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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

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

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Abstract

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

Keywords

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

Introduction

Octocorals are ecologically important species which can be found in very diverse ecological conditions, from shallow to deep waters, and from tropical to cold waters (Fabricius and Alderslade 2001; Watling et al. 2011; Ledoux and Antunes 2018). Before the advent of molecular tools, the taxonomy of this group was solely based on morphological characters, including colony and sclerite shapes. The use of molecular phylogenies challenged the monophyly of most traditional clades inside the Octocorallia (McFadden et al. 2006). This illustrates the difficulty of relying on morphology alone for octocoral taxonomy. For example, molecular markers demonstrated the polyphyly of the Alcyoniidae family (McFadden and Van Ofwegen 2013), and recently discovered species morphologically similar to *Alcyonium* indeed corresponded to a new genus, *Complexum* Van Ofwegen et al. 2014.

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

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

A molecular phylogeny based on nuclear rDNA 18S placed *D. paucispina* Opresko & Bayer, 1991 among octocorals (Berntson et al. 1999). In this last study, *Dendrobrachia* appeared close to the pennatulacean *Umbellula* Gray, 1870, but with long branches for both taxa, and with a reduced number of octocorals (11) included in the dataset. A subsequent study using more octocoral species (41), again with 18S, indicated that *Dendrobrachia* could be phylogenetically related to *Corallium* Cuvier, 1798 and *Paragorgia* Milne Edwards, 1857 (Berntson et al. 2001). In this later study, *D. paucispina* even appeared positioned between two *Corallium* species, although with poor bootstrap support. A similar grouping of *Dendrobrachia* with *Corallium* was recovered in Strychar et al. (2005) based on 18S. Even if there are some similarities in polyp morphology for these three genera, this positioning is puzzling considering the lack of sclerites and the very specific structure of the skeletal axis in *Dendrobrachia* (proteinaceous without hollow core). In their second study, Berntson *et al.* (2001) also included one representative of the Chrysogorgiidae, which grouped with primnoids rather than with *Dendrobrachia* and the scleraxonians *Corallium* and *Paragorgia*. Though confirming that *Dendrobrachia* species are indeed octocorals, these results did not solve the question of their phylogenetic positioning within the subclass Octocorallia. The affinities of *Dendrobrachia* in octocorals therefore remained to be refined as underlined by Berntson et al. (2001).

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

Material and methods

Museum collections

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

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

Complementary sampling

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

Molecular analyses

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

Phylogenetic analyses

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

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

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

We performed a Maximum Likelihood (ML) phylogenetic reconstruction with IQ-TREE 1.6.8 (Nguyen et al. 2014) and a Bayesian Inference (BI) with MrBayes 3.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). For ML we used the ModelFinder option of IQ-TREE (Kalyaanamoorthy et al., 2017) for all analyses. For *cox1* and *mtMutS* the retained models were K3Pu+F+I+G4 and TVM+F+R3 respectively. For 18S we performed a preliminary phylogenetic analysis, but regarding the puzzling results we did not go further with this marker (see results). For concatenated alignments, the best fitting data partitions and models of evolution were determined with PartitionFinder implemented in IQ-TREE, with each partition with its own evolution rate (Chernomor et al., 2016; Lanfear et al. 2012). The retained model was a partition of the two markers, with the K3Pu+F+G4 and TPM3+F+G4 for *cox1* and *mtMutS* respectively. For BI we used a GTR model of evolution, with a GAMMA model of rate heterogeneity, 2.10^6 generations, a sample frequency of 100 and a burnin of 50%. We assumed convergence of the MCMC analysis when the average standard of split frequency was below 0.01, when the log probability of the data did not show any trend, and when the potential scale reduction factors were close to 1.0. Trees were visualized with FigTree 1.4.4 (Rambaut 2012).

Results

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

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

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

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

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

Discussion

Phylogenetic position of *Dendrobrachia* among octocorals

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

The positioning of *Dendrobrachia* among octocorals was not clearly resolved with our datasets. Our *cox1* and *mtMutS* phylogenies positioned it in a sister position to most octocoral groups. This indicates that a more extended taxon sampling will be critical in establishing the proper phylogenetic placement of the genus. Including all the potential phynogenetic allies proposed by Opresko and Bayer (1991) in our analyses, we were able to reject this hypothesis: Dendrobrachia is not closely related to any of the nominal Chrysogorgiidae and Ifalukellidae. The long branches leading to *Dendrobrachia*, and its inner positioning, rather points to an ancient divergence of *Dendrobrachia* among octocorals. Such high divergence could also be responsible for the difficulty of getting well-resolved phylogenies. McFadden et al. (2006) obtained better support for inner relationships among octocorals by using more mitochondrial markers and species. It would be interesting to use additional nuclear markers (such as ultraconserved elements or exons; Quattrini *et al.*, 2018) to test the positioning of *Dendrobrachia*. Such approaches will allow the use of non-octocoral species, which will be particularly useful to root the tree and to clarify the most inner phylogenetic relationships. One hypothesis to test would be the lack of sclerites an ancestral character, appearance of sclerites one or multiple times during octocoral evolution. The alternative scenario would be that the *Dendrobrachia* organisation is a derived, though ancient (when considering the branch length) state in octocoral evolution. In this context one can note that there are other examples of octocorals without sclerites, at different positions in the octocorals phylogeny, and with cases where the absence of sclerites would be derived (Benayahu et al., 2017). This indicates that this character was modified several times during evolution. A reconstruction of ancestral states would be interesting here, but it will require a well resolved phylogeny.

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

Acknowledgements

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

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Figures

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

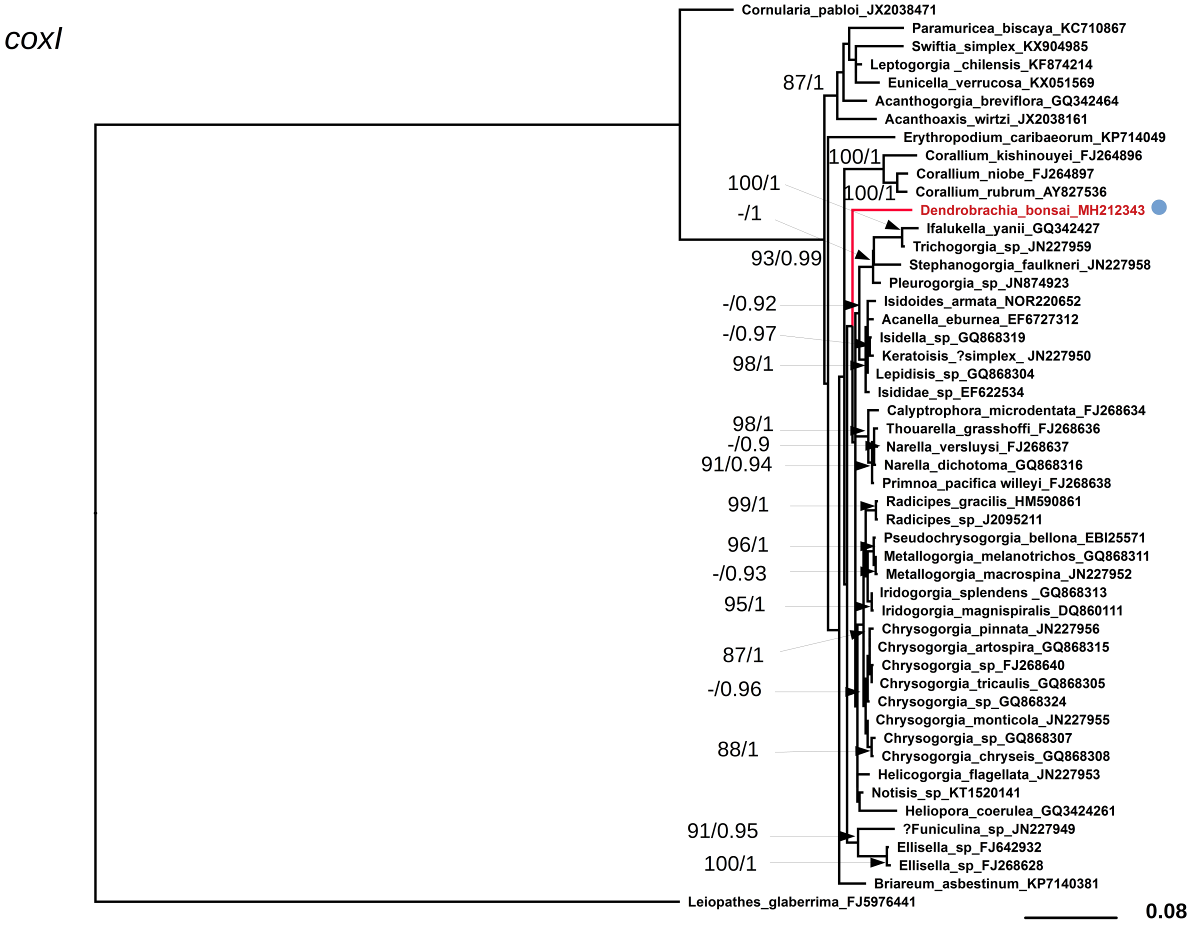
Figure 2. ML tree for *mtMutS*. Only bootstrap proportions and posterior probabilities higher than 80% and 0.9 (respectively) are presented, at the left of the corresponding groupings. *Dendrobrachia* sequences are indicated with with a filled circle. For clarity reasons, the support values of some inner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

Figure 3.

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

Supplementary material

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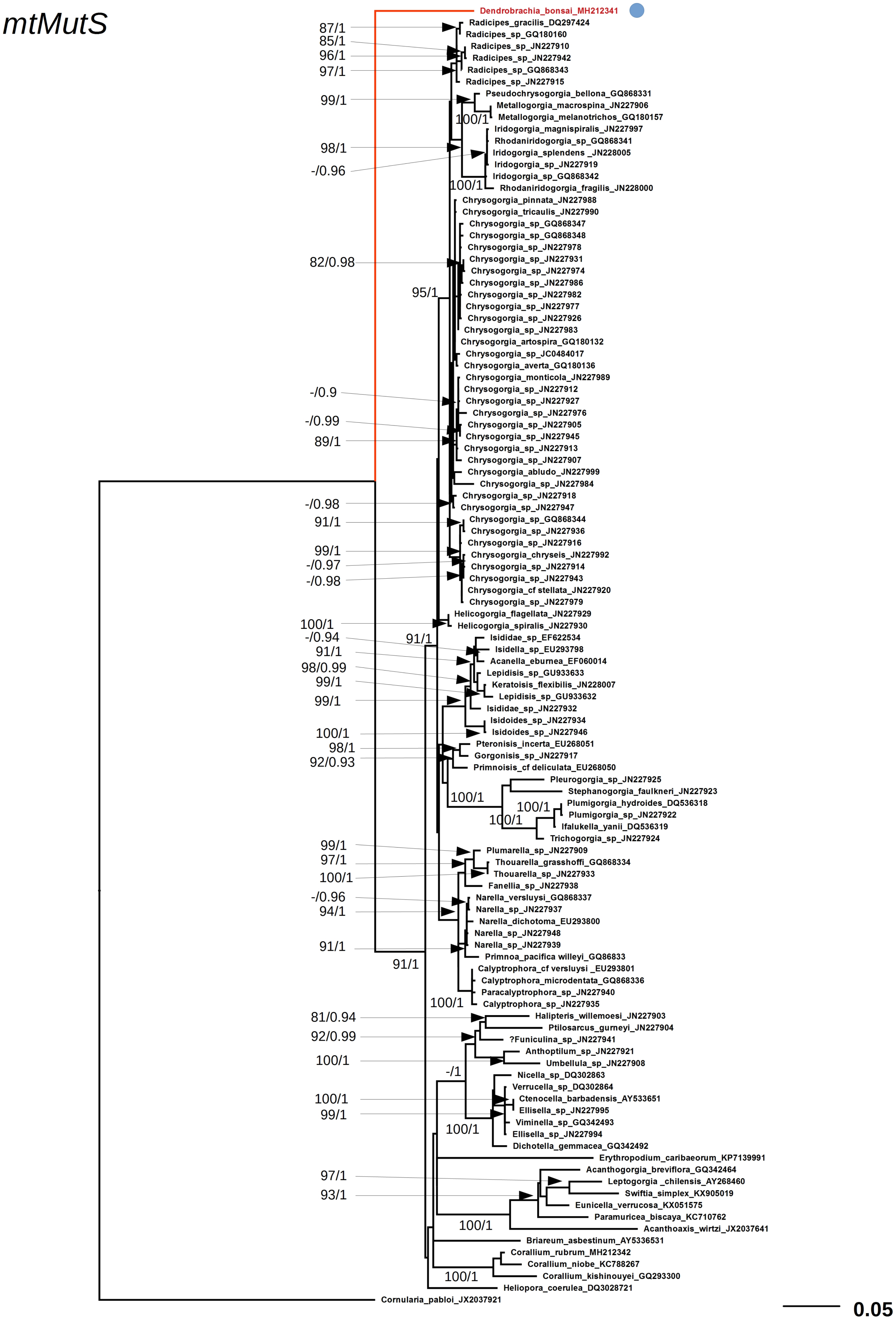
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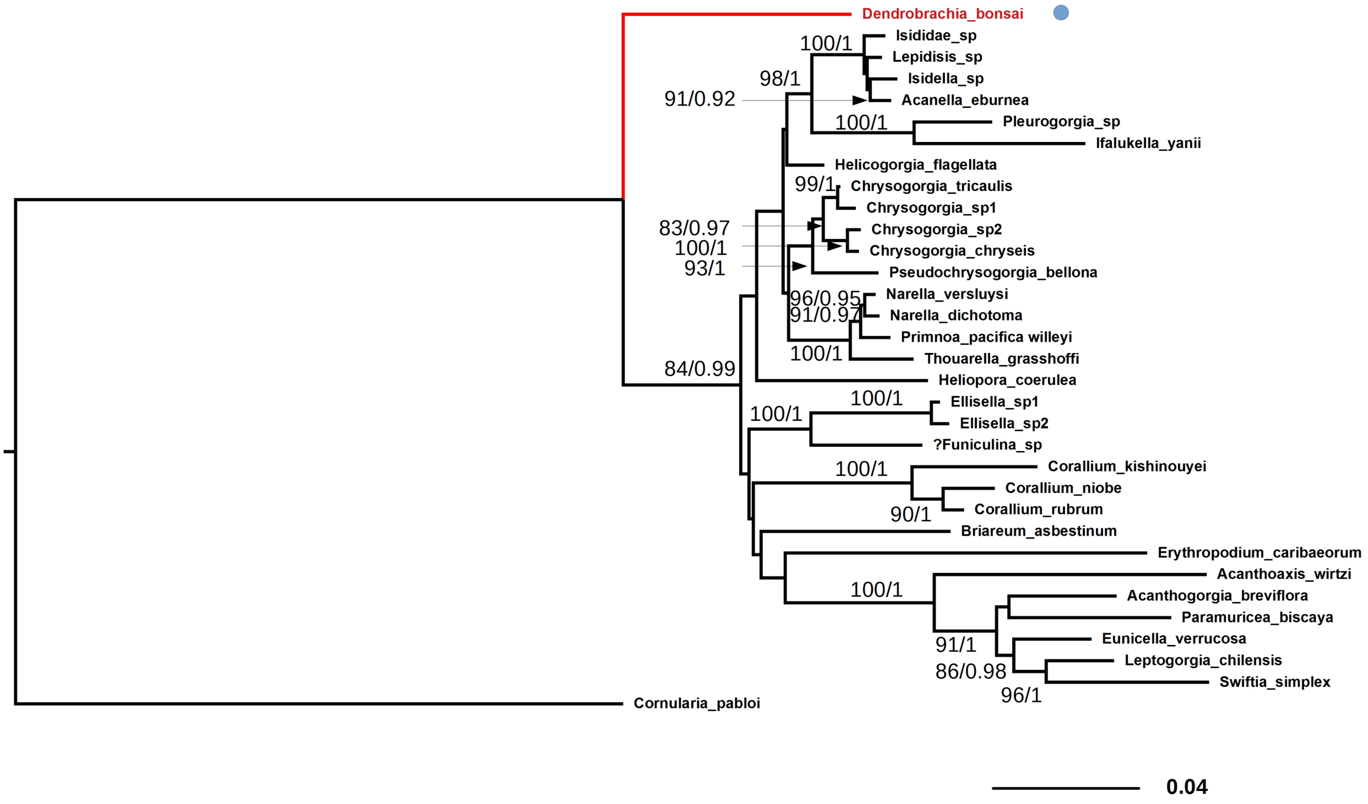
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