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► To cite this version:

Didier Aurelle, Eric Pante, Jean-Baptiste Ledoux, Stéphane Sartoretto. Advances on the phylogenetic placement of the enigmatic octocoral *Dendrobrachia* Brook 1889. *Zootaxa*, 2019, 4674 (1), pp.117-126. 10.11646/zootaxa.4674.1.6 . hal-02320200

HAL Id: hal-02320200

<https://hal.sorbonne-universite.fr/hal-02320200v1>

Submitted on 18 Oct 2019

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1 Advances on the phylogenetic placement of the enigmatic octocoral *Dendrobrachia* Brook
2 1889

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29

30 **Abstract**

31

32 The monogeneric family Dendrobrachiidae has been a taxonomic curiosity since its
33 original description in 1889. Using one nuclear (18S) and two mitochondrial (*mtMutS* and
34 *cox1*) genes, the phylogenetic placement of Dendrobrachiidae within the Octocorallia was
35 investigated based on recently-collected specimens and museum collections. In particular,
36 the relationship between *Dendrobrachia* and its suspected close allies from the
37 Chrysogorgiidae and Ifalukellidae was examined. Phylogenetic inferences based on
38 nuclear 18S sequences were inconclusive. On the basis of mitochondrial *cox1* and
39 *mtMutS*, the hypothesis that *Dendrobrachia* is closely related to the Chrysogorgiidae or the
40 Ifalukellidae could be rejected with confidence. *Dendrobrachia* appeared distantly related
41 to all octocoral groups considered here. However, the phylogenetic placement of
42 *Dendrobrachia* could not be further clearly resolved.

43

44 **Keywords**

45 Octocorallia, Antipatharia, Dendrobrachiidae, Chrysogorgiidae, Ifalukellidae, mitochondrial
46 DNA, Mediterranean Sea

47

48 **Introduction**

49

50 Octocorals are ecologically important species which can be found in very diverse
51 ecological conditions, from shallow to deep waters, and from tropical to cold waters
52 (Fabricius and Alderslade 2001; Watling et al. 2011; Ledoux and Antunes 2018). Before

53 the advent of molecular tools, the taxonomy of this group was solely based on
54 morphological characters, including colony and sclerite shapes. The use of molecular
55 phylogenies challenged the monophyly of most traditional clades inside the Octocorallia
56 (McFadden et al. 2006). This illustrates the difficulty of relying on morphology alone for
57 octocoral taxonomy. For example, molecular markers demonstrated the polyphyly of the
58 Alcyoniidae family (McFadden and Van Ofwegen 2013), and recently discovered species
59 morphologically similar to *Alcyonium* indeed corresponded to a new genus, *Complexum*
60 Van Ofwegen et al. 2014.

61 The family Dendrobrachiidae Brook 1889, with a single genus (*Dendrobrachia*) and
62 originally a single species (*D. fallax*), has presented a taxonomic challenge since its
63 description. The first two specimens of this family, collected off Ascension Island (South
64 Atlantic) during the Challenger expedition (1872-1876), were first considered as unusual
65 antipatharians by Brook (1889) due to the structure of their spiny proteinaceous axis
66 covered with ridges and spines and the lack of a hollow core (Daly et al. 2007). Brook
67 recognized *Dendrobrachia* as harbouring “a curious medley of characters.” While polyp
68 characteristics (and notably the number of tentacles and mesenteries) could not be studied
69 due to poor preservation, it was nevertheless noted by Brook (1889) that the taxon had
70 retractile, pinnate tentacles (making him hesitate between a placement in the Octocorallia
71 and a placement in the Antipatharia) and that the specimens entirely lacked sclerites. Van
72 Beneden (1897) observed that *Dendrobrachia*'s tentacles were typical of octocorals, but
73 noted that without additional information about their number, as well as the number and
74 arrangement of mesenteries and the overall organisation of polyps, its taxonomic status as
75 antipatharian should remain unchanged. Four new specimens were collected in 1901 off
76 Cape Verde (North Atlantic) and examined by Thomson (1910) who was able to determine
77 the presence of eight tentacles, but leaving the taxonomic status unchanged.

78 Opresko and Bayer (1991), based on better-preserved material from Australia and Florida,
79 could unequivocally place *Dendrobrachia* in the Octocorallia. The authors described two
80 additional species (*D. paucispina* and *D. multispina*) and noted the close resemblance of
81 polyps from *Dendrobrachia* with two species of *Trichogorgia* Hickson, 1904 that also lack
82 sclerites, as well as anatomical similarities with the polyps of *Chrysogorgia* Duchassaing &
83 Michelotti, 1864 and *Stephanogorgia* Bayer & Muzik 1976, both belonging to the
84 Chrysogorgiidae Verrill, 1883. These authors also noted the similarity of *Dendrobrachia*
85 with *Ifalukella* Bayer, 1955, family Ifalukellidae Bayer, 1955. It is worth noting that the
86 *Dendrobrachia* specimens examined by Opresko and Bayer were found in the
87 *Chrysogorgia* collection of the South Australia Museum. Currently there are five described
88 species in the genus *Dendrobrachia* (see Material and methods).

89 A molecular phylogeny based on nuclear rDNA 18S placed *D. paucispina* Opresko &
90 Bayer, 1991 among octocorals (Berntson et al. 1999). In this last study, *Dendrobrachia*
91 appeared close to the pennatulacean *Umbellula* Gray, 1870, but with long branches for
92 both taxa, and with a reduced number of octocorals (11) included in the dataset. A
93 subsequent study using more octocoral species (41), again with 18S, indicated that
94 *Dendrobrachia* could be phylogenetically related to *Corallium* Cuvier, 1798 and *Paragorgia*
95 Milne Edwards, 1857 (Berntson et al. 2001). In this later study, *D. paucispina* even
96 appeared positioned between two *Corallium* species, although with poor bootstrap
97 support. A similar grouping of *Dendrobrachia* with *Corallium* was recovered in Strychar et
98 al. (2005) based on 18S. Even if there are some similarities in polyp morphology for these
99 three genera, this positioning is puzzling considering the lack of sclerites and the very
100 specific structure of the skeletal axis in *Dendrobrachia* (proteinaceous without hollow
101 core). In their second study, Berntson et al. (2001) also included one representative of the
102 Chrysogorgiidae, which grouped with primnoids rather than with *Dendrobrachia* and the
103 scleraxonians *Corallium* and *Paragorgia*. Though confirming that *Dendrobrachia* species

104 are indeed octocorals, these results did not solve the question of their phylogenetic
105 positioning within the subclass Octocorallia. The affinities of *Dendrobrachia* in octocorals
106 therefore remained to be refined as underlined by Berntson et al. (2001).

107 Up to now, no molecular study had been performed on Mediterranean *Dendrobrachia*,
108 thereby leaving uncertainties on their relationships with other species from the same
109 genus. Our first goal here was to precise the phylogenetic position of *Dendrobrachia* using
110 mitochondrial and nuclear markers. We were especially interested in the phylogenetic
111 relationships of *Dendrobrachia* in the octocorals group (McFadden et al. 2006), and to test
112 the relationship among *Dendrobrachia* and its suspected close allies from the
113 Chrysogorgiidae and Ifalukellidae (Opresko and Bayer 1991). A second goal was to gain
114 insight into the genetic divergence among *D. paucispina*, *D. multispina* and *D. bonsai*, for
115 which we could obtain specimens to analyse.

116

117

118 **Material and methods**

119 **Museum collections**

120

121 There are currently five species in the genus *Dendrobrachia*. In addition to the type
122 specimen described by Brook, *D. fallax*, *D. paucispina* and *D. multispina* were erected by
123 Opresko and Bayer. Type material from *D. paucispina* was utilized in Berntson et al.
124 (1999, 2001). Given the little material remaining from these legacy specimens, we have
125 not attempted genetic analysis. Two species were recently described by López-González
126 and Cunha (2010): *D. sarmentosa* and *D. bonsai*. The first species was proposed based
127 on the material examined by Thomson (1910), while the second, *D. bonsai*, was described
128 based on more recent collections (2007) made in the southern Mediterranean Sea. We
129 attempted to perform genetic analyses from material deposited by López-González and

130 Cunha (2010) at the Museum national d'Histoire Naturelle (MNHN, Paris, France; MNHN-
131 IK-2009-219, holotype, MNHN-IK-2009-220, paratype), without success. We also
132 attempted to perform genetic analyses from material obtained from the Zoological Museum
133 of the Smithsonian Institution: *D. multispina* (USNM 87770; holotype) and *D. paucispina*
134 (USNM 87768 and USNM 87769, syntypes). Amplifications and sequencing only
135 succeeded for the 18S locus of *D. multispina* (see results) and we did not get any
136 mitochondrial sequence for these samples.

137

138 **Complementary sampling**

139

140 In addition to museum specimens, Sartoretto (2012) described specimens of *D. bonsai*
141 collected from the northern Mediterranean Sea (Corsica) in 2010; these latter specimens
142 were sufficiently well preserved to attempt molecular analysis. Two samples were
143 collected in the Canyon of Porto (depth: 218 and 300m), using ROV 'Super Achille'
144 operated from the Research vessel 'Minibex' during the CORSEACAN cruise. The
145 presence of sexually mature polyps during summer in Corsica thus confirms the
146 observations of López-González and Cunha (2010) on the presence of reproductive
147 colonies in the Mediterranean Sea and Gulf of Gadiz. The full description of the samples
148 and sampling sites is available in Sartoretto (2012). The specimens analysed here were
149 deposited in the Cnidaria collection at the French National Museum of Natural History
150 (MNHN), with the voucher number IK-2012-13885.

151

152 **Molecular analyses**

153

154 Total DNA from recent and older museum specimens was extracted with a Qiagen
155 DNeasy kit following the manufacturer's instructions. The DNA of museum specimens was

156 extracted in a different room where no manipulation of octocorals DNA has been
157 performed before. The mitochondrial loci *cox1* and *mtMutS* were amplified with the primers
158 COICniF / R (Calderon et al. 2006) and ND42599F / Mut3458R (Sánchez et al. 2003),
159 respectively. The nuclear ribosomal 18S locus was amplified with primers A1 / B1
160 (Strychar et al. 2005). The PCR conditions for a 25 µL final volume and for all markers
161 were: Promega PCR buffer 1X, MgCl₂ 2.5 mM, 0.25 mM of each dNTP, 0.5 µM of each
162 primer, Flexigotaq polymerase (Promega) 0.625 U, and 2.5 µl of DNA. The PCR program
163 was: 5 min at 94°C, 35 cycles with [1 min at 94°C, 1 min at annealing temperature, 1 min
164 at 72°C], and a final extension of 10 min at 72°C. The annealing temperature was 45°C for
165 *cox1*, 53°C for *mtMutS*, and 50°C for 18S. The PCR products for *cox1* (as PCR bands
166 were faint) and 18S were cloned with the pGEM®-T Easy Vector (Promega) according to
167 manufacturer's instructions and subsequently sequenced with SP6 and T7 primers.

168

169 **Phylogenetic analyses**

170

171 In the present phylogenetic study, we included all genera cited by Opresko and Bayer
172 (1991) as potential allies to the Dendrobrachiidae: *Chrysogorgia*, *Stephanogorgia*,
173 *Trichogorgia* and *Ifalukella*. Additional sequences from these genera were downloaded
174 from GenBank mainly on the basis of the dataset of Pante et al. (2012). We added to this
175 dataset multiple sequences of *Corallium*, because of the potential affinities of
176 *Dendrobrachia* with this genus (GenBank accession numbers, Table S1); the *Corallium*
177 species included here (*C. kishinouyei* Bayer, 1996, *C. niobe* Bayer, 1964, *C. rubrum*,
178 Linnaeus, 1758) are representative of the phylogenetic diversity of the genus (clades 1A,
179 1B and 2 from Tu et al. 2015).

180 The choice of an outgroup is not easy for building octocoral phylogenies, especially for the
181 *mtMutS* gene which is not found in any other mitochondrial genome among metazoans

182 (Pont-Kingdon et al. 1998). We choose the stoloniferous octocoral *Cornularia pabloi*
183 McFadden and van Ofwegen 2012 as outgroup for other octocorals, as a phylogeny based
184 on concatenated mitochondrial and nuclear genes and 130 octocoral taxa, and rooted to
185 multiple species of hexacorals, revealed the genus *Conularia* as a sister group to all other
186 octocorals (McFadden and van Ofwegen 2012). For *cox1*, based on a BLAST search on
187 Genbank, we used the antipatharian *Leiopathes glaberrima* (Esper, 1788) as outgroup. At
188 last, for 18S, the same BLAST search with our newly generated *Dendrobrachia* sequence
189 led to the choice of the Scleractinian *Phyllangia americana mouchezii* Lacaze-Duthiers,
190 1897 as an outgroup. Sequences were aligned with the MUSCLE (Edgar 2004) software
191 implemented in UGENE (Okonechnikov et al., 2012). For *mtMutS*, considering some
192 uncertainties in the alignment, we used GBLOCK (Castresana 2000) on Phylogeny.fr
193 (Dereeper et al., 2008) with options allowing smaller final blocks, gap positions within the
194 final blocks and less strict flanking positions. We also used a dataset with concatenated
195 sequences of *cox1* and *mtMutS*. For all phylogenetic analyses, we kept only one
196 representative of each sequence type when different specimens had the same sequence.
197 The details on the complete dataset including GenBank accession numbers are provided
198 in Table S1.

199 We performed a Maximum Likelihood (ML) phylogenetic reconstruction with IQ-TREE
200 1.6.8 (Nguyen et al. 2014) and a Bayesian Inference (BI) with MrBayes 3.2 (Huelsenbeck
201 & Ronquist 2001, Ronquist & Huelsenbeck 2003). For ML we used the ModelFinder option
202 of IQ-TREE (Kalyaanamoorthy et al., 2017) for all analyses. For *cox1* and *mtMutS* the
203 retained models were K3Pu+F+I+G4 and TVM+F+R3 respectively. For 18S we performed
204 a preliminary phylogenetic analysis, but regarding the puzzling results we did not go
205 further with this marker (see results). For concatenated alignments, the best fitting data
206 partitions and models of evolution were determined with PartitionFinder implemented in
207 IQ-TREE, with each partition with its own evolution rate (Chernomor et al., 2016; Lanfear

208 et al. 2012). The retained model was a partition of the two markers, with the K3Pu+F+G4
209 and TPM3+F+G4 for *cox1* and *mtMutS* respectively. For BI we used a GTR model of
210 evolution, with a GAMMA model of rate heterogeneity, $2 \cdot 10^6$ generations, a sample
211 frequency of 100 and a burnin of 50%. We assumed convergence of the MCMC analysis
212 when the average standard of split frequency was below 0.01, when the log probability of
213 the data did not show any trend, and when the potential scale reduction factors were close
214 to 1.0. Trees were visualized with FigTree 1.4.4 (Rambaut 2012).

215

216

217 **Results**

218

219 The numbers of sequences for the final alignment were 47, 34 and 110 for 18S, *cox1* and
220 *mtMutS* respectively, with the corresponding alignment lengths of 233, 600 and 671 bp.
221 For 18S and *cox1*, the two *D. bonsai* sequences obtained by cloning and sequencing in
222 both directions were identical. The two 18S sequences obtained for *D. multispina* were
223 also identical.

224 With 18S, we obtained a puzzling placement of two *C. rubrum* sequences
225 (originating from the same individual and produced by molecular cloning), one clustering
226 with *D. multispina* and *D. paucispina*, the other clustering other *Corallium* sequences.
227 These two *Dendrobrachia* sequences were well separated from the 18S sequence
228 obtained from the Mediterranean *D. bonsai*. These results could be due to the short length
229 of the sequences included in the analysis, of very high intra-genomic variation for
230 ribosomal sequences, as previously reported for cnidarians (e.g. Vollmer and Palumbi
231 2004; Calderon et al. 2006; Aurelle et al. 2011), or, more probably, from contaminations,
232 especially when considering old museum specimens.

233 The *cox1* phylogenetic reconstruction (Fig. 1) gave generally low bootstrap and
234 posterior probabilities for inner nodes, whereas external groups were better supported.
235 Nevertheless, the group of octocoral sequences (including *Dendrobrachia*) sister to *C.*
236 *pabloi* was well supported by BI and ML. In the ML reconstruction presented in Fig. 1, *D.*
237 *bonsai* was placed, though with low support, in a sister position to a clade containing
238 *Chrysogorgia*, *Isidella* Gray, 1857, *Narella* Gray, 1870, and *Heliopora* de Blainville, 1830
239 among other species. *Funiculina* Lamarck, 1816, *Ellisella* Gray, 1857 and *Corallium*
240 sequences were in sister position to this previous group. With BI, *D. bonsai* was in sister
241 position to all other octocorals, except *C. pabloi*.

242 On the basis of *mtMutS* (Fig. 2), *D. bonsai* was placed on a long branch, in a sister
243 position to all other octocorals except *C. pabloi* (used to root the tree). The grouping of
244 non-*Dendrobrachia* sequences was well supported. The next split among octocorals
245 separated *Heliopora coerulea* (Pallas, 1766) from other species, but with low support.
246 Again, shallow nodes were generally better supported than deep ones.

247 The concatenated *cox1* / *mtMutS* dataset included 33 sequences and 1271 bp
248 (Fig. 3), *Dendrobrachia bonsai* appeared again on a long branch, in a sister position to all
249 other octocorals except *C. pabloi* (used to root the tree). The relationships between groups
250 of other octocorals were generally poorly supported. Good support was observed for
251 external groupings such as for example Isididae Lamouroux, 1812, Coralliidae Lamouroux,
252 1812 or a clade including *Acanthoaxis* van Ofwegen & McFadden, 2009, *Paramuricea*
253 Kölliker, 1865, and *Eunicella* Verrill, 1869 among other species.

254

255

256 **Discussion**

257 **Phylogenetic position of *Dendrobrachia* among octocorals**

258

259 Since its discovery and its first assignation to the Order Antipatharia, the phylogenetic
260 position of *Dendrobrachia* remained unclear due to its unusual morphological
261 characteristics. Previous molecular studies confirmed *Dendrobrachia* as an octocoral
262 genus, on the basis of 18S nuclear sequences (Berntson et al. 1999, 2001). Nevertheless,
263 the peculiar characteristics of these species, as well as its puzzling position in the
264 octocoral 18S phylogeny (close to the pennatulacean *Umbellula* sp.), called for further
265 confirmation of this result. Our molecular data support the observation that *Dendrobrachia*
266 is a morphologically and genetically atypical octocoral. For the first time, we could amplify
267 and sequence the *mtMutS* locus in this genus. This locus is a synapomorphy of octocorals
268 (e.g. Bilewitch and Degnan 2011). The phylogeny obtained for *cox1*, rooted with an
269 antipatharian, independently positioned *D. bonsai* among octocorals, thus supporting the
270 result obtained for *D. paucispina* with 18S (Berntson et al. 1999, 2001).

271 The positioning of *Dendrobrachia* among octocorals was not clearly resolved with our
272 datasets. Our *cox1* and *mtMutS* phylogenies positioned it in a sister position to most
273 octocoral groups. This indicates that a more extended taxon sampling will be critical in
274 establishing the proper phylogenetic placement of the genus. Including all the potential
275 phynogenetic allies proposed by Opresko and Bayer (1991) in our analyses, we were able
276 to reject this hypothesis: *Dendrobrachia* is not closely related to any of the nominal
277 Chrysogorgiidae and Ifalukellidae. The long branches leading to *Dendrobrachia*, and its
278 inner positioning, rather points to an ancient divergence of *Dendrobrachia* among
279 octocorals. Such high divergence could also be responsible for the difficulty of getting well-
280 resolved phylogenies. McFadden et al. (2006) obtained better support for inner
281 relationships among octocorals by using more mitochondrial markers and species. It would
282 be interesting to use additional nuclear markers (such as ultraconserved elements or
283 exons; Quattrini *et al.*, 2018) to test the positioning of *Dendrobrachia*. Such approaches
284 will allow the use of non-octocoral species, which will be particularly useful to root the tree

285 and to clarify the most inner phylogenetic relationships. One hypothesis to test would be
286 the lack of sclerites an ancestral character, appearance of sclerites one or multiple times
287 during octocoral evolution. The alternative scenario would be that the *Dendrobrachia*
288 organisation is a derived, though ancient (when considering the branch length) state in
289 octocoral evolution. In this context one can note that there are other examples of
290 octocorals without sclerites, at different positions in the octocorals phylogeny, and with
291 cases where the absence of sclerites would be derived (Benayahu et al., 2017). This
292 indicates that this character was modified several times during evolution. A reconstruction
293 of ancestral states would be interesting here, but it will require a well resolved phylogeny.

294

295 One of our objectives here was to compare the sequences of three *Dendrobrachia*
296 species. Apart from *D. bonsai*, we could only obtain an 18S sequence for a museum
297 specimen of *D. multispina*, which we compared with the previously published 18S
298 sequence of *D. paucispina* (Berntson et al. 1999, 2001). Due to the previously mentioned
299 puzzling results obtained with 18S we could not go further on this topic. Nevertheless, it
300 would be very interesting to compare with informative markers the different *Dendrobrachia*
301 species. Due to their low evolution rate in octocorals, and its uniparental inheritance,
302 mitochondrial DNA alone may not be sufficient here. Testing the monophyly of this genus
303 would be useful to understand if their peculiar morphological characteristic evolved only
304 once, or could be another example of morphological convergence among octocorals (e.g.
305 the stoloniferous growth form; McFadden and van Ofwegen, 2012). Apart from analysing
306 more samples, it could be necessary to consider a large number of independent nuclear
307 markers (Herrera et al., 2016; Pante et al., 2015; Quattrini *et al.*, 2018). Considering the
308 difficulty of PCR amplification from museum samples, getting new live specimens would
309 probably be necessary for such protocol. The previously mentioned enrichment methods

310 for the targeted sequencing of numerous loci appears as a very promising tool in this
311 context (Quattrini et al., 2018).

312

313 **Acknowledgements**

314 We thank the molecular biology service of the IMBE (Marjorie Selva, Caroline Rocher,
315 Anne Haguenaer). We are thankful to Helmut Zibrowius for discussions on octocorals
316 taxonomy, as well as Ewan Berntson and Scott France for discussion on *Dendrobrachia*.
317 We thank the Smithsonian Institution for the *Dendrobrachia specimens* and Geoff Keel
318 (Smithsonian) and Anne Chenuil-Maurel (IMBE) for their help in obtaining specimens. We
319 thank Cathy McFadden for insightful discussions about *Dendrobrachia* at the MNHN
320 Octocoral Workshop held in Concarneau in 2017. We thank the project "Bibliothèque du
321 Vivant" for funding this project. This project was supported by the network "Bibliothèque du
322 Vivant" funded by the CNRS, the Muséum National d'Histoire Naturelle, the INRA and the
323 CEA (Centre National de Séquençage). We thank an anonymous reviewer who helped
324 improving the manuscript.

325

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345 Figures

346

347 **Figure 1.** ML tree for *cox1*. Only bootstrap proportions and posterior probabilities higher
348 than 80% and 0.9 (respectively) are presented, at the left of the corresponding groupings.
349 *Dendrobrachia* sequences are indicated with a filled circle. Genbank accession numbers
350 are associated with each sequence.

351

352 **Figure 2.** ML tree for *mtMutS*. Only bootstrap proportions and posterior probabilities higher
353 than 80% and 0.9 (respectively) are presented, at the left of the corresponding groupings.
354 *Dendrobrachia* sequences are indicated with with a filled circle. For clarity reasons, the
355 support values of some inner nodes inside the *Chrysogorgia* group are not presented.
356 Genbank accession numbers are associated with each sequence.

357

358 **Figure 3.**

359 **Figure 2.** ML tree for *mtMutS* and *cox1* concatenated. Only bootstrap proportions and
360 posterior probabilities higher than 80% and 0.9 (respectively) are presented, at the left of
361 the corresponding groupings. *Dendrobrachia* sequences are indicated with a filled circle.

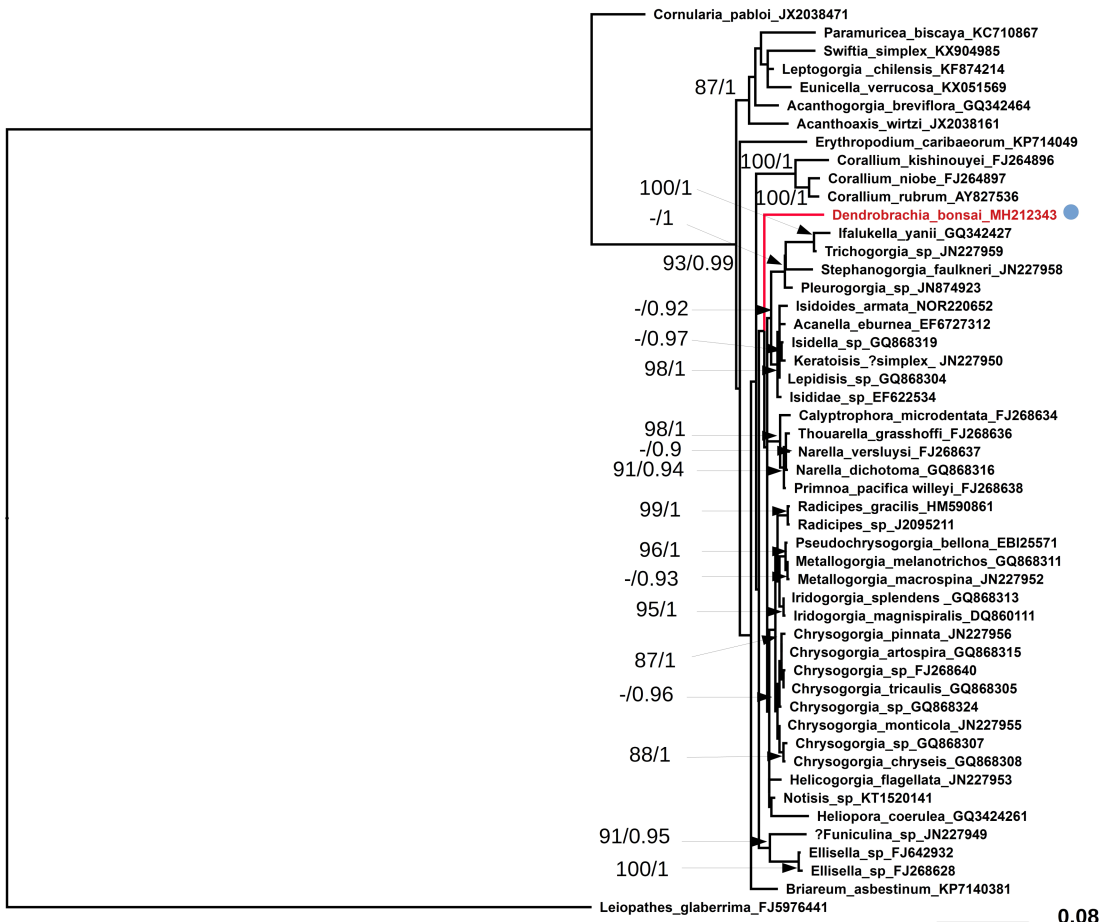
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363 Supplementary material

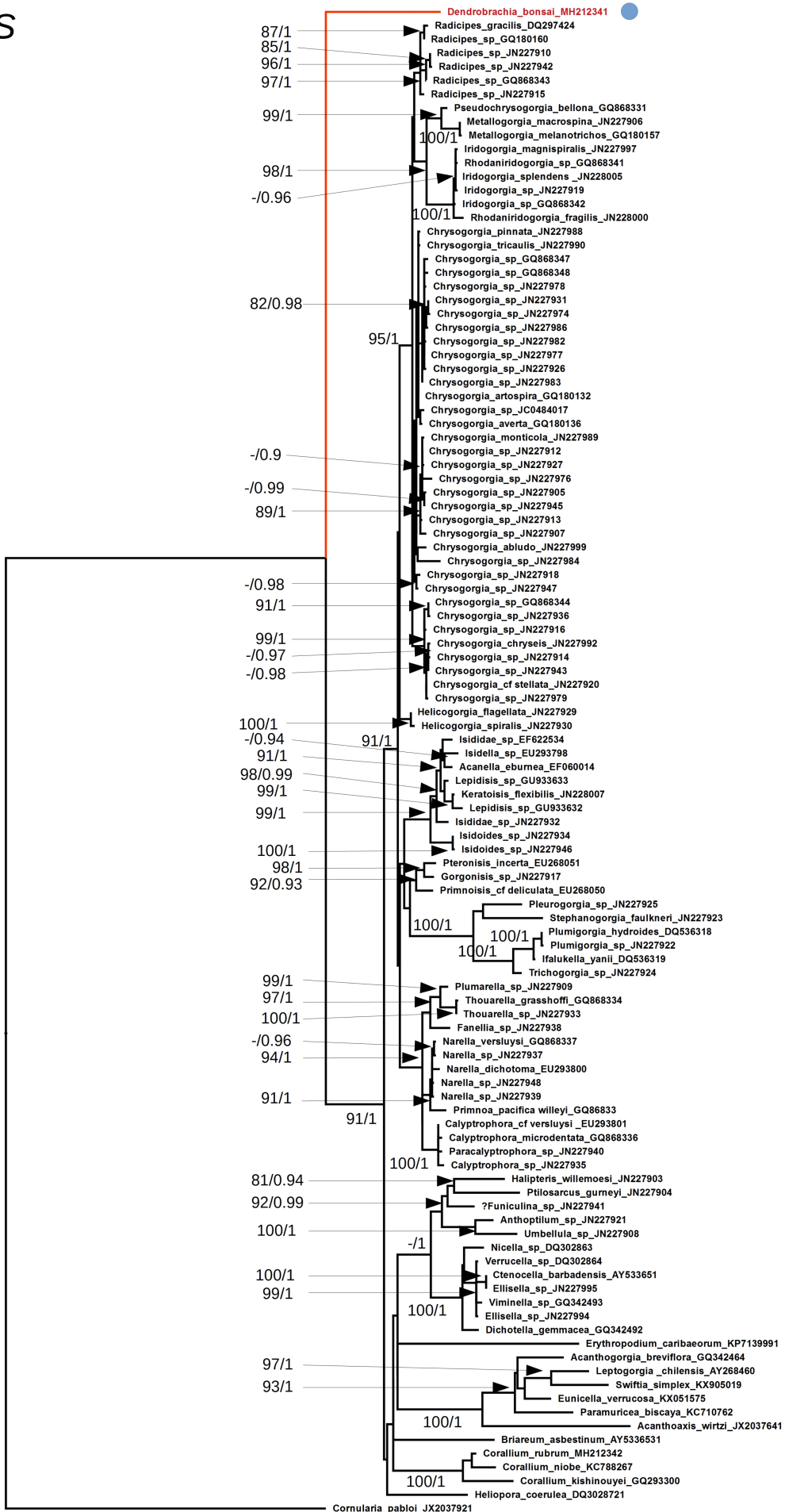
364

365 **Table S1.** Origin of all sequences initially used in the article. Collection date, geographic
366 coordinates, depth, and genetic markers sequenced for specimens used in this study.
367 GenBank accession numbers corresponding to each marker are given in the final three
368 columns.

COXI



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cox1 mtMutS

