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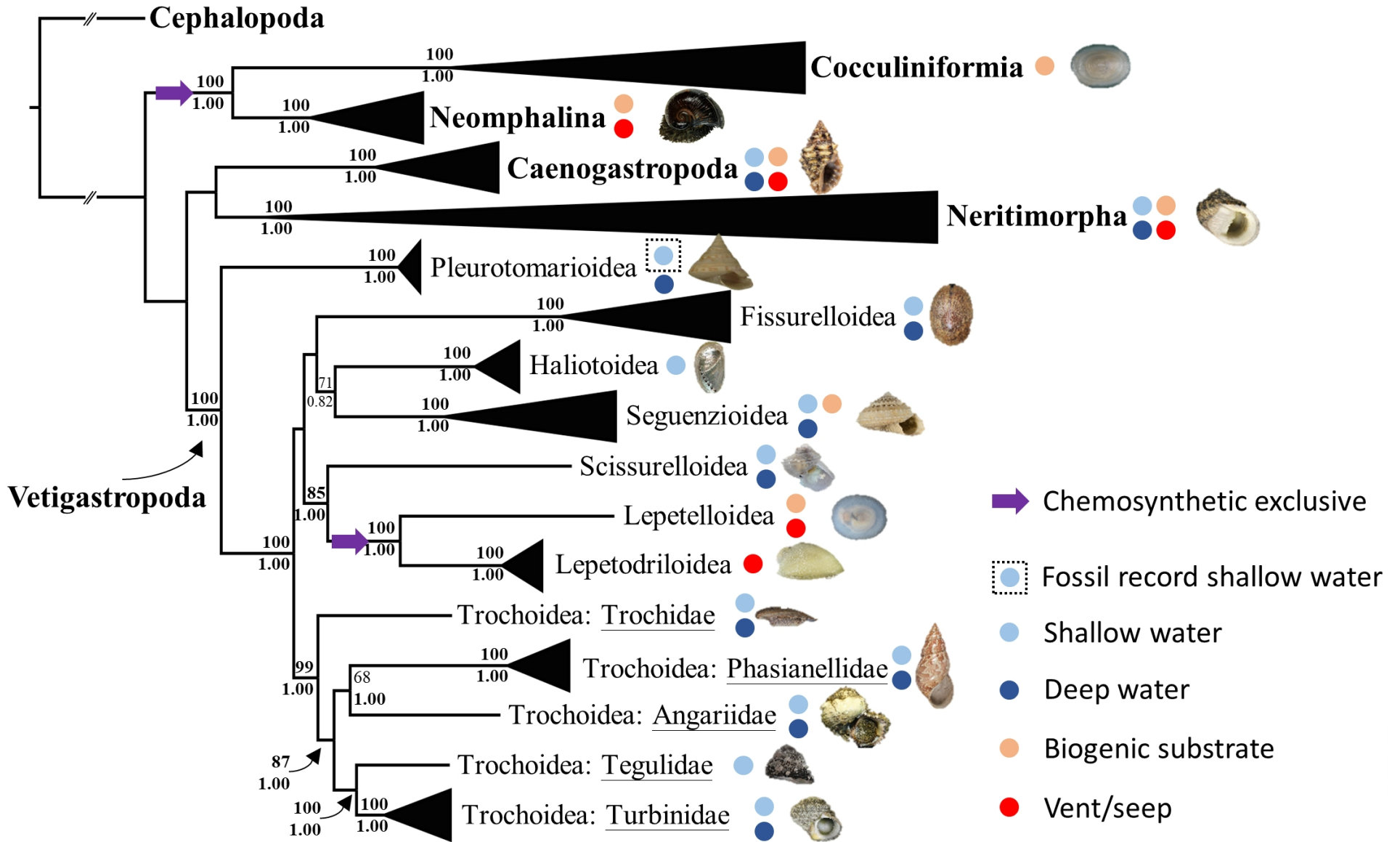
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1 **Incorporation of deep-sea and small-sized species provides new insights into**
2 **gastropods phylogeny**

3 Original Research Article

4

5 Hsin Lee^{a,b}, Wei-Jen Chen^{b*}, Nicolas Puillandre^a, Laetitia Aznar-Cormano^a, Mong-
6 Hsun Tsai^c, Sarah Samadi^a

7

8 *^a Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national*
9 *d'Histoire naturelle, CNRS, Sorbonne Université, EPHE CP 26, 57 rue Cuvier, 75005*
10 *Paris, France*

11 *^b Institute of Oceanography, National Taiwan University, No. 1, Sec. 4, Roosevelt*
12 *Road, Taipei 10617, Taiwan*

13 *^c Institute of Biotechnology, National Taiwan University, No. 1, Sec. 4, Roosevelt*
14 *Road, Taipei 10617, Taiwan*

15

16

17 *** Corresponding Author**

18 Wei-Jen Chen

19 Room 301, Institute of Oceanography, National Taiwan University, No.1 Sec. 4

20 Roosevelt Rd, Taipei 10617, Taiwan.

21 Phone number: +886 2 33661630

22 Fax number: +886 2 23637062

23 E-mail address: wjchen.actinops@gmail.com

24 **ABSTRACT**

25

26 The use of phylogeny with uneven or limited taxon sampling may bias our
27 interpretation of organismal evolution, for instance, the origin(s) of the deep-sea
28 animals. The Mollusca is the second most speciose phylum, in which the Gastropoda
29 forms the largest group. However, the currently proposed hypotheses of gastropod
30 phylogeny are mainly based on part of their taxonomic diversity, notable based on the
31 large-sized and shallow-water species. In this study, we aimed at correcting this bias
32 by reconstructing the phylogeny with new mitogenomes of deep-sea gastropods
33 including *Anatoma* sp., Bathysciadiidae sp., *Bayerotrochus teramachii*, *Calliotropis*
34 *micraulax*, *Cococrater* sp., *Cocculina subcompressa*, *Lepetodrilus guaymasensis*,
35 *Peltospira smaragdina*, *Perotrochus caledonicus*, Pseudococculinidae sp., and
36 *Shinkailepas briandi*. This dataset provided the first reports of the mitogenomes for
37 the Cocculiniformia, three vetigastropod superfamilies: Pleurotomarioidea,
38 Lepetelloidea, and Scissurelloidea, and the neritimorph family Phenacolepadidae. The
39 addition of deep-sea representatives also allowed us to evaluate the evolution of
40 habitat use in gastropods. Our results showed a strongly supported sister-group
41 relationship between the deep-sea lineages Cocculiniformia and Neomphalina. Within
42 the Vetigastropoda, the Pleurotomarioidea was revealed as the sister-group of the
43 remaining vetigastropods. Although this clade was presently restricted to the deep sea,
44 fossil records showed that it has only recently invaded this habitat, thus suggesting
45 that shallow waters was the ancestral habitat for the Vetigastropoda. The deep-sea
46 Lepetelloidea and Lepetodriolea formed a well-supported clade, with the
47 Scissurelloidea sister to it, suggesting an early transition from shallow water to deep
48 sea in this lineage. In addition, the switch between different chemosynthetic habitats

49 was also observed in deep-sea gastropod lineages, notably in Neomphalina and
50 Lepetelloidea. In both cases, the biogenic substrates appeared as the putative ancestral
51 habitat, confirming the previously proposed hypothesis of a wooden-step to deep-sea
52 vents scenario of evolution of habitat use for these taxa.

53

54 **Keywords.** Deep sea; Gastropoda; Phylogeny; Mitogenome; Next Generation
55 Sequencing; Chemosynthetic environment.

56

57 **1. Introduction**

58

59 The deep sea is the most extensive ecosystem on earth, but it is yet poorly
60 studied (Ramirez-Llodra et al., 2010). This vast area includes the water depths below
61 the light zone (> 200 meters). The deep-sea floor has long been thought to be infertile
62 (Anderson and Rice, 2006) and it is only with the great historical expeditions at the
63 end of the 19th century, notably the circumnavigations of the *Challenger*, that life was
64 shown to be present and diverse at every depths. In the late seventies, the unexpected
65 discovery of the hydrothermal vents revealed moreover a dense community of
66 organisms living in very unusual environmental conditions and displaying original
67 morphological and physiological traits (Tunnicliffe et al., 1998; Van Dover, 2000).
68 The complete exploration of deep-sea habitats is far from being achieved (Higgs and
69 Attrill, 2015) and other habitats such as seamounts, cold seeps or biogenic substrates
70 have been recently explored and revealed diversified communities (Distel et al., 2000;
71 Richer de Forges et al., 2000; Smith and Baco, 2003). Some animal lineages are
72 restricted – or more diverse – in the deep sea but this diversity is poorly represented in
73 the phylogenetic reconstruction of entire phyla, classes, orders or even families. The
74 question of the evolutionary origin(s) of deep-sea organisms is thus very poorly
75 documented.

76 The Mollusca is the second largest phylum in the animal kingdom, next to the
77 Arthropoda, and the largest marine phylum (Aktipis et al., 2008). Molluscan species
78 are found in all the marine environments, from shallow water to deep sea. The best-
79 known species assemblages are relatively large in size and from shallow waters.
80 However, these species represent only a small part of the diversity of marine mollusks
81 (Bouchet et al., 2002, 2016). Some molluscan families and genera are less known

82 because their members are tiny or they are difficult to be collected, with some groups
83 known exclusively from the bathyal or the hadal zones (Warén, 1991, 1996; Warén
84 and Bouchet, 1993, 2001, 2009). Massive collecting efforts, especially from the deep
85 sea, are required to assess the magnitude of species richness, the biogeography and the
86 phylogenetic relationships.

87 The Gastropoda is the largest class in the phylum Mollusca. This class comprises
88 seven main groups: Caenogastropoda, Cocculiniformia, Heterobranchia,
89 Neomphalina, Neritimorpha, Patellogastropoda, and Vetigastropoda. While each
90 group contains deep-sea lineages, the members of Cocculiniformia and Neomphalina
91 are mostly found in deep-sea habitats (Marshall, 1985; McLean, 1992; Warén and
92 Bouchet, 1993; McLean and Harasewych, 1995; Warén, 1996; Leal and Harasewych,
93 1999; Warén and Bouchet, 2001; Kiel and Goedert, 2006; Heß et al., 2008; Sasaki et
94 al., 2010; Warén, 2011). The Vetigastropoda (including abalones, slit snails, true
95 limpets, keyhole limpets, seguenzid snails and turban snails) is the most diverse group
96 with approximately 3,700 described living species occurring in a wide range of
97 marine habitats from all oceans (Aktipis et al., 2008), yet it has not been exclusively
98 studied. Among the eight superfamilies (Fissurelloidea, Haliotoidea, Lepetelloidea,
99 Lepetodriloidea, Pleurotomarioidea, Scissurelloidea, Seguenzioidea, and Trochoidea)
100 and the currently recognized 37 families (Bouchet et al., 2017), several are
101 exclusively found in the deep sea (e.g., Lepetodriloidea and Seguenziidae). The
102 Neritimorpha is supposedly a relic lineage of an early radiation with a morphological
103 and ecological diversity equivalent to that achieved by all the other gastropods
104 (Lindberg, 2008)

105 During the last decade many studies exploring the phylogenetic relationships
106 within the Gastropoda were based on Next Generation Sequencing (NGS) techniques

107 to improve the accuracy for the inference by increasing the character sampling
108 (Williams et al., 2014; Zapata et al., 2014; Osca et al., 2015; Lee et al., 2016; Uribe et
109 al., 2016a, 2016b, 2017; Wort et al., 2017). Noteworthy, Zapata et al. (2014) re-
110 evaluated the phylogenetic relationships among the five main gastropod clades
111 (Vetigastropoda, Caenogastropoda, Heterobranchia, Neritimorpha, and
112 Patellogastropoda) by analyzing a 56-taxon matrix comprising forty new
113 transcriptomes, completed by publicly available data. This study confirmed the
114 Apogastropoda clade (Caenogastropoda + Heterobranchia) and rejected the
115 monophyletic Orthogastropoda (including all major main groups except
116 Patellogastropoda). In this latter study, Cocculiniformia and Neomphalina were
117 lacking and the rooting of the reconstructed tree remained under debate. In Aktipis
118 and Giribet (2012), the authors re-examined the phylogenetic relationships within the
119 Vetigastropoda based on a multi-gene dataset (five genes) and a dense taxonomic
120 sampling, which included 69 terminal taxa of the Vetigastropoda, covering all the
121 vetigastropod superfamilies and 22 out of the 37 vetigastropod families (Bouchet et
122 al., 2017). The authors of this study suggested excluding the Pleurotomarioidea and
123 the deep-sea vetigastropod lineage Lepetelloidea from the Vetigastropoda *sensu*
124 *stricto*. However, the relationships were not robustly resolved in this and other
125 previous studies; further investigations are required. Similarly, Uribe et al (2016b)
126 examined the relationships within the Neritimorpha based on mitogenomic
127 information, but here again deep-sea lineages were lacking.

128 Overall, recent molecular studies investigating gastropod phylogeny and/or
129 specific lineages such those within the Vetigastropoda focused more on the shallow
130 water species (e.g. Zapata et al., 2014; Lee et al., 2016; Uribe et al., 2016a; Uribe et
131 al., 2016b) and used often only a few number of genetic markers (e.g., in Aktipis and

132 Giribet, 2012). Deep-sea representatives were indeed only occasionally included and
133 generally restricted to a few species or specimens (Colgan et al., 2003; Geiger and
134 Thacker, 2005; Lee et al., 2016; Osca et al., 2015; Smith et al., 2011; Uribe et al.,
135 2016a, 2017; Zapata et al., 2014). Such a bias in the taxonomic or character sampling
136 may strongly distort our understanding of the causes of the observed pattern of
137 diversity and thus of the evolution of the Gastropoda. For instance, although some
138 phylogenetic studies included many (>20) deep-sea taxa, they generally suffered from
139 a lack of resolution on deep nodes (e.g. Kano, 2008; Aktipis and Giribet, 2012;
140 Geiger, 2012).

141 In this study we reexamined the evolutionary relationships of the Gastropoda
142 based on a dataset enriched with deep-sea gastropods from the Vetigastropoda
143 (notably from Lepetelloidea, Scissurelloidea and Pleurotomarioidea),
144 Cocculiniformia, Neomphalina and Neritimorpha. These taxa are rare and difficult to
145 collect, making them the least-studied groups of gastropods. We focused on
146 mitogenomic data that have been successfully used for resolving deep phylogenies of
147 several gastropod groups (Grande et al., 2008; Cunha et al., 2009; Allcock et al.,
148 2011; Medina et al., 2011; White et al., 2011; Kocot et al., 2013; Williams et al.,
149 2014; Osca et al., 2015; Lee et al., 2016; Uribe et al., 2016a, 2016b, 2017; Wort et al.,
150 2017) to investigate the phylogenetic relationships among deep- and shallow-water
151 gastropods. In addition, the data from three independent nuclear gene markers, *18S*
152 *rRNA* (*18S*), *28S rRNA* (*28S*), and *Histone 3* (*H3*), were also used as additional data
153 for the phylogenetic hypothesis evaluation.

154

155 **2. Material and methods**

156 *2.1 Genomic DNA extraction*

157 The eleven specimens used to reconstruct mitogenomes in this study were listed
158 in Table 1. The specimens were mainly collected during the biodiversity expeditions
159 under the *Tropical Deep-Sea Benthos* program and the cooperation project between
160 Taiwan and France, TFDeepEvo (Table 1).

Table

161 For most of the specimens, the genomic DNA was extracted using DNeasy
162 Blood and Tissue Kit (Qiagen, Hilden, Germany) or *NucleoSpin 96 Tissue* kit
163 microkit with the Eppendorf automated pipetting systems epMotion 5075 (Macherey-
164 Nagel, France) following the manufacturer's protocols. For the smaller specimens
165 (*Anatoma* sp. and Bathysciadiidae sp.), the genomic DNA was extracted using
166 QIAamp DNA Micro-Kit (Qiagen, Hilden, Germany) to ensure sufficient quantity for
167 subsequent molecular work. For *Bayerotrochus teramachii*, genomic DNA was
168 extracted using a phenol-chloroform extraction method as described in Lee et al.
169 (2016).

170

171 2.2 Mitogenome reconstruction

172 To reconstruct the mitogenome of *Bayerotrochus teramachii*, the long-range
173 PCR and primer-walking Sanger sequencing were used to obtain its whole
174 mitogenomic sequence by following the protocol described in Lee et al. (2016).

175 Seven gastropod mitogenomes were reconstructed by using whole genome
176 shotgun sequencing approach with NGS on Illumina platform (Table 1). The library
177 construction and the procedure for shotgun sequencing on Illumina platform followed
178 those described in Lee et al. (2016). The quality of the reads was checked using the
179 program FastQC v. 0.10.1 (Andrews, 2010). Low quality reads were trimmed
180 according to the Phred quality score (< 20) using the program Trimmomatic v.0.33
181 (Bolger et al., 2014). The raw data were deposited in the NCBI SRA (Sequence Read

182 Archive) database (accession number: PRJNA516567). The methods of the post-
183 sequencing assemblages of the mitogenomes followed also those described in Lee et
184 al. (2016).

185 Three other gastropod mitogenomes were reconstructed by using whole genome
186 shotgun sequencing approach with NGS on Ion Torrent platform (Table 1). Ion
187 Torrent libraries were constructed for three other specimens by using NEB next
188 Library preparation kit (New England Biolabs, MA, USA) for Ion Torrent. Template
189 preparation of these libraries was performed by emulsion PCR on an Ion OneTouch
190 robotic system, and the subsequent sequencing was performed by an Ion Torrent PGM
191 sequencer using Hi-Q chemistry (Life technologies, France). The quality of the reads
192 was checked by default program implemented in the sequencing analyzer and the
193 passed reads were exported for post-sequencing assemblages.

194 The assemblage of mitochondrial sequence reads exported from Ion Torrent
195 analyzer was performed using Geneious R9 assembler, in *de novo* mode with default
196 settings (Biomatters Ltd., Auckland, New Zealand). Contigs with matching ends
197 where circularized. To map their mitochondrial genes, individual gene sequences
198 from the reference genomes of *Nerita melanotragus* (Castro and Colgan, 2010),
199 *Bayerotrochus teramachii* (this study), and *Cocculina subcompressa* (this study) were
200 used. Bait mapping was performed as follows: twenty-five iterations with assembly
201 sensitivity set to ‘med-low’ (and max mismatch percentage ranging 15-20%), without
202 any postulate on the gene order. Individual contigs were compared and aligned to
203 generate larger contigs.

204

205 *2.3 Mitochondrial gene annotation*

206 The DNA sequences of each reconstructed mitogenome were edited with
207 sequence assembly and alignment software CodonCode Aligner v. 6.0.2 (Codoncode
208 Corporation, Dedham, MA, USA) and Se-Align v. 2.0 (Rambaut, 1996). Gene annotation
209 was carried out using MITOS Webserver (Bernt et al., 2013) with the invertebrate
210 genetic codes for protein coding genes and default settings. Gene boundaries were
211 further determined by eye using the mitogenome of *Lunella granulata* as the reference
212 (Lee et al., 2016).

213

214 *2.4 Nuclear gene assemblages*

215 Three nuclear genes, *18S*, *28S*, and *H3*, were also mapped and assembled from
216 the read-pools of each NGS sample using Geneious R9 (Biomatters Ltd., Auckland,
217 New Zealand). The reference sequences for baiting and mapping were published
218 sequences from species of the same family or superfamily as the target sample.
219 Reference sequences were selected from the dataset of Aktipis and Giribet (2012) and
220 retrieved from Genbank. Mapping was performed with twenty-five iterations with
221 assembly sensitivity set to ‘med-low’, and max mismatch percentage 15%.

222

223 *2.5 Phylogenetic inference*

224 *2.5.1 Datasets*

225 A master dataset (hereafter called ‘large mt dataset’) was first compiled from the
226 11 newly reconstructed gastropod mitogenomes together with 43 molluscan
227 mitogenomes retrieved from Genbank (Table 1; Supplementary table S1). The
228 samples included 28 vetigastropods, 20 other gastropod taxa from Neritimorpha,
229 Patellogastropoda, Heterobranchia, Caenogastropoda, and Neomphalina, and 6 out-
230 group taxa from 4 different molluscan classes, Polyplacophora, Scaphopoda,

231 Octopoda, and Bivalvia. The polyplacophoran *Katharina tunicata* was used as the
232 distant out-group to root the inferred tree.

233 From this master dataset, we further compiled another mitogenomic dataset
234 (called hereafter ‘small mt dataset’). The data included all gastropod mitogenomes
235 except some long-branch taxa that have been identified in the analysis with the ‘large
236 mt dataset’ and in several previous studies (Grande et al., 2008; Williams et al., 2014;
237 Uribe et al., 2016a). This 46 taxa data matrix was herein used to infer the phylogeny.
238 *Octopus vulgaris* (cephalopod) and *Graptacme eborea* (scaphopod) were chosen as
239 distant out-groups to root the inferred tree.

240 A nuclear dataset was also compiled for the three targeted nuclear gene markers
241 (*18S*, *28S*, and *H3*). Using both the sequences from this study and previously
242 published sequences, we compiled data for 45 species (Aktipis and Giribet, 2012)
243 (Supplementary table S2).

244 Finally, a combined dataset of the mitochondrial sequences (from the small mt
245 dataset) and the nuclear sequences was compiled by selecting the representative taxa
246 from each superfamily or family which were from the same genus or family in both
247 mitogenomic and nuclear gene datasets. The resulting dataset included 32 taxa
248 (Supplementary table S3).

249

250 2.5.2 Sequence alignment and phylogenetic analysis

251 Sequences for each gene in the four compiled datasets were first aligned using
252 the automatic multiple-alignment program MUSCLE (Edgar, 2004) and then adjusted
253 by eye. For protein-coding genes we translated the nucleotide sequences to amino
254 acids before aligning the sequences in order to avoid erroneous creation of gaps that
255 would lead to shifts in the open reading frame. Each gene block was modified using

256 Gblocks v. 0.91b (Castresana, 2000) to remove the ambiguous alignments gene-by-
257 gene, with default settings except that gap positions within the final blocks were
258 allowed. To reduce the impact of homoplasy at the third codon position sites on
259 phylogenetic inferences, RY-coding strategy was used by recoding “A” and “G” into
260 “R”, and “C” and “T” into “Y” at the third codon positions (Chen and Mayden, 2009)
261 for each protein-coding gene. The final alignments respectively consisted of 10,393
262 bp for the large mt dataset, 11,129 bp nucleotides for the small mt dataset, 3,313 bp
263 nucleotides for the nuclear dataset, and 14,442 bp nucleotides for the combined
264 dataset. Four partitions (three partitions for each codon position for mitochondrial
265 protein-coding genes and one partition for the *12S* plus *16S* rRNA genes) were set for
266 large mt dataset and small mt datasets. Five partitions were set for nuclear dataset (by
267 gene and by codon position). Finally, nine partitions were set for combined dataset
268 (Supplementary table S4).

269 Phylogenetic analyses were performed using both partitioned maximum
270 likelihood method (ML) and Bayesian inference (BI). ML was conducted by using the
271 RAxML v. 8.0 (Stamatakis, 2014) with the *GTR+G+I* model. Nodal support was
272 assessed by bootstrapping (Felsenstein, 1985) with 1,000 pseudo-replicates. BI was
273 performed with MrBayes V. 3.2.6 (Ronquist et al., 2012) on the CIPRES Science
274 Gateway (Miller et al., 2010) with best-fit nucleotide substitution models suggested
275 by model test implemented in PartitionFinder (Lanfear et al., 2012) (Supplementary
276 table S4). Four Markov chains were performed in each of two parallel runs for
277 30,000,000 generations for the large mt dataset, small mt dataset, and nuclear dataset,
278 and 60,000,000 generations for the combined dataset, with a sampling frequency of
279 one tree every one thousand generations. The default setting from MrBayes of the
280 burn-in value (0.25) was used. The convergence of the likelihood scores for

281 parameters was evaluated using Tracer v. 1.6 (Rambaut et al., 2014) to make sure that
282 all the ESS values were over 200.

283

284 **3. Results**

285 *3.1 Reconstructed mitogenomes and nuclear genes*

286 The size of the nearly complete mitogenome of *Bayerotrochus teramachii*,
287 reconstructed by the primer walking and Sanger Sequencing was 13,474 bp (Table 2).

Table

288 It contained 12 protein-coding genes, 2 rRNAs, and 11 tRNAs. Although we
289 assembled a final contig showing overlapping sequences from the two ends of the
290 circular genome, several genes were missing (*trnY*, *trnC*, *trnW*, *trnQ*, *trnG*, *trnE*,
291 *cox3*, *trnK*, *trnA*, *trnR*, *trnN*, *trnI* and part of *12S rRNA*). These genes are commonly
292 found next to each together (e.g. in Grande et al., 2008; Cunha et al., 2009; Stöger and
293 Schrödl, 2013; Schrödl and Stöger, 2014; Williams et al., 2014; Lee et al., 2016;
294 Uribe et al., 2016a, 2016b, 2017) and we thus suspected that a hairpin of
295 mitochondrial fragment occurred during the PCR leading to skip the twisted part
296 during the elongation.

297 Ten other new mitogenomes, yet not fully complete, were reconstructed using
298 the shotgun sequencing approach described in Lee et al (2016). After the assembly,
299 the depths of the contigs were mostly over 25x. The amino acid sequences of each
300 contig were further examined by comparing with the reference sequences to avoid the
301 possibility of shifts in reading frames, especially for those having lower coverage.
302 Finally, for the undetermined regions, Ns were used to replace the uncertain positions.
303 We assembled each read pool into a single contig for *Anatoma* sp., *Cocculina*
304 *subcompressa*, *Peltospira smaragdina*, Bathysciadiidae sp., *Shinkailepas briandi*, and
305 *Calliotropis micraulax*. For *Perotrochus caledonicus* we assembled four non-

306 overlapped contigs containing the mitochondrial sequences from two long segments,
307 and from two short fragments with *nd2* and *nd3*, respectively. For *Coccocrater* sp. we
308 were able to assemble three contigs. From both read pools of *Lepetodrilus*
309 *guaymasensis* and Pseudococculinidae sp., we assembled two non-overlapping final
310 contigs. Finally, for *Peltospira smaragdina*, the final contig we assembled showed
311 overlapping sequences from the two ends of the circular genome and a full set of
312 animal mitochondrial genes.

313 The evolution of animal mitogenomes in terms of gene content is generally
314 conservative. A typical animal mitogenome contains 13 protein-coding genes, 2
315 ribosomal RNAs, and 22 transfer RNAs; this gene content was observed in most of
316 our reconstructed mitogenomes with a few exceptions. In the mitogenome of
317 *Cocculina subcompressa*, a duplicate *trnD* was found. The *trnM* and *trnY* could not be
318 detected in the reconstructed mitogenome of Bathysciadiidae sp. In the reconstructed
319 mitogenome of Pseudococculinidae sp., the *trnQ*, *trnG*, and *trnE* could not be found.
320 Besides, a large segment could not be assembled from the read pool of *Anatoma* sp.,
321 containing partial *16S rRNA*, *trnV*, *12S rRNA*, and the tRNA series MYCWQGE. In
322 the reconstructed mitogenome of *Perotrochus caledonicus*, the segment containing
323 *cox3*, the tRNA series YCWQGE and KARNI, and one *trnS* could not be found. In
324 the mitogenome of *Shinkailepas briandi*, the segment of the tRNA series
325 MYCWQGE, *trnV*, and *12S rRNA* could not be detected. For *Coccocrater* sp., the
326 segment of partial *nd5*, *trnH*, *nd4*, *nd4l*, *trnT*, and *trnS* could not be found. The main
327 structures of the reconstructed mitogenomes were shown in Table 2 and the gene
328 orders of the newly reconstructed mitogenomes were shown in Supplementary figure
329 S1.

330 For the three nuclear genes targeted in this study, sequences were assembled
331 from only four read pools. In the read pool of Bathysciadiidae sp., we assembled the
332 18S. In the read pool of Pseudococculinidae sp., H3 was assembled. For *Perotrochus*
333 *caledonicus*, we assembled the 18S and the H3. Lastly, the 18S and 28S were
334 assembled from the read pool of *Shinkailepas briandi* (Supplementary table S1).

335

336 3.2 Inferred phylogenetic trees

337 The topologies of the inferred ML and BI trees based on the big mt dataset were
338 almost identical except for the position of *Stomatella planulata* (Supplementary figure
339 S2), however, both positions were not supported. In these trees, Gastropoda was not
340 monophyletic. The cephalopod (*Octopus vulgaris*), scaphopod (*Graptacme eborea*),
341 bivalves (*Pyganodon grandis*, *Mytilus edulis*, *Chlamys farreri*), heterobranchs (*Pupa*
342 *strigosa*, *Peronia peronii*, *Siphonaria pectinata*), patellogastropod (*Lottia digitalis*),
343 and one neritimorph (*Pleuropoma jana*) were grouped together, but this clade was not
344 meaningfully supported (bootstrap value [BP] below 50%; posterior probability [PP]
345 = 0.9). This clade was placed as the sister-group of the rest (except Polyplacophora)
346 and included the taxa of patellogastropod and bivalves with extreme long branches.
347 We thus removed these taxa from the subsequent analyses.

348 The phylogenetic trees inferred with respectively the small mt, the nuclear, and
the combined datasets are shown in figures 1-3 and supplementary figure S3. From all
of the analyses, the Gastropoda and all the main groups within gastropods, including
the Neritimorpha that was observed to be non-monophyletic in the inferred tree based
on the big mt dataset (Supplementary figure S2), were resolved as monophyletic
groups with mediocre or strong nodal supports. As to their inter-relationships, none
were well resolved with an exception for the sister-group relationship between

349
350
351
352
353
354
Fig. 1

Fig. 2

Fig. 3

355 Cocculiniformia and Neomphalina (small mt dataset: BP = 100%, PP = 1.00; nuclear
356 dataset: BP = 70%, PP = 0.64; combined dataset: BP = 100%, PP = 1.00).

357 Within the Vetigastropoda, the Pleurotomarioidea was inferred to be the sister-
358 group of the clade containing the rest of the vetigastropod superfamilies in all the
359 analyses, and this relationship was highly supported in almost all the analyses (Figs 1-
360 3). Within the latter clade, two major groups could be delimited based on the results
361 from the analyses conducted with the small mt and combined datasets. The first group
362 included Fissurelloidea, Seguenzioidea, Haliotoidea, Scissurelloidea, Lepetelloidea,
363 and Lepetodriolea, whereas the second group included all the trochoidean families.
364 However, the first group was not well supported (Fig. 1 and 3). Within these two
365 major groups, some well-supported clades were resolved: the Fissurelloidea (full
366 support in all analyses), the clade containing the Haliotoidea and the Seguenzioidea
367 (small mt dataset: BP = 87%, PP = 0.98; combined dataset: BP = 71%, PP = 1.00), the
368 clade containing the Scissurelloidea, the Lepetelloidea, and the Lepetodriolea (small
369 mt dataset: BP = 92%, PP = 1.00; combined dataset: BP = 85%, PP = 1.00), the clade
370 grouping the Lepetelloidea and the Lepetodriolea (full support in all analyses), and
371 the clade containing Tegulidae and Turbinidae (full support in all analyses). In the
372 analyses based on the nuclear dataset, most of the clades mentioned above were
373 found, but support values were generally weak.

374

375 **4. Discussion**

376 *4.1 Mitogenomic phylogeny of the Gastropoda*

377 The mitogenome is widely used for reconstructing the molluscan phylogeny with
378 highly conserved sizes (Stöger and Schrödl, 2013). However, mitochondrial genes
379 have generally faster evolutionary rates than nuclear genes, leading to ambiguous

380 results due to saturation when considering deep phylogenetic relationships (Burton
381 and Barreto, 2012; Stöger and Schrödl, 2013; Wort et al., 2017). Stöger and Schrödl
382 (2013) have suggested that long-branch attraction might provide misleading
383 relationships in deep molluscan phylogeny. We detected such phenomenon when
384 using the large mt dataset with some gastropod branches clustering with the long-
385 branches of the bivalves. With this dataset, the non-monophyly observed for the
386 Gastropoda and Neritimorpha should result from a long-branch attraction (Grande et
387 al., 2008; Williams et al., 2014; Uribe et al., 2016a). Actually, the monophyly of the
388 Gastropoda as well as the Neritimorpha, supported by nuclear data set (Zapata et al.,
389 2014), was recovered when the long-branch taxa were removed (Figs. 1-3).

390 Another characteristic of mitogenomic datasets that should be taken into account
391 in phylogenetic reconstructions is the absence of recombination. In fact,
392 mitochondrial genes as a whole should be regarded as a single locus that experienced
393 the same evolutionary history. Consequently, a particular regime of selection,
394 different rate of evolution or introgression in a given lineage may distort the
395 reconstructed tree. In this context, nuclear genes that are not linked to mitochondrial
396 genes and thanks to recombination not linked among them, may be used as
397 independent evidence to evaluate the reliability of the phylogenetic reconstruction,
398 especially when mitochondrial introgression occurred (Chen and Mayden, 2010). In
399 our dataset, for the well supported branches, we found congruent results between the
400 nuclear and mitochondrial datasets (Figs 1-3).

401 Finally, the most critical issue that may affect phylogenetic reconstructions on
402 gastropods is the taxonomic sampling bias. Many recent mitogenomic studies
403 investigating the gastropod phylogeny were conducted with only shallow-water
404 lineages (Grande et al., 2008; Cunha et al., 2009; Williams et al., 2014; Oscala et al.,

405 2015; Uribe et al., 2016b; Wort et al., 2017) or a few deep-sea taxa (Lee et al., 2016;
406 Uribe et al., 2016a). In Uribe et al. (2016a), the authors presented that the deep-sea
407 Neomphalina was the sister-group of the clade containing all other gastropods
408 sampled in the study, but this topology was considered as an artefact. In the present
409 study, we reconstructed 11 nearly complete mitogenomes from deep-sea gastropods
410 that included novel reports of the mitogenomes from taxa difficult to collect, such as
411 the Cocculiniformia, Pleurotomarioidea, Scissurelloidea, and Lepetelloidea. Our
412 results demonstrated that the two major deep-sea gastropod groups Cocculiniformia
413 (not sampled in Uribe et al., 2016a) and Neomphalina are each monophyletic and
414 together form a strongly supported clade (Figs 1-3), supporting the results of Aktipis
415 and Giribet (2012). This implies that during the early diversifications of gastropods
416 colonization of the deep sea occurred only once. The topology does not exclude the
417 hypothesis of deep-sea origin of the entire Gastropoda or Vetigastropoda. However,
418 this hypothesis is just unrealistic notably from a paleontological point of view. This
419 topology is better interpreted as a transition to the deep sea occurring at the latest for
420 the common ancestor of the Cocculiniformia and Neomphalina. Our results revealed
421 that multiple transitions between shallow water and deep-sea habitats occurred later
422 during the evolution of the vetigastropods (Fig. 1-3) (see discussion below).

423 Within the Neritimorpha, deep-sea taxa (*Bathynnerita*, *Olgasolaris* and
424 *Shinkailepas*) are placed in the Phenacolepadidae that, together with the Neritidae,
425 belong to the superfamily Neritoidea. In our study *Shinkailepas* branches with
426 Neritidae species, this result was congruent with the fossil records and the
427 phylogenetic reconstruction based on partial 28S *rRNA* sequence (Kano et al., 2002).

428

429 *4.2 The evolutionary significance of the deep-sea taxa among vetigastropods*

430 The definition of the Vetigastropoda was unsettled mainly due to an uncertain
431 placement of a deep-sea lineage, the Pleurotomarioidea. It was placed as the sister-
432 group of the remaining vetigastropod superfamilies in most molecular studies but the
433 support for this relationship was not robust (Colgan et al., 2003; McArthur and
434 Harasewych, 2003; Geiger and Thacker, 2005; Williams and Ozawa, 2006; Kano,
435 2008; Williams et al., 2008). Aktipis and Giribet, (2012), using molecular data, even
436 suggested excluding it from the Vetigastropoda. Conversely, several morphological
437 analyses found it to be nested within the Vetigastropoda (Ponder and Lindberg, 1997;
438 Sasaki, 1998). With a denser character- and taxon-sampling strategy, the hypothesis
439 of a sister-group relationship between the Pleurotomarioidea and the rest of the
440 vetigastropods is confirmed with high support values in this study.

441 Our analyses resolve some other conflicting issues about the phylogenetic
442 relationships and classification of the Vetigastropoda. For instance, Aktipis and
443 Giribet (2012) suggested removing the deep-sea Lepetelloidea from Vetigastropoda
444 *sensu stricto*. However, in accordance with Zapata et al. (2014), we found this
445 superfamily to be sister to the monophyletic Lepetodriloidea that also include deep-
446 sea taxa. Moreover, we further identified the Scissurelloidea as the closest allies of
447 this deep-sea vetigastropod clade (Figs 1-3). This particular finding thus resolved the
448 close relationships among the Scissurelloidea, Lepetodriloidea, and Lepetelloidea.
449 Actually, no Lepetelloidea has been included in the phylogenetic studies based on
450 which a close affinity between Lepetodriloidea and Scissurelloidea was proposed
451 (Geiger and Thacker, 2005; Williams and Ozawa, 2006; Williams et al., 2008; Geiger,
452 2012). However, some studies questioned the monophyly of the Scissurelloidea and
453 found that the scissurelloid family, Anatomidae, might be sister to the
454 Lepetodriloidea, and that together these two lineages should be the sister-group of the

455 other scissurelloid family, Scissurelloidea (Kano, 2008; Geiger, 2012). Our nuclear
456 gene results showed a similar topology (Fig. 2), although the concerned nodes were
457 not supported. The inclusion of more scissurelloid mitogenomes in the data analyses
458 is necessary to test the hypothesis of a scissurelloid monophyly.

459

460 4.3 Habitat use in gastropods

461 To evaluate the evolutionary significance of the deep-sea habitats in gastropods,
462 we examined the literature to evaluate the relative importance of four distinct habitats:

Fig. 4

shallow water, deep-sea floor, biogenic substrates, and hot vents and cold seeps (Fig.
464 4). Caenogastropoda, Neritimorpha and Vetigastropoda are present in all four habitats
465 whereas the sister-clades Cocculiniformia and Neomphalina are mainly inhabit two
466 deep-sea habitats (biogenic substrates, and vents and seeps), which are recognized as
467 chemosynthetic environments.

468 Cocculiniform species are all restricted to biogenic substrates (Marshall, 1985;
469 Haszprunar, 1987; McLean and Harasewych, 1995; Lesicki, 1998; Warén, 2011)
470 whereas the members of Neomphalina can be found in both biogenic substrates (most
471 of the species of Melanodrymiidae except those in *Melanodrymia*) and vents or seeps
472 (species of Neomphalidae, and Peltospiridae) (Heß et al., 2008). The sunken wood
473 associated species in *Leptogyra* and *Leptogyropsis* (Neomphalina, Melanodrymiidae)
474 display putatively plesiomorphic characters in the morpho-anatomy, which led Heß et
475 al. (2008) to conclude that the biogenic substrates might be the ancestral habitat of the
476 Neomphalina. From our phylogenetic results, we found that the Neomphalina is sister
477 to the Cocculiniformia, which suggests that the biogenic substrates might serve as an
478 (ancestral) 'step' for the deep-sea gastropod colonization of chemosynthetic

479 environments (Fig. 4), and thus support the stepping stone hypothesis (Distel et al.,
480 2000).

481 In our analysis, the sister-clades Neomphalina and Cocculiniformia branches
482 with the Vetigastropoda based on the small mt dataset with mediocre supports (Fig.
483 1). In the Vetigastropoda most lineages are present in all three types of deep-sea
484 habitats, but only the two sister-clades Lepetelloidea and Lepetodriloidea are mainly
485 or exclusively inhabit the deep-sea chemosynthetic environments. Two potential
486 scenarios could be thus proposed. Either the common ancestor of Cocculiniformia,
487 Neomphalina and Vetigastropoda was restricted to deep-sea chemosynthetic
488 environments, and the colonization of other deep-sea habitats and shallow-waters
489 occurred later, or conversely, the colonization toward deep-sea chemosynthetic
490 environments occurred several time independently with two major colonization events
491 (i.e. the common ancestor of Cocculiniformia and Neomphalina, and the common
492 ancestor of Lepetelloidea and Lepetodriloidea).

493 Among Scissurelloidea, Lepetodriloidea, and Lepetelloidea, only one family
494 (Scissurellidae) mainly inhabit shallow waters (< 75m) (Geiger, 2012). Additional
495 sampling of mitogenomes within Scissurelloidea is required to determine if as
496 suggested by the nuclear gene analysis (Fig 2) and previous studies (e.g. Kano, 2008;
497 Geiger, 2012), the Scissurellidae is the sister-group of the other deep-sea lineages
498 from this clade. The members of the Lepetodriloidea inhabit mainly deep-sea
499 hydrothermal vents (McLean, 1988; Sasaki et al., 2010) and most of the Lepetelloidea
500 can be found on biogenic substrates from bathyal to hadal zones (Marshall, 1985;
501 Haszprunar, 1987; McLean and Harasewych, 1995; Lesicki, 1998; Warén, 2011,
502 Kano et al. 2016) and some, namely the Pyropeltidae, inhabit deep-sea vents or seeps
503 (Sasaki et al., 2010). In addition, Kano et al. (2016) suggested that sunken wood

504 habitat might be the ancestral habitat of the Lepetelloidea based on the potentially
505 plesiomorphic radula in this superfamily, which includes species mostly associated
506 with woods. Although additional data are still required, the available results suggest
507 an evolution from shallow waters (Scissurellidae) to deeper habitat (Anatomidae,
508 Lepetelloidea, Lepetodriloidea), with sunken-wood (Lepetelloidea) serving as
509 evolutionary stepping stones to vent and seeps (Lepetodriloidea).

510 In addition to the main deep-sea vetigastropod groups mentioned above, a few
511 particular deep-sea lineages or species within each other vetigastropod superfamily
512 can be found and some of them inhabit chemosynthetic environments (Fig. 4). There
513 are, for example, some species in *Cornisepta* (Fissurelloidea) (Araya and Geiger,
514 2013) found in cold seeps (Araya and Geiger, 2013) and in hydrothermal vents
515 (Sasaki et al., 2010), the species in *Puncturella* found on sunken woods
516 (Fissurelloidea) (Warén, 2011; Pante et al., 2012) and from hydrothermal vents
517 (Sasaki et al., 2010); most of the species attributed to Seguenziidae (Seguenzioidea)
518 are from the deep-sea floor, and all the species of Cataegidae (Seguenzioidea) are
519 from chemosynthetic environments (e.g. Warén and Bouchet, 2009; Olu et al., 2010;
520 Warén, 2011). The Pleurotomarioidea were first known from the fossil records. It was
521 thought to be one of the most ancient gastropod clades (Geiger et al., 2008). They
522 have diversified in shallow water habitats during the Paleozoic and Mesozoic and
523 during these periods they dominated the shallow water gastropod fauna (Harasewych,
524 2002). Only a single family (Pleurotomariidae) survived the Cretaceous extinction and
525 the recent species are now restricted to bathyal depth (Harasewych, 2002). Therefore,
526 together the position of Pleurotomariidae within Vetigastropoda and the fossil data
527 suggest that vetigastropods originated from shallow water ancestors and that the

528 colonization of deep-sea habitats, including chemosynthetic environments happened
529 later.

530 Our investigation of the taxonomic literature combined with new phylogenetic
531 results offers a first glimpse into the evolution of habitat use among gastropods.
532 However, in each lineage, more taxa from the different habitats are required to
533 reconstruct the ancestral states of habitat use at the major nodes in the phylogenetic
534 tree of gastropods. Moreover, the phylogenetic relationships among and within
535 gastropod superfamilies/families are far from being complete, especially for those
536 groups containing the deep-sea lineages. For example, the Fissurellidae contains 55
537 described genera (Aktipis et al., 2011), including 7 genera restricted to the deep-sea
538 habitats (references shown in Fig. 4) but only one was included in the recent
539 phylogenetic study of Fissurellidae (Aktipis et al., 2011). Conversely, the scissurelloid
540 species inhabit all kinds of marine habitats (Fig. 4) but we included so far only the
541 deep-sea floor representative from the genus *Anatoma*. Mitogenomic data from other
542 habitats and lineages are still lacking because of their very small size, these
543 gastropods are difficult to collect and to identify, whatever the habitat. The
544 scissurelloid case emphasizes that the size of organisms is another important sampling
545 bias in the reconstruction of the evolutionary history of the Gastropoda. Our study
546 provides a new framework for the study of the evolution of the Gastropods by
547 indicating the needed sampling efforts: sampling more thoroughly the deep-water
548 habitats and the smaller organisms.

549

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575

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870

871 **Figure captions**

872

873 **Figure 1.** Phylogenetic relationships of the Gastropoda inferred using partitioned
874 maximum-likelihood (ML) methods based on 11,129 bp nucleotide sequences
875 combined from 13 mitochondrial protein-coding genes and 2 ribosomal RNA genes
876 (small mt dataset). Nodal supports are shown as bootstrap (BP) values in percentage
877 (above) and posterior probabilities (PP) (below). Values below 50% in BP and 0.8 in
878 PP are not shown. Values higher than 80% in BP and 0.95 in PP are considered
879 significant and shown in bold. Taxa names in bold represent the deep-sea lineages.

880 **Figure 2.** Phylogenetic tree reconstructed using the partitioned maximum-likelihood
881 (ML) methods based on 3,313 bp nucleotide sequences combined from *18S*, *28S*, and
882 *H3* (nuclear dataset). Numbers above/below the nodes are bootstrap (BP) values in
883 percentage / posterior probabilities (PP). Values within superfamily and values below
884 50% (BP) and 0.8 (PP) are not shown. Values higher than 80% (BP) and 0.95 (PP) are
885 shown in bold. Asterisk indicates the superfamilies not found monophyletic in the
886 tree.

887 **Figure 3.** Partitioned maximum-likelihood (ML) tree based on 14,442 bp nucleotide
888 sequences combined from 13 mitochondrial protein-coding genes, 2 ribosomal RNA
889 genes, and nuclear genes including *18S*, *28S*, and *H3* (combined dataset). Nodal
890 supports are shown as bootstrap (BP) values in percentage / posterior probability (PP).
891 Values below 50% in BP and 0.8 in PP are not shown. Values higher than 80% in BP
892 and 0.95 in PP are considered significant and shown in bold. Taxa from
893 Cocculiniformia, Neomphalina, Caenogastropoda, Neritimorpha, and from the same
894 vetigastropod superfamily or family are collapsed. The uncollapsed tree is shown in
895 supplementary figure S3.

896 **Figure 4.** On the left: a simplified phylogeny modified from the inferred tree based on
897 the combined gene dataset shown in Fig. 3. The nodes with support values below 75%
898 (BP) are collapsed and shown as polytomies. Main gastropod groups are shown in
899 bold. The family-rank taxa are underlined. The red arrows indicate the two major
900 events of habitat switch. On the middle: the habitats for each taxon. Four distinct
901 habitats are described: shallow water, deep-sea floor, biogenic substrate, and vent &
902 seep. The colored-circle represents the taxon presents majorly in the habitat. If there is
903 only a single or several species in a single genus that are present in one habitat,
904 'minor' is plotted under the habitat. On the right: the references of the taxon record.

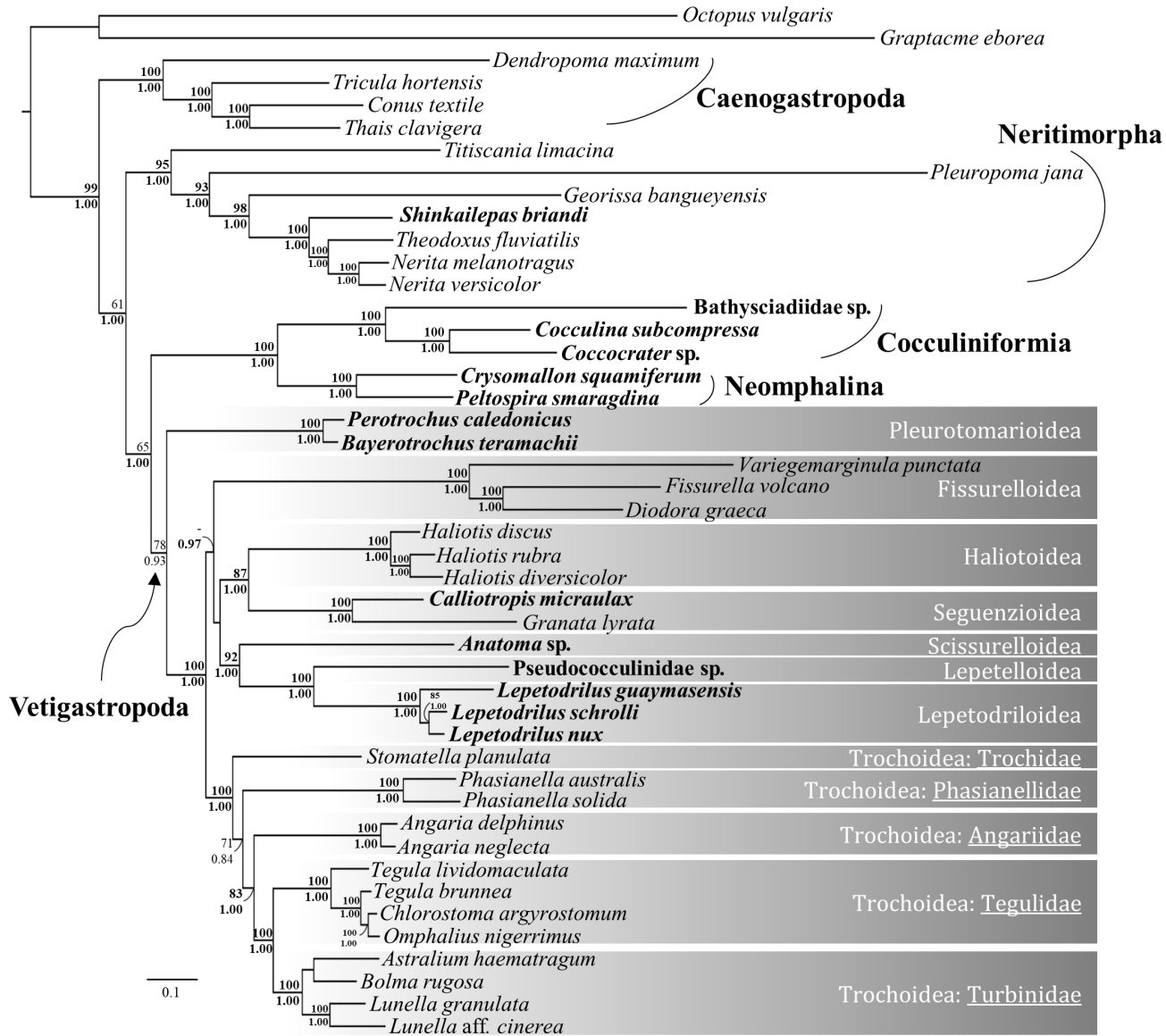
Table 1. New gastropod mitogenomes assembled in this study. MNHN: Muséum National d’Histoire Naturelle. NTUM: National Taiwan University Museums. The corresponding field data of the specimens from MNHN are found at <https://expeditions.mnhn.fr/>

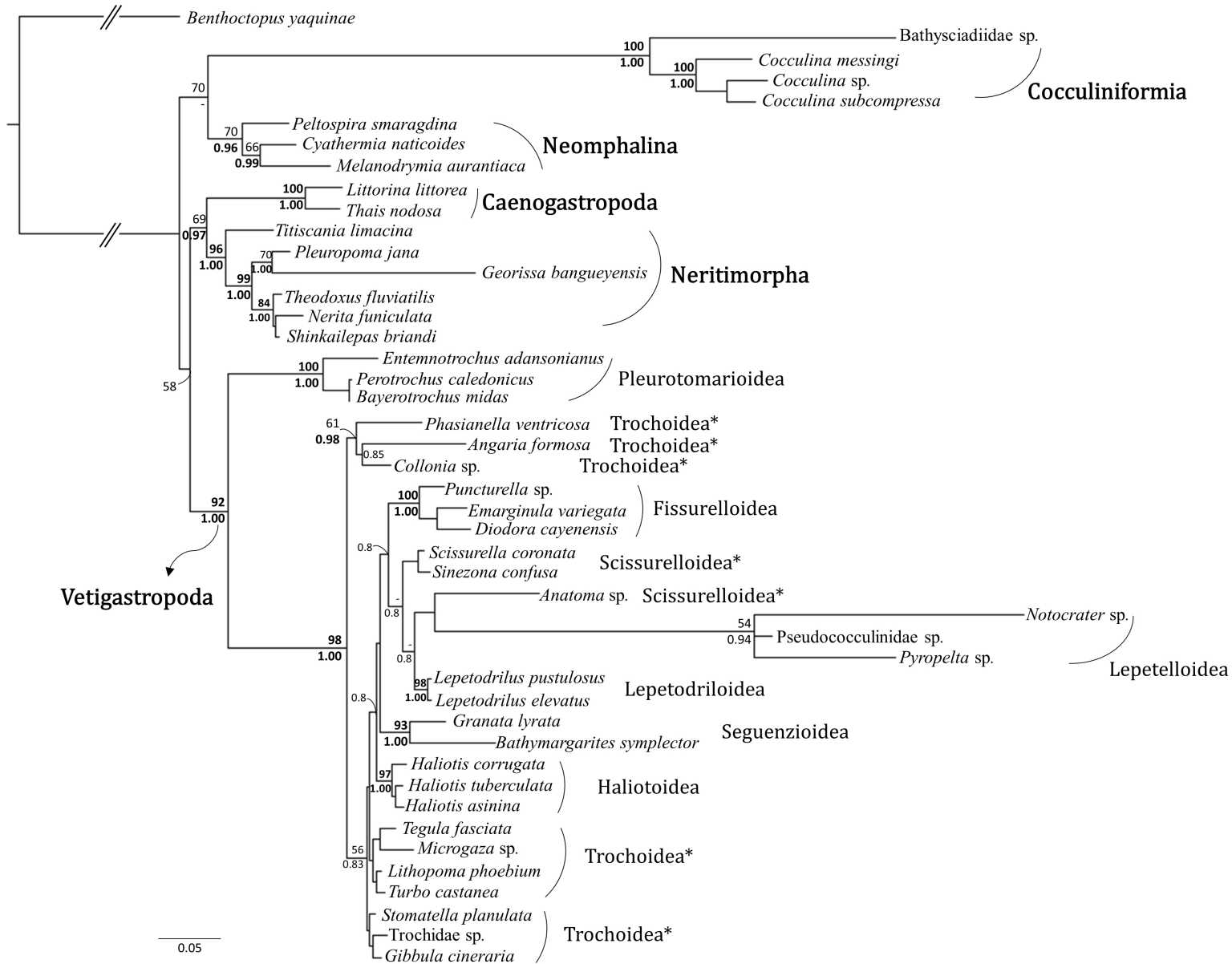
	Species	Voucher number	mitogenome	Sequencing method	Expedition, station, and locality (depth)	Habitat
Cocculiniformia,						
Cocculinoidea						
Bathysciadiidae	Bathysciadiidae sp.	MNHN-IM-2013-40843	MH837532	NGS, Illumina	EXBOBI, CP3791, Canal de la Havannah, New Caledonia (806m)	cephalopod beak
Cocculinidae	<i>Cocculina subcompressa</i>	MNHN-IM-2013-40775	MH837536	NGS, Illumina	BIOPAPUA, CP3645, Huon Gulf, Papua New Guinea (410m)	sunken wood
Cocculinidae	<i>Cococrater</i> sp.	MNHN-IM-2013-41044	MH837535	NGS, Iron Torrent	PAPUA NIUGINI, CP3967, Sek Island, Papua New Guinea (980m)	sunken wood
Neomphalina,						
Neomphaloidea						
Peltospiridae	<i>PeltoSPIra smaragdina</i>	NTUM-Inv-00001	MH837538	NGS, Illumina	DIVA 1, DV09, Lucky Strike vent, Mid-Atlantic Ridge (1653m)	hydrothermal vent
Neritimorpha,						
Neritoidea						
Phenacolepadidae	<i>Shinkailepas briandi</i>	MNHN-IM-2013-41914	MH837541	NGS, Iron Torrent	BISCOSE 1, PL568 ASPI2, Snake Pit, Mid-Atlantic Ridge (3466m)	hydrothermal vent
Vetigastropoda,						
Lepetelloidea						
Pseudococculinidae	Pseudococculinidae sp.	MNHN-IM-2013-40847	MH837540	NGS, Illumina	AROURA 2007, CP2736, East Philippines (346m)	sunken wood
Lepetodriloida						
Lepetodrilidae	<i>Lepetodrilus guaymasensis</i>	NTUM-Inv-00002	MH837537	NGS, Illumina	Alvin 2009, AT 15-59 sta. dive 4590, Off Punta Arenas, Costa Rica (1800m)	methane seep
Pleurotomarioidea						
Pleurotomariidae	<i>Bayerotrochus teramachii</i>	N/A	MH837533	LR-PCR	North-East of Taiwan (unknown)	dee-sea floor
Pleurotomariidae	<i>Perotrochus caledonicus</i>	MNHN-IM-2009-7483	MH837539	NGS, Iron Torrent	NORFOLK 2, DW2156, Ile des Pins, New Caledonia (484m)	dee-sea floor
Scissurelloidea						
Anatomidae	<i>Anatoma</i> sp.	MNHN-IM-2013-42003	MH837531	NGS, Illumina	CONCALIS, DW3025, Grand Passage, New Caledonia (398m)	dee-sea floor
Seguenzioidea						
Calliotropidae	<i>Calliotropis micraulax</i>	MNHN-IM-2009-31774	MH837534	NGS, Illumina	EXBODI, CP3842, Passe de la Sarcelle, New Caledonia (763m)	dee-sea floor

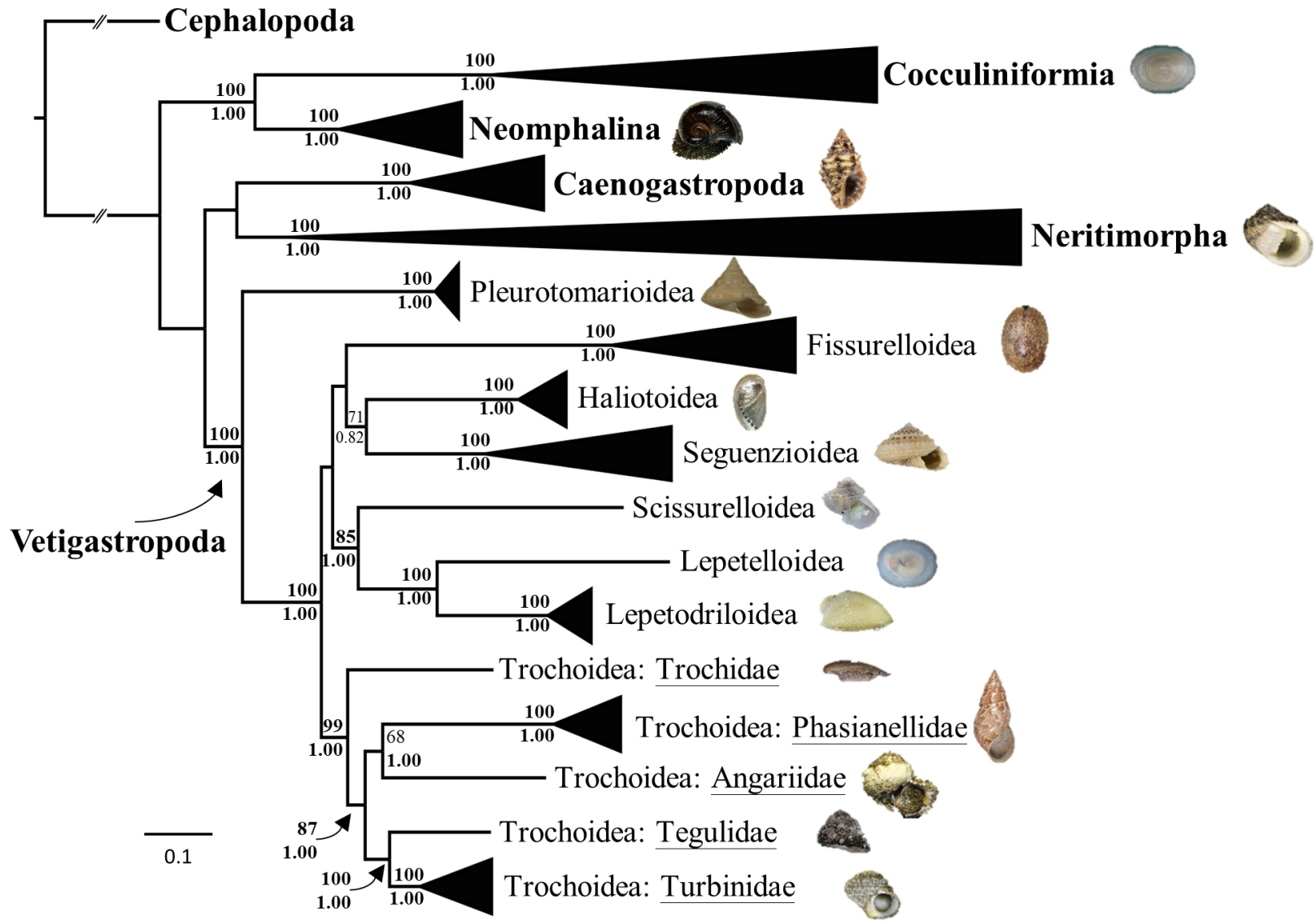
Table 2. Summary of features of the new gastropod mitogenomes, including total size of the genome (bp), percentage of A and T (AT %), and the sizes of protein-coding genes (bp).

	<i>Anatoma</i> sp.	<i>Bathysciadiid</i> <i>ae</i> sp.	<i>Calliotropis</i> <i>micraulax</i>	<i>Cococrater</i> sp.	<i>Cocculina</i> <i>subcompressa</i>	<i>Lepetodrilus</i> <i>guaymasensis</i>	<i>Bayerotrochu</i> <i>s teramachii</i>	<i>PeltoSPIra</i> <i>smaragdina</i>	<i>Perotrochus</i> <i>caledonicus</i>	<i>Pseudococculinid</i> <i>ae</i> sp.	<i>Shinkailepas</i> <i>briandi</i>
size	13,568	17,138	17,040	13,783	18,067	17,060	13,473	15,112	13,782	15,380	13,618
AT%	61.0	63.9	63.3	65.8	70.6	63.4.	63.6	69.4	60.0	72.0	61.7
<i>cox1</i>	1,548	1,539	1,554	1,533	1,542	1,545	1,536	1,542	1,536 ^b	1,548	1,548
<i>cox2</i>	699	684	684	690	690	708	693	702	702	711	690
<i>cox3</i>	780	774	780	780	780	780	- ^a	780	- ^a	774	780
<i>atp6</i>	633	504	309 ^b	579	717	714	696	678	696	495	696
<i>atp8</i>	165	339	207	225	249	222	174	162	174	231	165
<i>cytb</i>	1,137	1,149	1,164	348 ^b	1,137	1,137	1,140	1,140	1,140	1,137	1,137
<i>nd1</i>	945	948	1,002	852 ^b	948	939	921	948	936	951	933
<i>nd2</i>	1,086	1,038	1,095	1,116	1,119	1,089	1,059	1,095	1,099	1,002	1,131
<i>nd3</i>	354	357	354	354	372	351	354	381	323 ^b	354	354
<i>nd4</i>	1,347	1,344	1,302	- ^a	1,359	1,386	1,305	1,227	1,324 ^b	1,383	1,398
<i>nd4l</i>	300	285	297	- ^a	300	300	276	300	297	303	297
<i>nd5</i>	1,737	1,743	1,746	1,351 ^b	1,725	1,734	1,784	1,701	1,731	1,701	1,716
<i>nd6</i>	489	525	510	495	516	519	507	498	507	504	507

a: gene could not be sequenced; b: incomplete sequence







	<i>Shallow water</i>	<i>Deep-sea floor</i>	<i>Biogenic substrate</i>	<i>Vent & seep</i>	<i>Reference</i>	
<i>Vetigastropoda</i>	→		●		Marshall, 1985; McLean, 1992; McLean & Harasewych, 1995; Warén, 1995; Lesicki, 1998; Leal & Harasewych, 1999; Warén, 2011	
			●	●	Biogenic substrate: Kiel & Goedert, 2006; Heß, 2008; Warén, 2011; Vent & Seep: Fretter et al., 1981; Warén & Bouchet, 1993, 2001; Warén et al., 2003; Sasaki et al., 2010	
		●	●	●	Ponder et al., 2008; Sasaki et al., 2008; Warén, 2011	
		●	●	●	Fretter, 1984; Warén & Bouchet, 2001; Lindberg, 2008; Sasaki et al., 2010; Warén, 2011; Kano et al., 2013	
			●		Harasewych, 2002; Anseeuw et al., 2015	
		●	●	minor	minor	Shallow water: Aktipis et al., 2011; Deep-sea floor: McLean & Geiger, 1998; Biogenic substrate: Warén, 2011; Vent and seep: Warén and Bouchet, 2009; Sasaki et al., 2010; Araya & Geiger, 2013
		●			Brown, 1993	
		●	●	●	minor	Shallow water: Herbert, 2012; Deep-sea floor: Kano, 2008 Biogenic substrate: Warén, 2011; Vent and seep: Warén & Bouchet, 1993, 2001; Kano et al., 2009; Olu et al., 2010
		●	●	minor	minor	Geiger & Thacker, 2005; Geiger, 2012 Biogenic substrates and Vent & seep: Warén, 2011
				●	●	Biogenic substrate: Marshall, 1985; McLean, 1992; Marshall, 1996; Warén, 2011; Vent and seep: Warén and Bouchet, 2009; Sasaki et al., 2010
				minor	●	Biogenetic substrate: Warén, 2011; Amon et al., 2013; Vent and seep: McLean, 1988; Sasaki et al., 2010
		●	●	minor		Shallow water: Hickman & McLean, 1990; Deep-sea floor: Herbert, 1993; Williams et al., 2010; Biogenic substrate: Warén, 2011
		●	●	minor	minor	Hickman & McLean, 1990 Biogenic substrate: Warén, 2011; Vent and Seep: Sasaki et al., 2010
		●	●			Hickman & McLean, 1990 Deep-sea floor: Rosenberg et al., 2009
		●				Hickman & McLean, 1990
		●	●			Hickman & McLean, 1990

Supplementary table S1. Available mitogenomes retrieved from Genbank and analyzed in the study. Deep-sea habitats are shown in **bold**.

	superfamily	family	species	accession no.	reference	habitats
Polyplacophora,						
Chitonida	Mopalioidae	Mopaliidae	<i>Katharina tunicata</i>	U09810	Boore and Brown, 1994	intertidal, subtidal
Scaphopoda,						
Dentaliida		Dentaliidae	<i>Graptacme eborea</i>	AY484748	Boore et al., 2004	intertidal, subtidal
Octopoda,						
Octopoda	Octopodoidea	Octopodidae	<i>Octopus vulgaris</i>	AB158363	Yokobori et al., 2004	shallow water
Bivalvia,						
Palaeoheterodonta	Unionoidea	Unionidae	<i>Pyganodon grandis</i> (female)	FJ809754	Breton et al., 2009	fresh or brackish water
Pteriomorphia	Mytiloidea	Mytilidae	<i>Mytilus edulis</i> (female)	AY484747	Boore et al., 2004	intertidal, subtidal
	Pectinoidea	Pectinidae	<i>Chlamys farreri</i>	EF473269	Ren et al., 2010	intertidal, subtidal
Gastropoda,						
Heterobranchia	Acteonoidea	Acteonidae	<i>Pupa strigosa</i>	AB028237	Kurabayashi and Ueshima, 2000	intertidal, subtidal
	Onchidioidea	Onchidiidae	<i>Peronia peronii</i>	JN619346	White et al., 2011	intertidal
	Siphonarioidea	Siphonariidae	<i>Siphonaria pectinata</i>	AY345049	Grande et al., 2008	intertidal
Patellogastropoda	Lottioidea	Lottiidae	<i>Lottia digitalis</i>	DQ238599	Simison et al., 2006	intertidal, subtidal
Caenogastropoda	Conoidea	Conidae	<i>Comus textile</i>	DQ862058	Bandyopadhyay et al., 2008	intertidal, subtidal
	Muricoidea	Muricidae	<i>Thais clavigera</i>	DQ159954	Jung et al. (unpublished)	intertidal, subtidal
	Truncatelloidea	Pomatiopsidae	<i>Tricula hortensis</i>	EU440735	Zhao et al. (unpublished)	freshwater
	Vermetoidea	Vermetidae	<i>Dendropoma maximum</i>	HM174253	Rawlings et al., 2010	intertidal, subtidal
Neritimorpha	Neritoidea	Neritidae	<i>Theodoxus fluviatilis</i>	KU342667	Uribe et al., 2016a	freshwater
	Neritoidea	Neritidae	<i>Nerita versicolor</i>	KF728890	Arquez et al., 2014	intertidal, subtidal
	Neritoidea	Neritidae	<i>Nerita melanotragus</i>	GU810158	Castro and Colgan, 2010	intertidal, subtidal
	Neritopsoidea	Neritopsidae	<i>Titiscania limacina</i>	KU342669	Uribe et al., 2016a	intertidal, subtidal
	Hydrocenoidea	Hydrocenidae	<i>Georissa banguyensis</i>	KU342664	Uribe et al., 2016a	terrestrial
	Helicinoidea	Heliminidae	<i>Pleuropoma jana</i>	KU342666	Uribe et al., 2016a	terrestrial
Neomphalina	Neomphaloidea	Peltospiridae	<i>Crysmallon squamiferum</i>	AP013032	Nakagawa et al., 2014	hydrothermal vent
Vetigastropoda	Fissurelloidea	Fissurellidae	<i>Fissurella volcano</i>	JN790612	Simison (unpublished)	intertidal, subtidal
	Fissurelloidea	Fissurellidae	<i>Diodora graeca</i>	KT207825	Uribe et al., 2016b	intertidal, subtidal
	Haliotoidea	Haliotidae	<i>Haliotis discus</i>	EU595789	Ren et al. (unpublished)	intertidal, subtidal
	Haliotoidea	Haliotidae	<i>Haliotis diversicolor</i>	HQ832671	Xin et al., 2011	intertidal, subtidal
	Haliotoidea	Haliotidae	<i>Haliotis rubra</i>	AY588938	Maynard et al., 2005	intertidal, subtidal
	Lepetodriloidae	Lepetodrilidae	<i>Lepetodrilus schrolli</i>	KR297250	Uribe et al., 2016b	hydrothermal vent
	Lepetodriloidae	Lepetodrilidae	<i>Lepetodrilus nux</i>	LC107880	Nakajima et al., 2016	hydrothermal vent
	Seguenzioidea	Chilodontidae	<i>Granata lyrata</i>	KR297249	Uribe et al., 2016b	intertidal, subtidal
	Trochoidea	Angariidae	<i>Angaria neglecta</i>	KR297248	Uribe et al., 2016b	intertidal, subtidal
	Trochoidea	Phasianellidae	<i>Phasianella solida</i>	KR297251	Uribe et al., 2016b	intertidal, subtidal
	Trochoidea	Tegulidae	<i>Chlorostoma argyrostomum</i>	KX298892	Lee et al., 2016	intertidal, subtidal
	Trochoidea	Tegulidae	<i>Omphalius nigerrimus</i>	KX298895	Lee et al., 2016	intertidal, subtidal
	Trochoidea	Tegulidae	<i>Tegula brunnea</i>	JN790613	Simison (unpublished)	intertidal, subtidal
	Trochoidea	Tegulidae	<i>Tegula lividomaculata</i>	KT207826	Uribe et al., 2016b	intertidal, subtidal
	Trochoidea	Turbinidae	<i>Astralium haematragum</i>	KX298891	Lee et al., 2016	intertidal, subtidal
	Trochoidea	Turbinidae	<i>Bolma rugosa</i>	KT207824	Uribe et al., 2016b	intertidal, subtidal
	Trochoidea	Turbinidae	<i>Lunella aff. cinerea</i>	KF700096	Williams et al., 2014	intertidal, subtidal
	Trochoidea	Turbinidae	<i>Lunella granulata</i>	KX298890	Lee et al., 2016	intertidal, subtidal

Supplementary table S2. Nuclear genes used in the analyses. Multiple specimens used for creating chimeric sequences of terminal taxon in data matrix are shown with an asterisk (*).

	superfamily	family	species	reference	18S	28S	H3
Cephalopoda,							
Coleoidea	Octopodoidea	Enteroctopodidae	<i>Benthoctopus yaquinae</i>	Passamaneck et al., 2004	AY145366	AH012195	-
Gastropoda,							
Neritimorpha	Neritoidea	Neritidae	<i>Nerita funiculata</i>	Aktipis and Giribet, 2012	DQ093429	GQ160660	DQ093497
	Neritoidea	Neritidae	<i>Theodoxus fluviatilis</i>	Aktipis and Giribet, 2012	AF120515	GQ160659	-
	Neritoidea	Phenacolepadidae	<i>Shinkailepas briandi</i>	this study	MK457140	MK457137	-
	Neritopsoidea	Neritopsidae	<i>Titiscania limacina</i>	Uribe et al., 2016a	KU342683	KU342684	-
	Hydrocenoidea	Hydrocenidae	<i>Georissa bangueyensis</i>	Uribe et al., 2016a	KU342673	KU342674	KU342676
	Helicinoidea	Helininidae	<i>Pleuropoma jana</i>	Uribe et al., 2016a	KU342679	KU342680	KU342682
Caenogastropoda	Littorinoidea	Littorinidae	<i>Littorina littorea</i>	Aktipis and Giribet, 2012	DQ093437	FJ977692	DQ093507
	Muricoidea	Muricidae	<i>Thais nodosa</i>	Couto et al., 2016	KT753639	KT753772	KT754133
Cocculiniformia	Cocculinoidea	Cocculinidae	<i>Cocculina messingi</i>	Aktipis and Giribet, 2012	AF120508	AY377696	AY377777
	Cocculinoidea	Cocculinidae	<i>Cocculina subcompressa</i>	Aktipis and Giribet, 2012	GQ160773	GQ160621	GQ160708
	Cocculinoidea	Cocculinidae	<i>Cocculina</i> sp.	Aktipis and Giribet, 2012	GQ160774	GQ160622	GQ160709
	Cocculinoidea	Bathysciadiidae	<i>Bathysciadium</i> sp.	this study	MK457138	-	-
Neomphalina	Neomphaloidea	Peltospiridae	<i>Peltospira smaragdina</i>	Aktipis and Giribet, 2012	GQ160806	GQ160657	GQ160741
	Neomphaloidea	Melanodrymiidae	<i>Melanodrymia aurantiaca</i>	Aktipis and Giribet, 2012	GQ160805	GQ160656	GQ160740
	Neomphaloidea	Neomphalidae	<i>Cyathermia naticoides</i>	Aktipis and Giribet, 2012	DQ093430	FJ977685	DQ093498
Vetigastropoda	Lepetelloidea	Pyropeltidae	<i>Pyropelta</i> sp.	Aktipis and Giribet, 2012	-	GQ160633	GQ160719
	Lepetelloidea	Pseudococculinidae	<i>Notocrater</i> sp.	Aktipis and Giribet, 2012	GQ160784	GQ160632	GQ160718
	Lepetelloidea	Pseudococculinidae	Pseudococculinidae sp.	this study	-	-	MK457142
	Pleurotomarioidea	Pleurotomariidae	<i>Entemnotrochus adansonianus</i>	Aktipis and Giribet, 2012	AF120509	FJ977667	AY377774
	Pleurotomarioidea	Pleurotomariidae	<i>Bayerotrochus midas</i> *	Aktipis and Giribet, 2012	AF120510	FJ977668	DQ093500
	Pleurotomarioidea	Pleurotomariidae	<i>Perotrochus caledonicus</i>	this study	MK457139	-	MK457141
	Seguenzioidea	Chilodontidae	<i>Bathymargarites symplector</i>	Aktipis and Giribet, 2012	DQ093433	GQ160653	DQ093503
	Seguenzioidea	Chilodontidae	<i>Granata lyrata</i>	Williams et al., 2008	EU530064	EU530010	-
	Fissurelloidea	Fissurellidae	<i>Emarginula variegata</i>	Aktipis and Giribet, 2012	GQ160792	GQ160640	GQ160726
	Fissurelloidea	Fissurellidae	<i>Diodora cayenensis</i>	Aktipis and Giribet, 2012	GQ160788	GQ160636	GQ160722
	Fissurelloidea	Fissurellidae	<i>Puncturella</i> sp.	Aktipis and Giribet, 2012	FJ977641	FJ977672	FJ977733
	Scissurelloidea	Anatomidae	<i>Anatoma</i> sp.	Kano, 2008	AB365302	-	AB365260
	Scissurelloidea	Scissurellidae	<i>Scissurella coronata</i>	Williams and Ozawa, 2006	AM048637	AM048696	-
	Scissurelloidea	Scissurellidae	<i>Sinezona confusa</i>	Aktipis and Giribet, 2012	AF120512	DQ279981	AY377773
	Lepetodriloida	Lepetodrilidae	<i>Lepetodrilus pustulosus</i>	Aktipis and Giribet, 2012	FJ977652	FJ977683	FJ977744
	Lepetodriloida	Lepetodrilidae	<i>Lepetodrilus elevatus</i>	Aktipis and Giribet, 2012	DQ093432	GQ160654	DQ093501
	Lepetodriloida	Lepetodrilidae	<i>Gorgoleptis spiralis</i>	Aktipis and Giribet, 2012	GQ160804	GQ160655	GQ160739

Supplementary table S2. (Continued).

	superfamily	family	species	reference	18S	28S	H3
Vetigastropoda	Haliotoidea	Haliotidae	<i>Haliotis corrugata</i>	Aktipis and Giribet, 2012	FJ977644	FJ977675	FJ977736
	Haliotoidea	Haliotidae	<i>Haliotis asinina</i>	Aktipis and Giribet, 2012	GQ160786	GQ160634	GQ160720
	Haliotoidea	Haliotidae	<i>Haliotis tuberculata*</i>	Aktipis and Giribet, 2012	GQ160787	GQ160635	GQ160721
	Trochoidea	Angariidae	<i>Angaria formosa</i>	Williams and Ozawa, 2006	AM048648	AM048708	-
	Trochoidea	Colloniidae	<i>Collonia</i> sp.	Aktipis and Giribet, 2012	GQ160800	GQ160649	GQ160735
	Trochoidea	Phasianellidae	<i>Phasianella ventricosa</i>	Williams and Ozawa, 2006	AM048659	AM048720	-
	Trochoidea	Trochidae	Trochidae sp.	Aktipis and Giribet, 2012	GQ160794	GQ160643	GQ160729
	Trochoidea	Trochidae	<i>Stomatella planulata</i>	Williams et al., 2008	EU530078	EU530029	-
	Trochoidea	Trochidae	<i>Gibbula cineraria</i>	Aktipis and Giribet, 2012	FJ977645	FJ977676	FJ977737
	Trochoidea	Tegulidae	<i>Microgaza</i> sp.	Aktipis and Giribet, 2012	GQ160797	GQ160646	GQ160732
	Trochoidea	Tegulidae	<i>Tegula fasciata</i>	Aktipis and Giribet, 2012	GQ160801	GQ160650	GQ160736
	Trochoidea	Turbinidae	<i>Turbo castanea</i>	Aktipis and Giribet, 2012	FJ977650	FJ977681	FJ977742
	Trochoidea	Turbinidae	<i>Lithopoma phoebium</i>	Aktipis and Giribet, 2012	FJ977649	FJ977680	FJ977741

Supplementary table S3. Mitogenomes and nuclear gene sequences used in the combined dataset. Reference data for each sequences are shown in the supplementary table 1 (mitogenomes) and 2 (nuclear genes).

examined taxon	mitogenome used	accession num.	nuclear gene used	18S	28S	H3
Cephalopoda	<i>Octopus vulgaris</i>	AB158363	<i>Benthoctopus yaquinae</i>	AY145366	AH012195	-
Cocculiniformia	<i>Cocculina subcompressa</i>	MH837536	<i>Cocculina subcompressa</i>	GQ160773	GQ160621	GQ160708
Cocculiniformia	Bathysciadiidae sp.	MH837532	Bathysciadiidae sp.	MK457138	-	-
Neomphalina	<i>Peltoispira smaragdina</i>	MH837538	<i>Peltoispira smaragdina</i>	GQ160806	GQ160657	GQ160741
Neomphalina	<i>Cryosmallon squamiferum</i>	AP013032	<i>Cyathermia naticoides</i>	DQ093430	FJ977685	DQ093498
Caenogastropoda	<i>Tricola hortensis</i>	EU440735	<i>Littorina littorea</i>	DQ093437	FJ977692	DQ093507
Caenogastropoda	<i>Thais clavigera</i>	DQ159954	<i>Thais nodosa</i>	KT753639	KT753772	KT754133
Neritimorpha	<i>Titiscania limacina</i>	KU342669	<i>Titiscania limacina</i>	KU342683	KU342684	-
Neritimorpha	<i>Pleuropoma jana</i>	KU342666	<i>Pleuropoma jana</i>	KU342679	KU342680	KU342682
Neritimorpha	<i>Georissa bangueyensis</i>	KU342664	<i>Georissa bangueyensis</i>	KU342673	KU342674	KU342676
Neritimorpha	<i>Theodoxus fluviatilis</i>	KU342667	<i>Theodoxus fluviatilis</i>	AF120515	GQ160659	-
Neritimorpha	<i>Nerita versicolor</i>	KF728890	<i>Nerita funiculata</i>	DQ093429	GQ160660	DQ093497
Neritimorpha	<i>Shinkailepas briandi</i>	MH837541	<i>Shinkailepas briandi</i>	MK457140	MK457137	-
Pleurotomarioidea	<i>Perotrochus caledonicus</i>	MH837539	<i>Perotrochus caledonicus</i>	MK457139	-	MK457141
Pleurotomarioidea	<i>Bayerotrochus teramachii</i>	MH837533	<i>Bayerotrochus midas</i>	AF120510	FJ977668	DQ093500
Fissurelloidea	<i>Varietegmarginula punctata</i>	KX298889	<i>Emarginula variegata</i>	GQ160792	GQ160640	GQ160726
Fissurelloidea	<i>Diodora graeca</i>	KT207825	<i>Diodora cayenensis</i>	GQ160788	GQ160636	GQ160722
Haliotoidea	<i>Haliotis rubra</i>	AY588938	<i>Haliotis corrugata</i>	FJ977644	FJ977675	FJ977736
Haliotoidea	<i>Haliotis discus</i>	EU595789	<i>Haliotis asinina</i>	GQ160786	GQ160634	GQ160720
Seguenzioidea	<i>Granata lyrata</i>	KR297249	<i>Granata lyrata</i>	EU530064	EU530010	-
Seguenzioidea	<i>Calliotropis micraulax</i>	MH837534	<i>Bathymargarites symplector</i>	DQ093433	GQ160653	DQ093503
Scissurelloidea	<i>Anatoma</i> sp.	MH837531	<i>Anatoma</i> sp.	AB365302	-	AB365260
Lepetelloidea	Pseudococculinidae sp.	MH837540	Pseudococculinidae sp.	-	-	this study
Lepetodrilioidea	<i>Lepetodrilus guaymasensis</i>	MH837537	<i>Lepetodrilus pustulosus</i>	FJ977652	FJ977683	FJ977744
Lepetodrilioidea	<i>Lepetodrilus schrolli</i>	KR297250	<i>Lepetodrilus elevatus</i>	DQ093432	GQ160654	DQ093501
Phasianellidae	<i>Phasianella solida</i>	KR297251	<i>Collonia</i> sp.	GQ160800	GQ160649	GQ160735
Phasianellidae	<i>Phasianella australis</i>	KX298888	<i>Phasianella ventricosa</i>	AM048659	AM048720	-
Angariidae	<i>Angaria delphinus</i>	KX298893	<i>Angaria formosa</i>	AM048648	AM048708	-
Trochidae	<i>Stomatella planulata</i>	KX298894	<i>Stomatella planulata</i>	EU530078	EU530029	-
Tegulidae	<i>Tegula brunnea</i>	JN790613	<i>Tegula fasciata</i>	GQ160801	GQ160650	GQ160736
Turbinidae	<i>Lunella granulata</i>	KX298890	<i>Turbo castanea</i>	FJ977650	FJ977681	FJ977742
Turbinidae	<i>Astrarium haematragum</i>	KX298891	<i>Lithopoma phoebium</i>	FJ977649	FJ977680	FJ977741

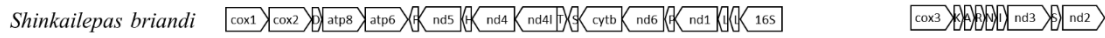
Supplementary table S4. Partitions and best-fit models in RAxML and MrBayes given by PartitionFinder v.1.1.0.

Partitions and best-fit models in RAxML		Partitions and best-fit models in MrBayes	
<i>Big mt dataset</i>		<i>Big mt dataset</i>	
<i>Model used</i>		<i>Model used</i>	
protein-coding genes 1 st codon	GTR+I+G	protein-coding genes 1 st codon	GTR+I+G
protein-coding genes 2 nd codon	GTR+I+G	protein-coding genes 2 nd codon	GTR+I+G
protein-coding genes 3 rd codon	GTR+I+G	protein-coding genes 3 rd codon	F81+I+G
<i>12S + 16S</i>	GTR+I+G	<i>12S + 16S</i>	GTR+I+G
<i>Small mt dataset</i>		<i>Small mt dataset</i>	
protein-coding genes 1 st codon	GTR+I+G	protein-coding genes 1 st codon	GTR+I+G
protein-coding genes 2 nd codon	GTR+I+G	protein-coding genes 2 nd codon	GTR+I+G
protein-coding genes 3 rd codon	GTR+I+G	protein-coding genes 3 rd codon	F81+I+G
<i>12S + 16S</i>	GTR+I+G	<i>12S + 16S</i>	GTR+I+G
<i>Nuclear dataset</i>		<i>Nuclear dataset</i>	
<i>18S</i>	GTR+I+G	<i>18S</i>	K80+I+G
<i>28S</i>	GTR+I+G	<i>28S</i>	GTR+I+G
<i>H3 1st codon</i>	GTR+I+G	<i>H3 1st codon</i>	GTR+I+G
<i>H3 2nd codon</i>	GTR+I+G	<i>H3 2nd codon</i>	JC+I+G
<i>H3 3rd codon</i>	GTR+I+G	<i>H3 3rd codon</i>	GTR+I+G

Hypothetical ancestral gene order of gastropods (Stöger and Schrödl, 2013)



Neritimorpha



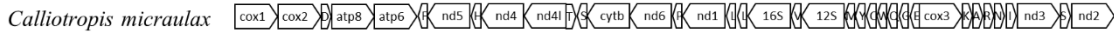
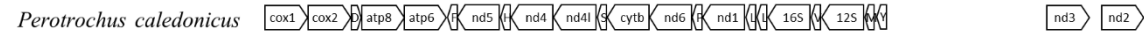
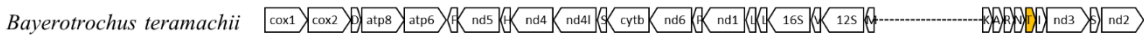
Cocculiniformia



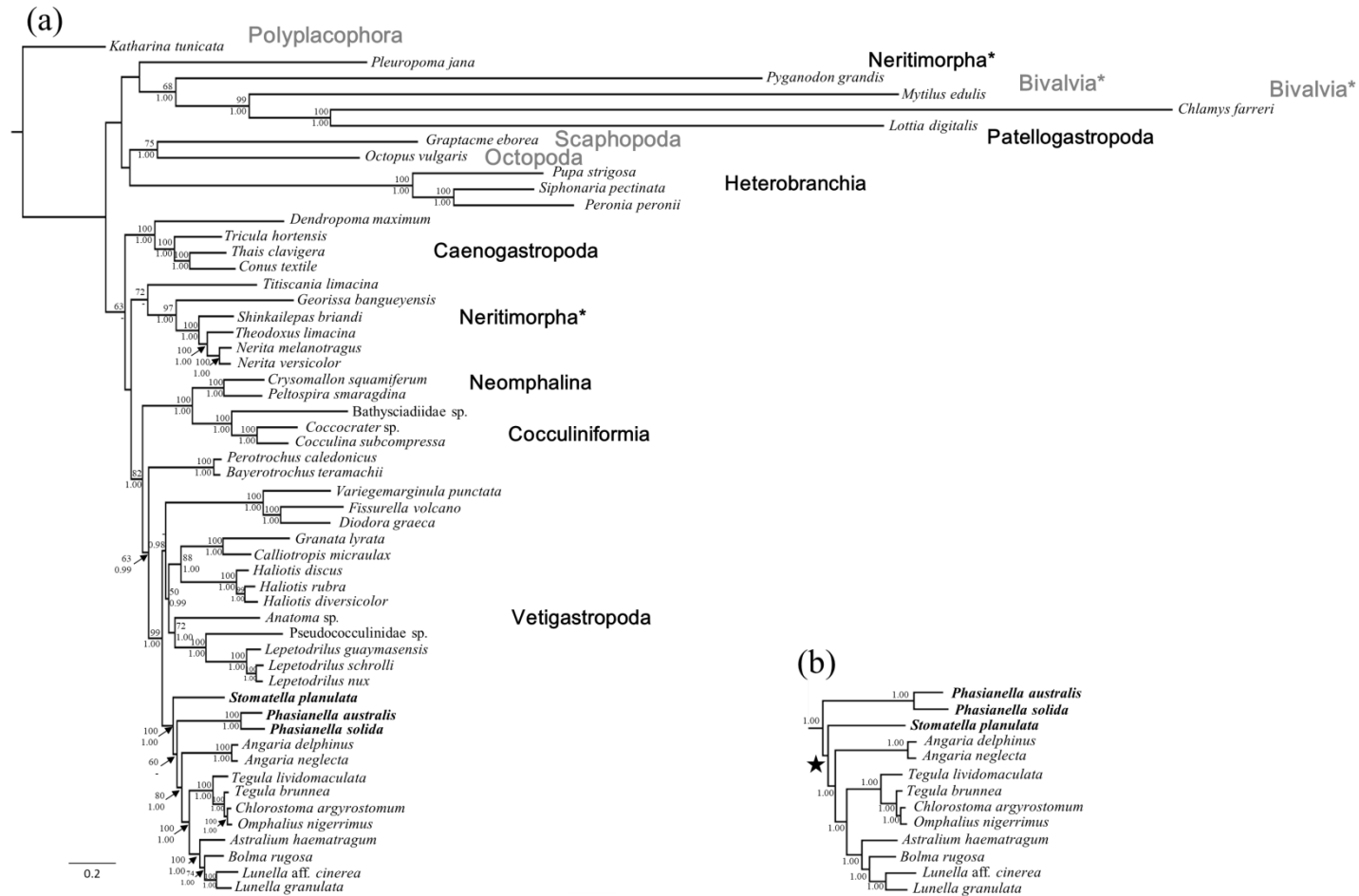
Neomphalina



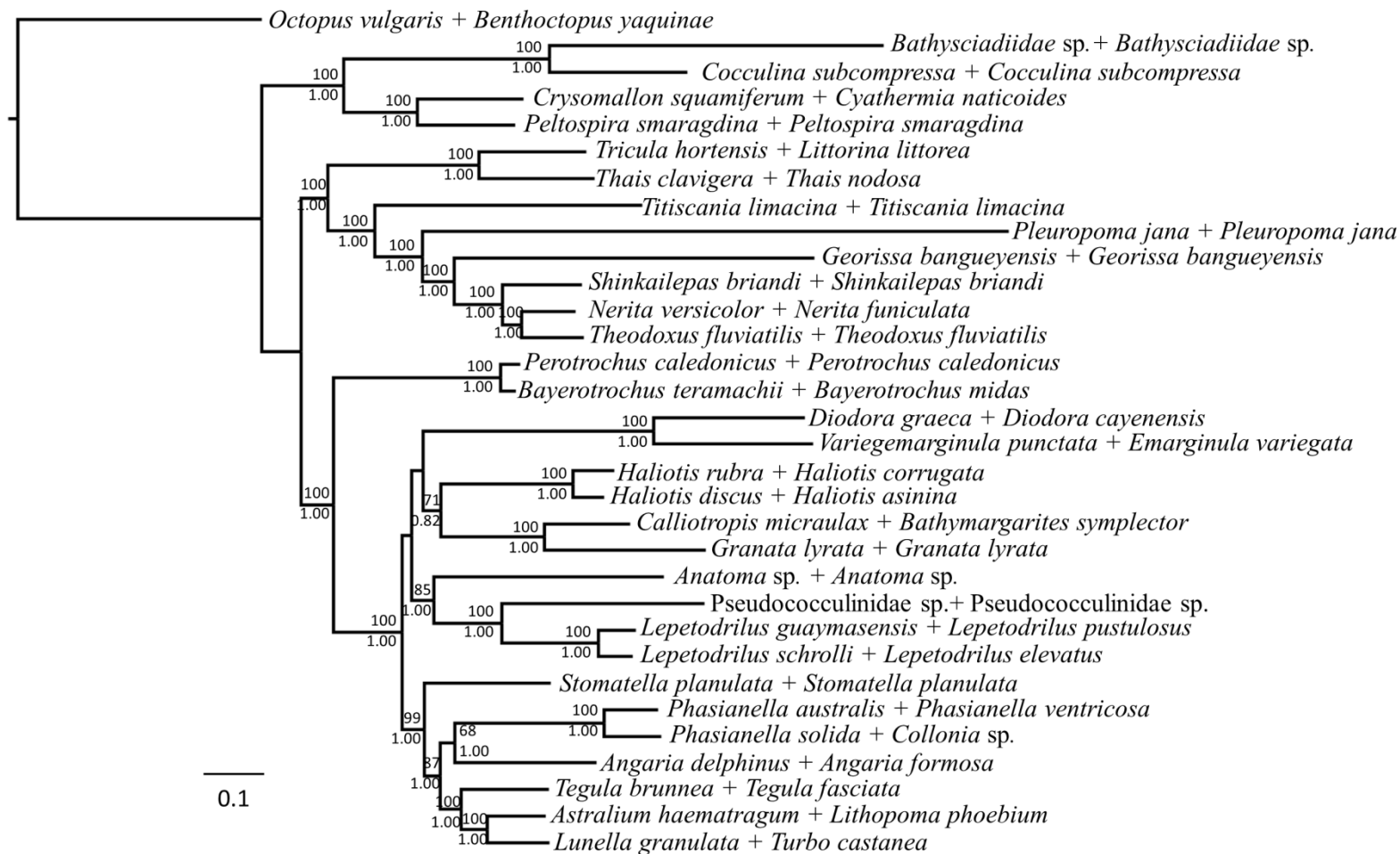
Vetigastropoda



Supplementary figure S1. Gene order of the newly reconstructed mitogenomes of deep-sea gastropods. White gaps separate the contigs obtained from NGS reads, these regions might have the missing genes (see text). The dashed line represents there was no gap in LR-PCR. Protein-coding genes with blue and tRNAs with yellow show different arrangements/directions to the hypothetical ancestral gastropod gene order. Genes without color correspond to the hypothetical ancestral gastropod gene order.



Supplementary figure S2. Phylogenetic relationships within Gastropoda inferred from the large mt dataset using partitioned ML and BI methods. (a) ML tree based on 10,393 bp nucleotide sequences combined from 13 protein-coding genes and two rRNA genes. Nodal support is shown as BP in percentage and PP; (b) partial BI tree based on the same dataset as in (a). Asterisk in (b) indicates the difference topology compare to the ML tree (a), where PP < 0.8.



Supplementary figure S3. Partitioned maximum-likelihood (ML) tree based on 14,442 bp nucleotide sequences combined from 13 mitochondrial protein-coding genes, 2 ribosomal RNA genes, and nuclear genes including *18S*, *28S*, and *H3* (combined dataset). This phylogenetic tree is identical to figure 3 without collapsing the nodes. The format of taxon names is: mitogenome used taxon + nuclear genes used taxon. Nodal supports are shown as bootstrap (BP) values in percentage / posterior probabilities (PP). Values below 50% in BP and 0.8 in PP are not shown.