7138, Systématique, adaptation, évolution, UPMC,  
24 IRD, MNHN, CNRS, Service de systématique moléculaire (CNRS, IFR 101), Département  
25 Systématique et Evolution, Muséum National d’Histoire Naturelle, CP26, 57 rue Cuvier,  
26 75231 Paris, Cedex 05, France.

27 E-mail address: puillandre@mnhn.fr (N. Puillandre).

28  
29

30 **Abstract**

31

32 The superfamily Conoidea is one of the most speciose groups of marine mollusks, with  
33 estimates of about 340 recent valid genera and subgenera, and 4000 named living species.  
34 Previous classifications were based on shell and anatomical characters, and clades and  
35 phylogenetic relationships are far from well assessed. Based on a dataset of ca. 100 terminal  
36 taxa belonging to 57 genera, information provided by fragments of one mitochondrial (COI)  
37 and three nuclear (28S, 18S and H3) genes is used to infer the first molecular phylogeny of  
38 this group. Analyses are performed on each gene independently as well as for a data matrix  
39 where all genes are concatenated, using Maximum Likelihood, Maximum Parsimony and  
40 Bayesian approaches. Several well-supported clades are defined and are only partly  
41 identifiable to currently recognized families and subfamilies. The nested sampling used in our  
42 study allows a discussion of the classification at various taxonomical levels, and several  
43 genera, subfamilies and families are found polyphyletic.

44

45

46 Keywords: 18S rRNA; 28S rRNA; Classification; COI gene; Conoidea; Conidae; H3 gene;  
47 Molecular phylogeny; Toxoglossa; Turridae; West Pacific

48

## 49 1. Introduction

50

51 The superfamily Conoidea (= Toxoglossa) includes small to medium (3–50 mm on average)  
52 sized species of marine snails that are specialist predators on annelids, other mollusks, and  
53 even fishes, and occupy all marine habitats from the tropics to the poles, from shallow to deep  
54 water, and from hard to soft substrates. This is the most diverse groups of marine mollusks,  
55 with almost 700 recent and fossil nominal genera and 10,000 described species (Bouchet,  
56 1990), and current estimates of about 340 recent valid genera and subgenera (Taylor et al.,  
57 1993) and 4000 named living species (Tucker, 2004). *Conus* alone includes over 500 valid  
58 species, making it the most speciose genus of marine animals (Kohn, 1990; Duda and Kohn,  
59 2005). The monophyly of the Conoidea, characterized by a venom apparatus, is not  
60 questioned (Taylor et al., 1993), but subdivisions within Conoidea, and relationships between  
61 them are controversial, mostly because the extensive morphological and anatomical variation  
62 encountered is itself not well understood. In this context, molecular data can bring new  
63 characters, allowing to root the classification of Conoidea in an evolutionary perspective  
64 using a phylogenetic analysis.

65 During most of the 19th and 20th century, classifications (e.g., Fischer, 1887; Cossmann,  
66 1896; Hedley, 1922; Thiele, 1929; Wenz, 1938–1944) were based on characters of the shell  
67 and of the radula, and Powell (1942, 1966) later gave emphasis on characters of the  
68 protoconch (larval shell). All these authors traditionally recognized three families of recent  
69 Conoidea: (i) Conidae, only containing the genus *Conus*, (ii) Terebridae containing species  
70 with acuminate shells without a siphonal canal, and (iii) Turridae, including the rest, i.e., the  
71 vast majority of the group. Turridae was considered by Hedley (1922) to be “more perplexing  
72 than any other molluscan family”. Powell’s (1942, 1966) subdivision of the Turridae in nine  
73 subfamilies (see Table 1) was the basis for turrid classifications in the latter half of the 20th  
74 century. Subsequent authors diverged on the number of subfamilies they recognized, mostly  
75 splitting one subfamily into several: working mainly on East Pacific faunas, McLean (1971)  
76 thus recognized 15 subfamilies of Turridae; Kilburn (various papers from 1983 to 1995)  
77 recognized eight subfamilies in the South African fauna; while in their monograph of  
78 European deep-sea turrids, Bouchet and Ware´n (1980) criticized the use of “more or less  
79 randomly selected shell characters” and did not use subfamilies at all. Other shell- and radula-  
80 based classifications, mostly regional, include Morrison (1965), Shimek and Kohn (1981) and  
81 Chang (1995, 2001). A turning point in toxoglossate classification was the work of Taylor et  
82 al. (1993) who extensively used anatomical characters, in addition to radulae. Their entirely  
83 novel classification recognized six families (Conidae, Turridae, Terebridae, Drilliidae,  
84 Pseudomelatomidae and Strictispiridae), the salient point being that Conidae was by then  
85 enlarged beyond Coninae (*Conus*) to include five subfamilies previously placed in Turridae,  
86 and the newly restricted Turridae included a further five subfamilies. Bouchet and Rocroi’s  
87 (2005) recent review of gastropod classification essentially kept Taylor’s classification with  
88 updates based mainly on Rosenberg (1998) and Medinskaya and Sysoev (2003): Clavatulinae  
89 was raised to the family level; Taraninae was synonymized with Raphitominae; and the novel  
90 subfamily Zemaciinae was accepted in the Turridae. Thereafter, we use “Turridae s.l.” to  
91 designate all Conoidea except *Conus* and Terebridae (i.e., Turridae sensu Powell (1966) and  
92 most 20th century authors) and “Turridae s.s.” to designate the family as restricted by Taylor  
93 et al. (1993), while “Conidae” designates the expanded family after Taylor et al. (1993).  
94 Since Taylor et al. (1993), several anatomical studies have highlighted the high level of  
95 homoplasy of the characters of the shell and the radula (e.g., Kantor and Taylor, 1994; Kantor  
96 et al., 1997; Taylor, 1994), but although *Conus* itself has been subjected to intensive  
97 molecular studies (e.g., Duda and Kohn, 2005), the phylogeny of the broader Conoidea has  
98 not yet been addressed based on molecular characters. The present paper is thus the first

99 molecular phylogeny, based on fragments of one mitochondrial and three nuclear genes, of  
100 the crown clade of the Caenogastropoda. It provides insights at several taxonomic levels  
101 (generic, subfamilial and familial) and the adequacy of previous classifications is thus re-  
102 evaluated.

103

## 104 **2. Materials and methods**

105

### 106 *2.1. Taxon sampling*

107

108 Because of the instability of the taxonomy of the group, currently accepted synonymies  
109 cannot be taken for certain and must be re-evaluated. Ideally, a molecular sampling should  
110 thus include several representatives of all the nominal family group-names, including their  
111 type genera, whether they are currently regarded as taxonomically valid or not. In practice,  
112 this goal is difficult or impossible to reach because (a) a number of nominal (sub)families are  
113 based on fossil type genera (e.g., Borsoniinae, Conorbinae), and (b) a number of type genera  
114 are restricted in distribution and/or live in deep water and are difficult to obtain alive (e.g.,  
115 Pseudomelatomidae, Thatcheriidae). To overcome these difficulties, our taxon sampling  
116 includes several genera for as many as possible of the subfamilies proposed in the literature  
117 (see detail in Table 1). Of the 114 specimens sequenced, few were replicates and the taxon  
118 sampling represents about 100 species in 57 valid genera.

119

### 120 *2.2. Materials*

121

122 The bulk of the material was obtained during expeditions carried out in the tropical western  
123 Pacific during research expeditions by the Muséum National d'Histoire Naturelle (MNHN)  
124 and the Institut de Recherche pour le Développement (IRD) (see Table 2). Living specimens  
125 were anesthetized using MgCl<sub>2</sub>, a piece of tissue was cut from the head-foot, and fixed in  
126 95% ethanol. This dataset was supplemented by specimens collected in West Africa by Serge  
127 Gofas in the mid 1980s. Shells were kept intact for identification. Identifications were carried  
128 to genus level using the classically admitted shell-based genus definitions, but, given the  
129 chaotic state of turrid systematics, no attempt was made to identify our material to species  
130 level; a number of species, especially from deep water, probably represent new species. Even  
131 so, eight specimens could not confidently be attributed to a genus and are denoted thereafter  
132 “cf. Genus”. Conversely, specimens of Terebridae and Conus were identified to species level.  
133 A specimen of a species of Nassaria and a specimen of a species of Cancellopolia, both in the  
134 neogastropod family Buccinidae, closely related to Conoidea (Harasewych et al., 1997;  
135 Colgan et al., 2007), were used as outgroups. Littorina littorea, belonging in the non-  
136 neogastropod family Littorinidae, was used as a third outgroup, with sequences taken from  
137 GenBank (GenBank Accession Nos: AJ622946.1, Q279985.1, AJ488712.1 and  
138 DQ093507.1). Outgroups were chosen to form a non-monophyletic group, as recommended  
139 by Darlu and Tassy (1993). All vouchers are kept in MNHN.

140

### 141 *2.3. Sequencing*

142

143 DNA was extracted from a piece of foot, using 6100 Nucleic Acid Prepstation system  
144 (Applied Biosystem) or  
145 DNeasy

146

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147 96 Tissue kit (Qiagen) for smaller specimens. A fragment of 658 bp of Cytochrome Oxidase I  
148 (COI) mitochondrial gene was amplified using the universal primers LCO1490 and HCO2198

149 developed by Folmer et al. (1994). Three nuclear gene fragments were also analyzed: (i) 900  
150 bp of the rDNA 28S gene, involving D1, D2 and D3 domains (Hassouna et al., 1984), using  
151 the primers C1 and D3 (Jovelin and Justine, 2001); (ii) 328 bp of the H3 gene using the  
152 primers H3aF and H3aR (Okusu et al., 2003); (iii) 1770 bp of the 18S gene using three pairs  
153 of primers: 1F and 5R, 3F and Bi, A2 and 9R (Giribet et al., 1996; Okusu et al., 2003). All  
154 PCR reactions were performed in 25  $\mu$ l, containing 3 ng of DNA, 1 reaction buffer, 2.5 mM  
155 MgCl<sub>2</sub>, 0.26 mM dNTP, 0.3  $\mu$ M of each primer, 5% DMSO and 1.5 U of Q-Bio Taq  
156 (Qbiogene) for all genes. Amplifications consisted of an initial denaturation step at 94  
157 \_\_\_\_\_C for 40, followed by 30 cycles of denaturation at 94  
158 \_\_\_\_\_C for 3000, annealing at 52 \_\_\_\_\_C for  
159 28S gene and first and third fragment of 18S gene, and 53 \_\_\_\_\_C for  
160 H3 gene and second fragment of 18S gene for 4000 and extension at 72  
161 \_\_\_\_\_C for 10. The final extension was at 72  
162 \_\_\_\_\_C for 100. COI gene amplifications followed description of  
163 Hebert et al. (2003). PCR products were purified using ExonucleaseI and Phosphatase and  
164 sequenced using BigDyeTerminator V3.1 kit (Applied biosystem) and the ABI3730XL  
165 sequencer. Because of the length of the 28S PCR product, two internal primers (D2 and C20,  
166 Dayrat et al., 2001) were used for sequencing, in addition of primers used for PCR. All genes  
167 were sequenced for both directions to confirm accuracy of each sequence. The overlap of the  
168 three fragments of 18S gene made it possible to check for consistency. Sequences were  
169 deposited in GenBank (GenBank Accession Nos: EU015417–EU015858).

170

#### 171 *2.4. Phylogenetic analyses*

172

173 COI and H3 genes were manually aligned whereas 28S and 18S genes were automatically  
174 aligned using ClustalW multiple alignment implemented in BioEdit version 7.0.5.3 (Hall,  
175 1999). The accuracy of automatic alignments was confirmed by eye. Hyper-variable regions  
176 of 28S gene and 30 extremity of 18S gene were excluded from further analyses due to  
177 ambiguities in the alignments. For protein coding genes (COI and H3), saturation according to  
178 codon position was tested by plotting genetic distances against patristic distances calculated  
179 from a Maximum Parsimony (MP) tree with a heuristic search option, 10 random  
180 taxonaddition (RA) and tree-bisection and reconnection (TBR) branch-swapping using PAUP  
181 4.0b10 (Swofford, 2002).

182 Nucleotide substitution models were selected for each gene separately and for each combined  
183 dataset using the program Modeltest (Posada and Crandall, 2001), in conjunction with PAUP  
184 4.0b10 (Swofford, 2002). Best models and parameters as estimated by the AIC criterion were  
185 used for Maximum Likelihood (ML) analyses; only the model was fixed for Bayesian  
186 Analyses (BA). Analyses were conducted using three different approaches. A heuristic MP  
187 search was executed with 100 RA, TBR branchswapping, all sites equally weighted and  
188 indels treated as fifth states, using PAUP 4.0b10 (Swofford, 2002). ML heuristic search was  
189 conducted with 100 replicates with TBR branch-swapping using PhyML 2.4.4 (Guindon and  
190 Gascuel, 2003). Robustness of the nodes was assessed using nonparametric bootstrapping  
191 (Felsenstein, 1985) with 100 bootstraps replicates for MP analysis and 1000 for ML analysis,  
192 TBR branch-swapping and 100 RA replicates. BA consisted of six Markov chains (8,000,000  
193 generations each with a sampling frequency of one tree each hundred generations) run in two  
194 parallel analyses using Mr. Bayes (Huelsenbeck et al., 2001). When the log-likelihood scores  
195 were found to stabilize, a consensus tree was calculated after omitting the first 25% trees as  
196 burn-in. For the treatment of combined data using BA, the data were separated into four  
197 unlinked partitions corresponding to the four genes analyzed, each following the best fitting  
198 model of substitution estimated for each gene.

199

## 200 2.5. Turning the phylogeny into a classification

201

202 There are currently 41 available family-group names in the Conoidea, of which 19 are  
203 considered valid at family or subfamily ranks (Bouchet and Rocroi, 2005). In a nomenclatural  
204 perspective, only the occurrence of the type genus of a family-group name in a clade allows  
205 an unequivocal application of this name to that clade. For example, the clade containing the  
206 genus *Raphitoma* can unambiguously carry the name Raphitominae. However, many type  
207 genera are not represented in our taxon sampling and many of our molecular clades do not  
208 include a type genus. In such cases, we have relied on the traditional allocation of non-type  
209 genera to a subfamily to link clade and name. For example, a clade containing three genera  
210 classically classified in the family Drilliidae (Taylor et al., 1993; Tippet and Tucker, 1995)  
211 can carry the name Drilliidae, even though *Drillia* itself is not part of our taxon sampling.  
212 However, this approach does not lead to an unequivocal application of names when genera (or  
213 subfamilies) as traditionally construed prove to be non-monophyletic; in that case, only the  
214 type species (or the type genus) is the legitimate bearer of the name.

215

## 216 3. Results

217

218 For COI and H3 genes, 658 and 328 bp were sequenced, respectively, and no indels were  
219 found. After the alignment, we obtained a fragment of 933 and 1729 bp in length for the 28S  
220 and 18S genes, respectively. Sequencing of specimens belonging to genera *Clavatula*,  
221 *Pusionella* and *Perrona* was successful only for the COI gene: the prolonged conservation in  
222 the museum collections (more than 20 years) may have altered the quality of the DNA. Only  
223 one specimen (17855) failed to sequence for COI gene, and three others (17842, 17919 and  
224 17920, genus *Cochlespira*) for H3 gene. No bias was detected in base composition. The  
225 saturation analyses for the two protein coding genes revealed that the COI gene was highly  
226 saturated on the third position of codon, thus we used only the first and second positions in  
227 the phylogenetic analyses. Best model and parameters estimated for each gene and genes  
228 combinations are shown in Table 3. Independent analyses of each of the four genes provided  
229 very poorly resolved trees, with few well-supported clades (Table 4).

230 The only incongruencies found between the independent gene analyses corresponded to  
231 poorly supported nodes. The most supported incongruency concerned relationships between  
232 three specimens attributed to the genus *Bathytoma* (17700, 17865 and 17857). In the ML  
233 analysis of H3 gene 17700 was the sister-group of 17865 and 17857 whereas in the ML  
234 analysis of the 18S gene 17865 was the sister-group of 17700 and 17857. These two nodes were  
235 supported by bootstrap value of, respectively, 61 and 67, values weaker than the bootstrap  
236 value allowing the recognition of a supported clade (e.g., Hillis and Bull, 1993; Soltis and  
237 Soltis, 2003).

238 Since no incongruency was revealed among the single gene analyses, we constructed two  
239 combined datasets comprising the data of the 4 gene fragments resulting in a sequence of  
240 3428 bp length. For both combined datasets we excluded the taxa attributed to *Clavatula*,  
241 *Pusionella* and *Perrona* for which only the COI gene was successfully obtained. For the first  
242 combined dataset (CD1) we also excluded the specimens 17855, 17842, 17919 and 17920, not  
243 sequenced for all genes, to avoid potential perturbation of phylogenetic reconstruction by  
244 missing data (Wiens, 1998). Thus, the CD1 included 104 ingroups and the second combined  
245 dataset (CD2) included 108 ingroups. In CD2, missing sequences were treated as missing  
246 characters in all analyses. For CD1 and CD2, respectively, 662 and 671 sites were variable  
247 among which 454 and 460 were parsimony informative.

248 The Conoidea were found monophyletic, at least with the two combined analyses, although  
249 not always strongly supported (for CD2, MP and ML bootstraps, respectively: 65 and 79,  
250 Posterior Probabilities PP: 1). Within the Conoidea, two clades could be distinguished: clade  
251 A (MP bootstraps: 58, ML bootstraps: 68, PP: 0.73) and clade B (MP bootstraps: 28, ML  
252 bootstraps: 52, PP: 1). Within the clade A, the clade C is found strongly supported with ML  
253 bootstraps (91) and PP (1). Each analysis of the two combined datasets allowed the definition  
254 of the same 21 higher level clades, each of them strongly supported: MP and ML bootstraps  
255 >80 and PP >0.99 (Mason-Gamer and Kellogg, 1996; Zander, 2004). They included from 1 to  
256 12 genera each (Tables 4 and 5, Fig. 1). Clades were numbered according to their position in  
257 the tree (Fig. 1). Clades 1–9 are included in clade A, and among them clades 1–4 are included  
258 in clade C. Clades 10–21 are included in clade B.  
259 As long branches, for example that displayed by clade 9, could potentially disturb  
260 phylogenetic reconstructions (Felsenstein, 2004), the three analyses (MP, ML and BA) were  
261 conducted for the whole CD2, excluding specimens 17701 and 17702 (clade 9). The  
262 Conoidea were again separated in two clades: A0 (including clades 1–8) and B. The bootstraps  
263 and PP were increased for both clades A0 (MP Bootstraps: 60, ML bootstraps: 77, PP: 1) and  
264 clade B (MP Bootstraps: 37, ML bootstraps: 60, PP: 1).  
265 The position of the representatives of Clavatula, Pusionella and Perrona, for which we  
266 obtained only the COI sequence, could be analyzed only in the single gene analysis. The taxa  
267 clustered in the weakly supported clade 22 in all the performed COI gene analyses (Table 4,  
268 tree not shown). The weak resolution of the trees obtained with the COI gene did not permit  
269 the placement of clade 22 in either clade A or B.  
270 All representatives of a genus clustered together in 1 of the 22 clades, except representatives  
271 of Borsonia, Comitas, Conus and Leucosyrinx. The representatives of Borsonia and Conus  
272 splitted, respectively, in clades 15, 16 and 19–21, each including only specimens from a  
273 single genus. The relationships between the two clades were not resolved and thus the  
274 monophyly of each of these genera cannot be rejected. Conversely, the monophyly of genera  
275 Leucosyrinx and Comitas (clades 3, 4 and 9) can be rejected, since representatives of the two  
276 genera clustered in the clade 4.

277

## 278 **4. Discussion**

279

### 280 *4.1. Classification of the Conoidea*

281

282 Although not strongly supported, our analysis suggests that the superfamily Conoidea is  
283 monophyletic. However, the Conoidea and two outgroups used here (Cancellapollia and  
284 Nassaria) both belong in the Neogastropoda, the phylogeny of which is not well resolved  
285 (Harasewych et al., 1997; Colgan et al., 2007), and the monophyly observed here could thus  
286 be an artifact due to under-sampling within Neogastropoda. Within Conoidea, the large  
287 amount of diversity included in our dataset allows us to discuss the current classification at  
288 genus, subfamily, and family levels.

289

### 290 *4.2. Accuracy of taxonomic delimitations at genus level*

291

292 The genus is the lowest level for which we can discuss taxonomic delimitations since most of  
293 our specimens are not identified at species level. Among the 57 genera identified in our  
294 dataset, monophyly can be rejected for only two of them (Leucosyrinx and Comitas), which  
295 indicates that in most cases shell morphology is an appropriate predictor of generic  
296 allocations. Two further genera (Borsonia and Conus) are found to be diphyletic, but the  
297 position of the two defined clades is unresolved and thus monophyly cannot be excluded.



298 Similarly, the polyphyly of some genera within the clades 1–22 can not be confirmed because  
299 of the lack of support for intra-clade nodes (results not shown).

300

#### 301 *4.3. Position of the genera within the subfamilies*

302

303 Our analysis confirms many previous assignments of genera to subfamilies as in Taylor et al.  
304 (1993) (Table 1) and subsequent refinements of their classification. We thus confirm a  
305 position of Conopleura in the Drilliidae (Tippet and Tucker, 1995), of Anacithara in the  
306 Crassispirinae (Kilburn, 1994), of Turridrupa in the Turrinae (Kantor et al., 1997), of  
307 Toxicochlespira in the Mangeliinae (Sysoev and Kantor, 1990), and of Glyphostomoides in  
308 the Raphitominae (Shuto, 1983). However, several results do not confirm established  
309 classifications (Tables 1 and 5). The genus Otitoma, tentatively retained by Kilburn (2004) in  
310 the Mangeliinae based on shell characters, is here found to be in the Crassispirinae. The genus  
311 Lienardia, earlier classified in the Mangeliinae, is here placed in clade 12, identified as a  
312 Clathurellinae. (Furthermore, specimens attributed to Lienardia display several types of  
313 protoconchs and Lienardia as currently understood is probably a highly polyphyletic  
314 assemblage of species, some belonging to Raphitominae—not represented in our molecular  
315 sampling—and others to Clathurellinae—as the specimens studied here). The position of  
316 Gemmuloborsonia, assigned to the Turrinae (Sysoev and Bouchet, 1996; Medinskaya, 2002),  
317 is unresolved.

318

#### 319 *4.4. Robustness of subfamilies delimitations*

320

321 We found discrepancies between our phylogeny and previous classifications at the subfamily  
322 level. Thus, crassispirine genera are present in two clades (2 and 7), one of them (clade 2)  
323 containing the type genus. The polyphyly of this subfamily is supported by the existence of  
324 clade C, which includes clade 2, but excludes clade 7. Since the relationships between clade 7  
325 and others clades within clade A are not resolved, it is inconclusive whether clade 7 must be  
326 ranked as its own subfamily or whether it must be grouped together with another existing  
327 subfamily. The subfamily Cochlespirinae as currently construed appears polyphyletic too,  
328 with four distinct clades (3, 4, 8 and 9), one of them (clade 8) containing the type genus. As  
329 for the Crassispirinae, the polyphyly of the Cochlespirinae is supported by the existence of  
330 clade C, which includes clades 3 and 4, but excludes clades 8 and 9. However, because of the  
331 limits of the resolution of the deeper nodes, it is inconclusive whether clades 3 and 4 should  
332 be allocated to the Crassispirinae or should constitute a new subfamily; the subfamily  
333 Cochlespirinae could be limited to clade 8, or could also include clade 9.

334

335 In the next three cases, polyphyly is possible but not demonstrated because of a general lack  
336 of support for deeper nodes in clade B. (a) Relationships between the two highly divergent  
337 clades (clades 11 and 17) of the Mangeliinae are not resolved and our results are inconclusive  
338 on the non-monophyly of the subfamily. (b) Coninae also ends up as two distinct clades  
339 (clades 19 and 21), a result already obtained by Duda and Kohn (2005). (c) The subfamily  
340 Clathurellinae is split into seven clades (clades 12, 13, 14, 15, 16, 18 and 20), but the non-  
341 monophyly of these clades is not demonstrated. With one exception, our molecular  
342 clathurelline clades correspond to intra-clathurelline “groups” defined by Taylor et al. (1993),  
343 suggesting that these may warrant formal naming as tribes. The exception is clade 18 which  
344 includes on one hand the genus Typhlomangelia (placed in the “borsoniid group” by Taylor  
345 et al., 1993) and on the other hand the genera Heteroturris and Microdrillia (placed in the  
346 “tomopleurid group” by Taylor et al., 1993).

347

348 *4.5. Robustness of families delimitations*

349

350 Finally, our results also permit a discussion of family classification within Conoidea. Taylor  
351 et al.'s (1993) anatomical study suggested a closer relationship of Clathurellinae, Conorbinae,  
352 Mangeliinae, Oenopotinae and Raphitominae to *Conus* than to other members of the family  
353 Turridae s.l. and their extension of Conidae included these turrid subfamilies. In our study,  
354 clade B, although weakly supported, corresponds to Taylor et al.'s (1993) family Conidae,  
355 thus supporting its monophyly.

356 Our study also revealed another weakly supported deep clade (clade A) that includes genera  
357 classified by Taylor et al. (1993) in three different families: Drilliidae, Terebridae and  
358 Turridae s.s. (consisting of Clavatulinae, Cochlespirinae, Crassispirinae, Turrinae and  
359 Zonulispirinae). Genera of the Drilliidae (clade 1) are included in clade C. This well-  
360 supported clade also contains taxa of the Turridae s.s. (Crassispirinae and *Comitas*), and  
361 excludes the other taxa of the Turridae s.s. Consequently, Turridae s.s. are not monophyletic.  
362 Furthermore, according to Kantor (2006), the radula of Drilliidae is not fundamentally  
363 different from that of Turridae s.s.

364 Within clade A, the monophyly of the Terebridae is supported but its relationships with other  
365 clades of Turridae s.s. is not resolved. The strong support obtained for clade A0 (clade A  
366 without clade 9) indicates that Terebridae are closely related to Turridae s.s. Moreover, the  
367 increase of clade support from A to A0 suggests an artifact effect of clade 9 on the  
368 phylogenetic reconstruction, e.g., a long branch attraction effect with the outgroups. This  
369 phenomenon could be avoided by increasing the amount of diversity included in the analysis  
370 (Bergsten, 2005). A close relationship between Terebridae and Turridae s.s. had already been  
371 suggested by Cossmann (1896), and Powell (1942, 1966), based on the resemblance of the  
372 shells of Terebridae and of the clavatuline genus *Pusionella*. Based on this observation and  
373 the fossil record, Powell (1966) speculated that Terebridae were derived from the  
374 Clavatulinae. Our results suggest that Turridae s.s. could be closer to Terebridae than to  
375 Conidae, but the question of whether Terebridae is included in Turridae s.s. or is its sister  
376 group still remains unresolved.

377

378 *4.6. Towards a stabilized system for Conoidea*

379

380 The weak support of neogastropod molecular phylogenies available in literature is supposed  
381 to be the consequence of an early radiation of the group (Harasewych et al., 1997; Colgan et  
382 al., 2003, 2007). Genes used in those studies were not adequate to resolve the relationships  
383 between clades that emerged during this radiation. In our study, we used the same genes,  
384 albeit at a lower taxonomic level, but deeper nodes are not resolved either. In view of the fact  
385 that most subfamilies of Turridae s.l. were already present in the Eocene, Powell (1966) dated  
386 their divergence before the Upper Cretaceous (before 65MY). As for other animal groups  
387 (e.g., Strugnell et al., 2005; Fry et al., 2006), resolving phylogenetic relationships between  
388 those early divergences seems to require slow-evolving genes. In this perspective, nuclear  
389 coding genes, rarely used in mollusk phylogenies, could be useful to resolve early  
390 relationships within Conoidea as well as deeper relationships within gastropods.

391 The taxonomic sampling used here allows an estimation of molecular variability within clades  
392 at each level: several genera are included in each subfamily, several subfamilies are included  
393 in each family, and most of the families defined by Taylor et al. (1993) are present. This  
394 strategy, where taxonomic sampling is hierarchically organized, is clearly required to discuss  
395 monophyly of each of those groups, and some problems are thus highlighted at each  
396 taxonomic level.

397 However, even with a dataset of 57 genera, covering most of the previously recognized  
398 families and subfamilies of Conoidea, the present study only brings preliminary results. At  
399 genus level, these 57 genera represent only 17% of the 340 already described recent genera  
400 and it is further clear that the shell-based current taxonomic extension of many genera will not  
401 stand after molecular testing. At subfamily and family levels, although a large part of the  
402 conoidean diversity is represented in this study, the families Strictispiridae and  
403 Pseudomelatomidae, the subfamilies Zonulispirinae and Zemaciinae in Turridae s.s., the  
404 Pervicaciinae in Terebridae and the Oenopotinae in Conidae, are not part of our taxon  
405 sampling. The highly divergent clades found here in several subfamilies as previously defined  
406 demonstrate the need for further research in order to better restrict the taxonomic extensions  
407 of the already known subfamilies and probably formally name new subfamilies and/or tribes.  
408 Finally, at family level, new relationships are suggested. As a remake of the Conus story, it  
409 now appears that the long recognized family Terebridae does not stand alone apart from the  
410 rest of the Conoidea, but could be the sister-group or even part of the Turridae s.s.

411

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413

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424 authors thank two anonymous referees for very constructive comments on the manuscript.

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573 Table 1: Evolution of Conoidea classification.

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	<b>Powell, 1966</b>	<b>McLean, 1971</b>	<b>Taylor et al., 1993</b>	<b>Actual system*</b>	
TURRIDAE s.l.	<b>Clavinae</b> <i>Ceritoturris</i> <i>Crassispira</i> <i>Horaiclavus</i> ? <i>Inquisitor</i> = <i>Ptychobela</i> <i>Microdrillia</i> <i>Splendrilla</i>	<b>Clavinae</b> <i>Splendrilla</i>	<b>DRILLIIDAE</b> <i>Clavus</i> <i>Horaiclavus</i> <i>Splendrilla</i>	<b>DRILLIIDAE</b> <i>Clavus</i> <i>Conopleura</i> : Tippet and Tucker, 1995 <i>Splendrilla</i>	TURRIDAE s.s.
		<b>Crassispirinae</b> <i>Inquisitor</i>	<b>Crassispirinae</b> <i>Ceritoturris</i> <i>Crassispira</i> <i>Funa</i> <i>Inquisitor</i> <i>Iwaoa</i> <i>Ptychobela</i> <i>Turridrupa</i>	<b>Crassispirinae</b> <i>Anacithara</i> : Kilburn, 2004 <i>Ceritoturris</i> <i>Crassispira</i> <i>Funa</i> <i>Horaiclavus</i> : Kantor, pers. com. <i>Inquisitor</i> <i>Iwaoa</i> <i>Ptychobela</i>	
		<b>Zonulispirinae</b>	<b>Zonulispirinae</b>	<b>Zonulispirinae</b>	
				<b>Zemaciinae</b>	
	<b>Turrinae</b> <i>Gemmula</i> <i>Lophiotoma</i> <i>Turridrupa</i> <i>Turris</i>	<b>Turrinae</b> <i>Gemmula</i> <i>Lophiotoma</i>	<b>Turrinae</b> <i>Gemmula</i> <i>Lophiotoma</i> <i>Turris</i>	<b>Turrinae</b> <i>Gemmula</i> <i>Gemmuloborsonia</i> : Sysoev and Bouchet, 1996 <i>Lophiotoma</i> <i>Turris</i> <i>Turridrupa</i> : Kantor et al., 1997	
	<b>Turriculinae</b> <i>Cochlespira</i> <i>Comitas</i> <i>Iwaoa</i> <i>Leucosyrinx</i>	<b>Turriculinae</b>	<b>Cochlespirinae</b> <i>Cochlespira</i> <i>Comitas</i> <i>Leucosyrinx</i>	<b>Cochlespirinae</b> <i>Cochlespira</i> <i>Comitas</i> <i>Leucosyrinx</i>	
		<b>Pseudomelatomidae</b>	<b>PSEUDOMELATOMIDAE</b>	<b>PSEUDOMELATOMIDAE</b>	
		<b>Strictispirinae</b>	<b>STRICTISPIRIDAE</b>	<b>STRICTISPIRIDAE</b>	
	<b>TEREBRIDAE</b>		<b>TEREBRIDAE</b>	<b>TEREBRIDAE</b> <i>Cinguloterebra</i> : Terryn, 2007 <i>Terebra</i>	
	TURRIDAE s.l.	<b>Clavatulinae</b> <i>Clavatula</i> <i>Perrona</i> <i>Pusionella</i>		<b>Clavatulinae</b> <i>Clavatula</i> <i>Perrona</i> <i>Pusionella</i>	
<b>Borsoniinae</b> <i>Bathytoma</i> <i>Borsonia</i> <i>Mitromorpha</i>		<b>Borsoniinae</b> <i>Borsonia</i>	<b>Clathurellinae</b> Borsoniid: <i>Borsonia</i> <i>Typhlomangelia</i> Mitromorphid: <i>Anarithma</i> <i>Mitromorpha</i>	<b>Clathurellinae</b> Borsoniid: <i>Borsonia</i> <i>Typhlomangelia</i> Mitromorphid: <i>Anarithma</i> <i>Mitromorpha</i>	
		<b>Mitromorphinae</b> <i>Mitromorpha</i>			
		<b>Clathurellinae</b>	Bathytomid: <i>Bathytoma</i> Clathurellid: <i>Etrema</i> ? <i>Nannodiella</i> Tomopleurid: <i>Heteroturris</i> <i>Microdrillia</i> <i>Tomopleura</i>	Bathytomid: <i>Bathytoma</i> Clathurellid: <i>Etrema</i> ? <i>Nannodiella</i> Tomopleurid: <i>Heteroturris</i> <i>Microdrillia</i> <i>Tomopleura</i>	
<b>Mangeliinae</b> <i>Anacithara</i> <i>Benthomangelia</i> <i>Conopleura</i> <i>Etrema</i> <i>Eucithara</i> <i>Guraleus</i> <i>Leiocithara</i> <i>Lienardia</i> <i>Macteola</i> <i>Mangelia</i>			<b>Mangeliinae</b> <i>Benthomangelia</i> <i>Eucithara</i> <i>Guraleus</i> <i>Leiocithara</i> <i>Lienardia</i> <i>Macteola</i> <i>Mangelia</i>	<b>Mangeliinae</b> <i>Benthomangelia</i> <i>Eucithara</i> <i>Guraleus</i> <i>Leiocithara</i> <i>Lienardia</i> <i>Macteola</i> <i>Mangelia</i> <i>Otitoma</i> : Kilburn, 2004 <i>Toxicochlespira</i> : Sysoev and Kantor, 1990	
			<b>Oenopotinae</b>	<b>Oenopotinae</b>	
<b>Daphnellinae</b> <i>Daphnella</i> <i>Eucyclotoma</i> <i>Gymnobela</i> <i>Kermia</i> <i>Pleurotomella</i> <i>Raphitoma</i> <i>Rimosodaphnella</i> <i>Vepracula</i>		<b>Daphnellinae</b> <i>Daphnella</i> <i>Kermia</i> <i>Philbertia</i> <i>Vepracula</i>	<b>Daphnellinae</b> <i>Rimosodaphnella</i> <i>Daphnella</i> <i>Eucyclotoma</i> <i>Gymnobela</i> <i>Kermia</i> <i>Pleurotomella</i> <i>Raphitoma</i> <i>Vepracula</i>	<b>Raphitominae</b> <i>Daphnella</i> <i>Eucyclotoma</i> <i>Glyphostomoides</i> : Shuto, 1983 <i>Gymnobela</i> <i>Kermia</i> <i>Pleurotomella</i> <i>Raphitoma</i> <i>Rimosodaphnella</i> <i>Teretiopsis</i> <i>Thatcheria</i> <i>Tritonoturris</i> <i>Vepracula</i>	
			<b>Thatcheriinae</b>		
			<b>Taraniiinae</b> ?		
<b>Conorbinae</b> <i>Benthofascis</i>			<b>Conorbinae</b> ? <i>Benthofascis</i>	<b>Conorbinae</b> <i>Benthofascis</i>	
<b>CONIDAE</b> <i>Conus</i>		<b>Coninae</b> <i>Conus</i>	<b>Coninae</b> <i>Conus</i>		

617 History of conoidean classification and position of the genera included in the present dataset  
618 in the classifications of Powell (1966), McLean (1971) and Taylor et al. (1993). Subfamilies  
619 are in bold, families in bold and capital. \*Recent modifications proposed since the  
620 classification of Taylor et al. (1993) (details given for each genus), resulting in the actual  
621 system used as a basis for our discussion. (See above-mentioned references for further  
622 information).

Table 2: Specimens of Conoidea used in this study.

ID	Cruise	Station ID	Coordinates, depth	Genus (or species) identification	COI	28S	18S	H3	Clades
17700*	BOA 1	CP2462	16°37.5'S, 167°57.4' E, 618-641m	<i>Bathytoma</i> Harris and Burrows, 1891	x	x	x	x	20 B
17701*	BOA 1	CP2432	14°59.7'S, 166°55.0' E, 630-705m	<i>Leucosyrinx</i> Dall, 1889	x	x	x	x	9 A
17702	BOA 1	CP2432	14°59.7'S, 166°55.0' E, 630-705m	<i>Leucosyrinx</i> Dall, 1889	x	x	x	x	9 A
17754*	Panglao 2004	R42	9°37.1'N, 123°52.6'E, 8-22m	<i>Turris</i> Roding, 1798	x	x	x	x	5 A
17755*	Panglao 2004	L46	9°30.9'N, 123°41.2'E, 90-110m	<i>Crassispira</i> Swainson, 1840	x	x	x	x	2, C A
17829	Angola	Ilha de Luanda	8°78'S, 13.23'E, 40-60m	<i>Clavatula</i> Lamarck, 1801	x				22 A
17830	Angola	Cacuaco	10°51'S, 14°23'E, 5-10m	<i>Pusionella</i> Gray, 1847	x				22 A
17831	Angola	Cacuaco	10°51'S, 14°23'E, 5-10m	<i>Pusionella</i> Gray, 1847	x				22 A
17832	Cameroun	Victoria	3°54'N, 9°08'E, 34-37m	<i>Pusionella</i> Gray, 1847	x				22 A
17833	Angola	Mocamedes	15°14'S, 12°29'E, 50m	<i>Perrona</i> Schumacher, 1817	x				22 A
17834	Gabon	Port-Gentil	1°17'S, 11°53'Em	<i>Pusionella</i> Gray, 1847	x				22 A
17835*	BOA 1	CP2462	16°37.5'S, 167°57.4' E, 618-641m	<i>Benthomangelia</i> Thiele, 1925	x	x	x	x	17 B
17836	BOA 1	CP2462	16°37.5'S, 167°57.4' E, 618-641m	<i>Rimosodaphnella</i> Cossmann, 1915	x	x	x	x	10 B
17837	EBISCO	DW2547	21°06'S, 158°36'E, 356-438m	<i>Inquisitor</i> Hedley, 1918	x	x	x	x	2, C A
17838	EBISCO	DW2533	22°18'S, 159°28'E, 360-370m	<i>Gemmula</i> Weinkauff, 1875	x	x	x	x	5 A
17839*	EBISCO	CP2557	21°07'S, 158°30'E, 800-923m	<i>Borsonia</i> Bellardi, 1839	x	x	x	x	16 B
17840*	EBISCO	DW2631	21°03'S, 160°44'E, 372-404m	<i>Horaiclavus</i> Oyama, 1954	x	x	x	x	7 A
17841	EBISCO	CP2648	21°32'S, 162°30'E, 750-458m	<i>Gymnobela</i> Verrill, 1884	x	x	x	x	10 B
17842*	EBISCO	DW2553	21°03'S, 158°36'E, 352-370m	<i>Cochlespira</i> Conrad, 1865	x	x	x		8 A
17843	EBISCO	DW2522	22°46'S, 159°21'E, 310-318m	<i>Funa</i> Kilburn, 1988	x	x	x	x	2, C A
17844	EBISCO	CP2645	20°58'S, 160°58'E, 641-652m	<i>Gymnobela</i> Verrill, 1884	x	x	x	x	10 B
17845	EBISCO	CP2651	21°29'S, 162°36'E, 883-957m	<i>Teretiopsis</i> Kantor and Sysoev, 1989	x	x	x	x	10 B
17846*	EBISCO	CP2600	19°38'S, 158°46'E, 603-630m	<i>Leucosyrinx</i> Dall, 1889	x	x	x	x	3, C A
17847*	EBISCO	DW2617	20°06'S, 160°22'E, 427-505m	<i>Splendrillia</i> Hedley, 1922	x	x	x	x	1, C A
17848	EBISCO	DW2625	20°05'S, 160°19'E, 627-741m	<i>Pleurotomella</i> Verrill, 1873	x	x	x	x	10 B
17849*	EBISCO	DW2619	20°06'S, 160°23'E, 490-550m	<i>cf. Gemmuloborsonia</i> Shuto, 1989	x	x	x	x	A
17850	EBISCO	DW2607	19°33'S, 158°40'E, 400-413m	<i>Turridrupa</i> Hedley, 1922	x	x	x	x	5 A
17851	EBISCO	DW2625	20°05'S, 160°19'E, 627-741m	<i>Inquisitor</i> Hedley, 1918	x	x	x	x	2, C A
17852	EBISCO	DW2625	20°05'S, 160°19'E, 627-741m	<i>Gemmula</i> Weinkauff, 1875	x	x	x	x	5 A
17853*	EBISCO	DW2629	21°06'S, 160°46'E, 569-583m	<i>Heteroturris</i> Powell, 1967	x	x	x	x	18 B
17855*	Norfolk 2	DW2155	22°52'S, 167°13'E, 453-455m	<i>Benthofascis</i> Iredale, 1936		x	x	x	B
17857	EBISCO	CP2551	21°06'S, 158°35'E, 637-650m	<i>Bathytoma</i> Harris and Burrows, 1891	x	x	x	x	20 B
17858	Panglao 2004	S12	9°29.4'N, 123°56.0'E, 6-8m	<i>Clavus</i> Monfort, 1810	x	x	x	x	1, C A
17859	Panglao 2004	S12	9°29.4'N, 123°56.0'E, 6-8m	<i>Turridrupa</i> Hedley, 1922	x	x	x	x	5 A
17860	Panglao 2004	R44	9°33.3'N, 123°43.9'E, 2m	<i>Lophiotoma</i> Casey, 1904	x	x	x	x	5 B
17861	Panglao 2004	B14	9°38.5'N, 123°49.2'E, 2-4m	<i>Kermia</i> Oliver, 1915	x	x	x	x	10 B
17862	Panglao 2004	T10	9°33.4'N, 123°49.6'E, 117-124m	<i>Gemmula</i> Weinkauff, 1875	x	x	x	x	5 A
17863	Panglao 2004	B16	9°37.6'N, 123°47.3'E, 20m	<i>Macteola</i> Hedley, 1918	x	x	x	x	11 B
17864	Panglao 2004	S18	9°35.7'N, 123°44.4'E, 0-2m	<i>cf. Guralaus</i> Hedley, 1918	x	x	x	x	11 B
17865	Panglao 2004	P2	9°39'N, 123°44'E, 400m	<i>Bathytoma</i> Harris and Burrows, 1891	x	x	x	x	20 B
17866*	Panglao 2004	S19	9°42.1'N, 123°51.4'E, 3-4m	<i>Mangelia</i> Risso, 1826	x	x	x	x	11 B
17867	Panglao 2004	B19	9°29.4'N, 123°56.0'E, 17m	<i>Borsonia</i> Bellardi, 1839	x	x	x	x	16 B
17868	Panglao 2004	B19	9°29.4'N, 123°56.0'E, 17m	<i>Anacithara</i> Hedley, 1922	x	x	x	x	7 A
17869	Panglao 2004	S21	9°41.7'N, 123°50.9'E, 4-12m	<i>Erema</i> Hedley, 1918	x	x	x	x	12 B
17870	Panglao 2004	S25	9°41.5'N, 123°51.0'E, 21m	<i>Otitoma</i> Jousseaume, 1898	x	x	x	x	2, C A
17871	Panglao 2004	S26	9°41.5'N, 123°51.0'E, 21m	<i>Kermia</i> Oliver, 1915	x	x	x	x	10 B



17872	Panglao 2004	S26	9°41.5'N, 123°51.0'E, 21m	<i>Macteola</i> Hedley, 1918	x	x	x	x	11	B
17873	Panglao 2004	T26	9°43.3'N, 123°48.8'E, 123-135m	<i>Guraleus</i> Hedley, 1918	x	x	x	x	11	B
17874	Panglao 2004	T26	9°43.3'N, 123°48.8'E, 123-135m	<i>Guraleus</i> Hedley, 1918	x	x	x	x	11	B
17875*	Panglao 2004	T26	9°43.3'N, 123°48.8'E, 123-135m	<i>Tomopleura</i> Casey, 1924	x	x	x	x	14	B
17876	Panglao 2004	B21	9°37.2'N, 123°46.4'E, 20-21m	<i>Lienardia</i> Jousseaume, 1928	x	x	x	x	12	B
17877*	Panglao 2004	B21	9°37.2'N, 123°46.4'E, 20-21m	<i>Mitromorpha</i> Carpenter, 1865	x	x	x	x	13	B
17878	Panglao 2004	B25	9°29.4'N, 123°56.1'E, 16m	<i>Kermia</i> Oliver, 1915	x	x	x	x	10	B
17879	Panglao 2004	T32	9°36.4'N, 123°53.8'E, 60-62m	<i>Inquisitor</i> Hedley, 1918	x	x	x	x	2, C	A
17880	Panglao 2004	L46	9°30.9'N, 123°41.2'E, 90-110m	<i>Kermia</i> Oliver, 1915	x	x	x	x	10	B
17881	Panglao 2004	L46	9°30.9'N, 123°41.2'E, 90-110m	<i>Daphnella</i> Hinds, 1844	x	x	x	x	10	B
17882*	Panglao 2004	L46	9°30.9'N, 123°41.2'E, 90-110m	<i>Raphitoma</i> Bellardi, 1848	x	x	x	x	10	B
17883	Panglao 2004	L46	9°30.9'N, 123°41.2'E, 90-110m	<i>Veprecula</i> Melvill, 1917	x	x	x	x	10	B
17884	Panglao 2004	L46	9°30.9'N, 123°41.2'E, 90-110m	<i>Leiocithara</i> Hedley, 1922	x	x	x	x	11	B
17885	Panglao 2004	T36	9°29.3'N, 123°51.5'E, 95-128m	<i>Ceritoturris</i> Dall, 1924	x	x	x	x	7 A	
17886	Panglao 2004	T36	9°29.3'N, 123°51.5'E, 95-128m	<i>Splendrillia</i> Hedley, 1922	x	x	x	x	1, C	A
17887	Panglao 2004	T36	9°29.3'N, 123°51.5'E, 95-128m	<i>Microdrillia</i> Casey, 1903	x	x	x	x	18	B
17888	Panglao 2004	T36	9°29.3'N, 123°51.5'E, 95-128m	<i>Ceritoturris</i> Dall, 1924	x	x	x	x	7 A	
17889	Panglao 2004	T41	9°29.7'N, 123°50.2'E, 110-112m	<i>Conopleura</i> Hinds, 1844	x	x	x	x	1, C	A
17890	Panglao 2004	L49	9°36.5'N, 123°45.3'E, 90m	<i>Raphitoma</i> Bellardi, 1848	x	x	x	x	10	B
17891	Panglao 2004	T39	9°30.1'N, 123°50.4'E, 100-138m	<i>cf. Tritonoturris</i> Dall, 1924	x	x	x	x	10	B
17892	Panglao 2004	T39	9°30.1'N, 123°50.4'E, 100-138m	<i>cf. Glyphostomoides</i> Shuto, 1983	x	x	x	x	10	B
17893	Panglao 2004	T41	9°29.7'N, 123°50.2'E, 110-112m	<i>cf. Mitromorpha</i> Carpenter, 1865	x	x	x	x	13	B
17894	Panglao 2004	B7	9°35.9'N, 123°51.8'E, 4-30m	<i>Lienardia</i> Jousseaume, 1928	x	x	x	x	12	B
17895	Panglao 2004	D5	9°33.6'N, 123°43.5'E, 0-3m	<i>Inquisitor</i> Hedley, 1918	x	x	x	x	2, C	A
17896	Panglao 2004	D5	9°33.6'N, 123°43.5'E, 0-3m	<i>Eucithara</i> Fischer, 1883	x	x	x	x	11	B
17897*	Panglao 2004	B8	9°37.1'N, 123°46.1'E, 3m	<i>Lienardia</i> Jousseaume, 1928	x	x	x	x	12	B
17898	Panglao 2004	B8	9°37.1'N, 123°46.1'E, 3m	<i>Mitromorpha</i> Carpenter, 1865	x	x	x	x	13	B
17899	Panglao 2004	B8	9°37.1'N, 123°46.1'E, 3m	<i>Eucithara</i> Fischer, 1883	x	x	x	x	11	B
17900	Panglao 2004	B8	9°37.1'N, 123°46.1'E, 3m	<i>Eucithara</i> Fischer, 1883	x	x	x	x	11	B
17901	Panglao 2004	S5	9°37.1'N, 123°46.1'E, 2-4m	<i>Anarithma</i> Iredale, 1916	x	x	x	x	13	B
17902	Panglao 2004	S6	9°38.5'N, 123°49.2'E, 1-4m	<i>Clavus</i> Monfort, 1810	x	x	x	x	1, C	A
17903	Panglao 2004	S12	9°29.4'N, 123°56.0'E, 6-8m	<i>Eucyclotoma</i> Boettger, 1895	x	x	x	x	10	B
17904	Panglao 2004	T9	9°33.5'N, 123°49.5'E, 97-120m	<i>cf. Nannodiella</i> Dall, 1919	x	x	x	x	12	B
17905	Panglao 2005	CP2348	9°29.6'N, 123°52.5'E, 196-216m	<i>Otitoma</i> Jousseaume, 1898	x	x	x	x	2, C	A
17906	Panglao 2005	CP2349	9°31.6'N, 123°55.7'E, 219-240m	<i>Prychobela</i> Thiele, 1925	x	x	x	x	2, C	A
17907	Panglao 2005	CP2349	9°31.6'N, 123°55.7'E, 219-240m	<i>Gemmula</i> Weinkauff, 1875	x	x	x	x	5	A
17908	Panglao 2005	CP2332	9°38.8'N, 123°45.9'E, 396-418m	<i>Iwaoa</i> Kuroda, 1953	x	x	x	x	7	A
17909	Panglao 2005	CP2343	9°27.4'N, 123°49.4'E, 273-356m	<i>Cinguloterebra cf. fujitai</i> Kuroda and Habe, 1952	x	x	x	x	6	A
17910	Panglao 2005	CP2349	9°31.6'N, 123°55.7'E, 219-240m	<i>Tomopleura</i> Casey, 1924	x	x	x	x	14	B
17911	Panglao 2005	CP2333	9°38.2'N, 123°43.5'E, 584-596m	<i>cf. Heteroturris</i> Powell, 1967	x	x	x	x	18	B
17912	Panglao 2005	CP2377	8°40.6'N, 123°20.3'E, 85-88m	<i>Conus praecellens</i> Adams, 1854	x	x	x	x	19	B
17913*	Panglao 2005	CP2377	8°40.6'N, 123°20.3'E, 85-88m	<i>Conus sulcatus</i> Hwass in Bruguière, 1792	x	x	x	x	19	B
17914	Panglao 2005	CP2380	8°41.3'N, 123°17.8'E, 150-163m	<i>Conus sulcatus</i> Hwass in Bruguière, 1792	x	x	x	x	21	B
17915	Panglao 2005	CP2381	8°43.3'N, 123°19.0'E, 259-280m	<i>Toxicochlespira</i> Sysoev and Kantor, 1990	x	x	x	x	17	B
17916*	Panglao 2005	CP2385	8°51.0'N, 123°10.0'E, 982-989m	<i>Comitas</i> Finlay, 1926	x	x	x	x	4, C	A
17917	Panglao 2005	CP2393	9°30.1'N, 123°41.6'E, 356-396m	<i>Terebra polygirata</i> Deshayes, 1859	x	x	x	x	6	A
17918	Panglao 2005	CP2388	9°26.9'N, 123°34.5'E, 762-786m	<i>Comitas</i> Finlay, 1926	x	x	x	x	4, C	A
17919	Panglao 2005	CP2340	9°29.4'N, 123°44.4'E, 271-318m	<i>Cochlespira</i> Conrad, 1865	x	x	x		8	A
17920	Panglao 2005	CP2340	9°29.4'N, 123°44.4'E, 271-318m	<i>Cochlespira</i> Conrad, 1865	x	x	x		8	A
17921*	Panglao 2005	CP2340	9°29.4'N, 123°44.4'E, 271-318m	<i>Conus orbigny</i> Kilburn, 1975	x	x	x	x	21	B

17922	Panglao 2005	DW2400	9°32.5'N, 123°41.8'E, 111-115m	<i>Conus wakayamaensis</i> Kuroda, 1956	x	x	x	x	21	B
17923	Panglao 2005	CP2395	9°36.2'N, 123°43.8'E, 382-434m	<i>Cinguloterebra cf. fenestrata</i> Hinds, 1844	x	x	x	x	6	A
17924	Salomon 2	CP2184	8°16,9' S, 159°59,7' E, 464-523m	<i>Thatcheria</i> Angas, 1877	x	x	x	x	10	B
17925	Salomon 2	CP2227	6°37,2' S, 156°12,7' E, 508-522m	<i>Toxicochlespira</i> Sysoev and Kantor, 1990	x	x	x	x	17	B
17926*	Salomon 2	CP2269	7°45,1' S, 156°56,3' E, 768-890m	<i>Borsonia</i> Bellardi, 1839	x	x	x	x	15	B
17927	Salomon 2	CP2260	8°03,5' S, 156°54,5' E, 399-427m	<i>Daphnella</i> Hinds, 1844	x	x	x	x	10	B
17928	Salomon 2	CP2216	7°45,3' S, 157°39,4' E, 930-977m	<i>Comitas</i> Finlay, 1926	x	x	x	x	3, C	A
17929	Salomon 2	CP2186	8°17,0' S, 160°00,0' E, 487-541m	<i>Bathytoma</i> Harris and Burrows, 1891	x	x	x	x	20	B
17930	Salomon 2	CP2269	7°45,1' S, 156°56,3' E, 768-890m	<i>Benthomangelia</i> Thiele, 1925	x	x	x	x	17	B
17931	Salomon 2	CP2269	7°45,1' S, 156°56,3' E, 768-890m	<i>cf. Typhlomangelia</i> Sars, 1878	x	x	x	x	18	B
17932	Salomon 2	CP2197	8°24,4' S, 159°22,5' E, 897-1057m	<i>Borsonia</i> Bellardi, 1839	x	x	x	x	15	B
17933	Salomon 2	CP2228	6°34,7' S, 156°10,5' E, 609-625m	<i>Comitas</i> Finlay, 1926	x	x	x	x	3, C	A
17934	Salomon 2	CP2176	9°09,4' S, 158°59,2' E, 600-875m	<i>Borsonia</i> Bellardi, 1839	x	x	x	x	16	B
17935	Salomon 2	CP2187	8°17,5' S, 159°59,8' E, 482-604m	<i>Inquisitor</i> Hedley, 1918	x	x	x	x	2, C	A
17936	Santo 2006	LD28	15°35,4'S, 166°58,7'E, 3-8m	<i>Conus generalis</i> Linne, 1758	x	x	x	x	19	B
17937	Santo 2006	NR52	15°35,6S, 167°01,9E, 15m	<i>Conus gauquini</i> Richard and Salvat, 1973	x	x	x	x	19	B
17938*	Santo 2006	LD28	15°35,4'S, 166°58,7'E, 3-8m	<i>Terebra textilis</i> Hinds, 1844	x	x	x	x	6	A
17939	Santo 2006	AT87	15°32,1'S, 167°16,1'E, 235-271m	<i>Conus consors</i> Sowerby, 1833	x	x	x	x	19	B
17854	Norfolk 2	DW2034	23°41'S, 167°41'E, 485-505m	<i>Nassaria</i> , Buccinidae	x	x	x	x		
17856	Norfolk 2	DW2081	25°54'S, 168°22'E, 500-505m	<i>Cancellopolia</i> , Buccinidae	x	x	x	x		
GenBank				<i>Littorina</i> , Littorinidae	x	x	x	x		

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Identification number (ID) corresponding to MNHN catalogue number, cruise and station of collection, with the coordinates and the depth, are given for each specimen. Specimens are identified at genus level, except *Conus* and Terebridae which are identified at species level. A cross indicates that the specimen was successfully sequenced for the gene. Allocation to clades A, B, C and 1–22, as defined by the molecular analysis, is given for each taxon. <sup>a</sup> This specimen has been chosen to illustrate the clade to which it belongs in Fig. 1.

632 Table 3: Models of evolution and parameters estimated using AIC implemented in Modeltest  
 633 for each gene separately and each combined dataset.

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635 Dataset	636 Model	637 Base frequencies	638 Substitution rates	639 I	640 G
637 COI	638 GTR+I+G	639 $\pi_A = 0.1922$ 640 $\pi_C = 0.245$ 641 $\pi_G = 0.2215$ 642 $\pi_T = 0.3413$	643 $r(A-C) = 0.8578$ 644 $r(A-G) = 5.3343$ 645 $r(A-T) = 0.3918$ 646 $r(C-G) = 0.9449$ 647 $r(C-T) = 35.0926$	648 0.6915	649 0.6794
641 28S	642 GTR+I+G	643 $\pi_A = 0.1563$ 644 $\pi_C = 0.3383$ 645 $\pi_G = 0.3502$ 646 $\pi_T = 0.1551$	647 $r(A-C) = 0.7256$ 648 $r(A-G) = 1.8046$ 649 $r(A-T) = 1.5931$ 650 $r(C-G) = 0.4122$ 651 $r(C-T) = 7.8933$	652 0.5957	653 0.6338
645 18S	646 TrNef+I+G		647 $r(A-C) = 1$ 648 $r(A-G) = 3.0918$ 649 $r(A-T) = 1$ 650 $r(C-G) = 1$ 651 $r(C-T) = 9.2099$	652 0.8620	653 0.5928
649 H3	650 GTR+I+G	651 $\pi_A = 0.2063$ 652 $\pi_C = 0.3261$ 653 $\pi_G = 0.3113$ 654 $\pi_T = 0.1563$	655 $r(A-C) = 1.4455$ 656 $r(A-G) = 3.2261$ 657 $r(A-T) = 2.663$ 658 $r(C-G) = 0.9033$ 659 $r(C-T) = 8.6701$	660 0.6233	661 0.9671
653 CD1	654 GTR+I+G	655 $\pi_A = 0.2154$ 656 $\pi_C = 0.2761$ 657 $\pi_G = 0.2803$ 658 $\pi_T = 0.2282$	659 $r(A-C) = 1$ 660 $r(A-G) = 2.8258$ 661 $r(A-T) = 1$ 662 $r(C-G) = 1$ 663 $r(C-T) = 10.8424$	664 0.7230	665 0.4565
657 CD2	658 GTR+I+G	659 $\pi_A = 0.2062$ 660 $\pi_C = 0.2772$ 661 $\pi_G = 0.2874$ 662 $\pi_T = 0.2292$	663 $r(A-C) = 1.3887$ 664 $r(A-G) = 3.1175$ 665 $r(A-T) = 1.1091$ 666 $r(C-G) = 0.986$ 667 $r(C-T) = 11.5743$	668 0.7192	669 0.4490

661

662 Proportion of invariable sites; G, gamma rate distribution; CD, combined dataset.

663 Table 4: Node supports of ML, MP and BA analyses for the four genes separately and for the  
 664 two combined datasets.  
 665

	COI			28S			18S			H3			CD1			CD2		
	ML	MP	BA	ML	MP	BA	ML	MP	BA	ML	MP	BA	ML	MP	BA	ML	MP	BA
Conoidea							35		0.94				85	71	0.98	79	65	1
Clade A	1						13			6		0.6	85	70	0.88	68	58	0.73
Clade B						1							53	33	0.52	52	28	1
Clade C				34	30	0.98				41	40		89	81	1	91	76	1
Clade 1				99	92	1	99		1	66	43	0.54	100	100	1	100	100	1
Clade 2	11	9					7	28	0.96			0.96	84	84	1	84	85	1
Clade 3	57	46		95	95	0.83			0.96	100	98	0.95	100	100	1	100	100	1
Clade 4	93	92	0.96	100	100	1			1	100	99	0.98	100	100	1	100	100	1
Clade 5	27	17	1	54	34	0.98				32	72	0.99	100	93	1	100	97	1
Clade 6	53	26	1	86	93	1	34	44	0.96	58	70	0.63	100	98	1	100	100	1
Clade 7		36	0.57	90	87	0.94				41	21	0.53	100	97	1	100	99	1
Clade 8	98	100	1	99	99	1	62	55	1							100	100	1
Clade 9	100	100	1	100	100	1		0		100	100	1	100	100	1	100	100	1
Clade 10				90	80	1					16		100	100	1	98	95	1
Clade 11				99	99	1				42	23	0.77	100	99	1	100	100	1
Clade 12				97	87	1	59	52	1	45	26	0.95	100	95	1	100	92	1
Clade 13	23	27	0.55	97	98	1	92	88	1	46	46		100	100	1	100	100	1
Clade 14	75	62	1	72	66	0.92				70	81	0.65	99	100	1	100	100	1
Clade 15	100	98	1	100	98	1	88	62	0.98	100	100	1	100	100	1	100	100	1
Clade 16	38	56		31						56	48	0.99	97	93	1	98	95	1
Clade 17		15		24	20		56	57	0.98	96	94	1	99	100	1	99	100	1
Clade 18	91	90	1		16					64	51	0.87	98	93	1	96	86	1
Clade 19				100	100	1	100	98	1	99	100	1	100	100	1	100	100	1
Clade 20				100	100	1				87	74	0.94	100	100	1	100	100	1
Clade 21	99	97	1	89	84	1				95	97	1	100	100	1	100	100	1
Clade 22	56	52	0.88															

666  
 667  
 668 Bootstraps values and Posterior Probabilities are given for 26 nodes (all Conoidea, clades A,  
 669 B, C and clades 1–22). CD, Combined dataset. Gray cells correspond to unavailable data  
 670 (sequences for specimens attributed to clade 8 were not obtained for H3 gene, and sequences  
 671 for those attributed to clade 22 were successfully sequenced only for COI gene).

672 Table 5: Genera included in the clades A, B, C and 1–22, and association to a taxonomic  
 673 name proposed in previous classifications (see Table 1).

674	Clade 1			
675	<i>Clavus</i>	<b>DRILLIIDAE</b>	}	<b>C</b>
676	<i>Conopleura</i>			
677	<i>Splendrillia</i>			
678	.....			
679	Clade 2			
680	<i>Crassispira</i>	<b>Crassispirinae</b>		
681	<i>Funa</i>			
682	<i>Inquisitor</i>			
683	<i>Otitoma</i>			
684	<i>Ptychobela</i>			
685	.....			
686	Clade 3 & 4			
687	<i>Comitas</i>			
688	Clade 3	<b>"Cochlespirinae"</b>		
689	<i>Leucosyrinx</i>			
690	.....			
691	Clade 5			
692	<i>Gemmula</i>	<b>Turrinae</b>	}	<b>A</b>
693	<i>Lophiotoma</i>			
694	<i>Turris</i>			
695	<i>Turridrupa</i>			
696	.....			
697	<i>Gemmuloborsonia</i>	<b>"Turrinae"</b>		
698	.....			
699	Clade 6			
700	<i>Cinguloterebra</i>	<b>TEREBRIDAE</b>		
701	<i>Terebra</i>			
702	.....			
703	Clade 7			
704	<i>Anacithara</i>			
705	<i>Ceritoturris</i>	<b>"Crassispirinae"</b>		
706	<i>Horaiclavus</i>			
707	<i>Iwaoa</i>			
708	.....			
709	Clade 8			
710	<i>Cochlespira</i>	<b>Cochlespirinae</b>		
711	.....			
712	Clade 9			
713	<i>Leucosyrinx</i>	<b>"Cochlespirinae"</b>		
714	.....			
715	Clade 10			
716	<i>Daphnella</i>			
717	<i>Eucyclotoma</i>	<i>Raphitoma</i>		
718	<i>Glyphostomoides</i>	<i>Rimosodaphnella</i>		
719	<i>Gymnobela</i>	<i>Teretiopsis</i>		
720	<i>Kermia</i>	<i>Thatcheria</i>		
721	<i>Pleurotomella</i>	<i>Tritonoturris</i>		
722	<i>Yeprecula</i>			
723	.....			
724	Clade 11			
725	<i>Eucithara</i>			
726	<i>Guraleus</i>			
727	<i>Leiocithara</i>	<b>Mangeliinae</b>		
728	<i>Macteola</i>			
729	<i>Mangelia</i>			
730	.....			
731	Clade 12			
732	<i>Lienardia</i>			
733	<i>Etrema</i>			
734	<i>Nannodiella</i>			
735	Clade 13			
736	<i>Mitromorpha</i>	<b>Clathurellinae</b>		
737	<i>Anarithma</i>			
738	Clade 14			
739	<i>Tomopleura</i>			
740	Clade 15 & 16			
741	<i>Borsonia</i>			
742	.....			
743	Clade 17			
744	<i>Benthomangelia</i>	<b>"Mangeliinae"</b>		
745	<i>Toxicochlespira</i>			
746	.....			
747	Clade 18			
748	<i>Heteroturris</i>			
749	<i>Microdrillia</i>	<b>Clathurellinae</b>		
750	<i>Typhlomangelia</i>			
751	.....			
752	<i>Benthofascis</i>	<b>Conorbinae</b>		
753	.....			
754	Clade 19			
755	<i>Comus</i>	<b>Coninae</b>		
756	.....			
757	Clade 20			
758	<i>Bathytoma</i>	<b>Clathurellinae</b>		
759	.....			
760	Clade 21			
761	<i>Comus</i>	<b>Coninae</b>		
762	.....			
763	Clade 22			
764	<i>Clavatula</i>	<b>CLAVATULIDAE</b>		
765	<i>Perrona</i>			
766	<i>Pusionella</i>			
767				<b>In TURRIDAE</b>
768				<b>or CLAVATULIDAE</b>

720 Subfamilies are in bold, families in bold and capital. Type genera present in our dataset are  
 721 underlined.

722 Fig. 1. Consensus tree of MP, ML and BA results obtained with CD2. Nodes presented here  
 723 were found with at least two of the three methods used. Top downwards, MP bootstraps, ML  
 724 bootstraps and Posterior Probabilities are specified for each node. Supports for intranodes of  
 725 clades 1–21 are not presented. Taxonomic names are attributed for each of the clades 1–21, as  
 726 explained in the text. One example of shell, corresponding to the type-genus when possible, is  
 727 given for each clade. Illustrated specimens are quoted in the Table 2.  
 728  
 729

