Phylogeny of Cladobranchia (Gastropoda: Nudibranchia): a total evidence analysis using DNA sequence data from public databases

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Abstract

Cladobranchia is a clade of charismatic and exclusively marine slugs (Gastropoda: Nudibranchia). Though Cladobranchia and its sister taxon, Anthobranchia, have been supported by molecular data, little resolution among the higher-level groups within these two clades has emerged from previous analyses. Cladobranchia is traditionally divided into three taxa (Dendronotida, Euarminida, and Aeolidida), none of which have been supported by molecular phylogenetic studies. Reconstructions of the evolutionary relationships within Cladobranchia have resulted in poorly supported phylogenies, rife with polytomies and non-monophyletic groups contradicting previous taxonomic hypotheses. In this study, we present a working hypothesis for the evolutionary history of Cladobranchia, utilizing publicly available data that have been generated since the last attempt at a detailed phylogeny for this group (we include approximately 200 more taxa and a total of five genes). Our results resolve Cladobranchia as monophyletic and provide support for a small proportion of genera and families, but it is clear that the presently available data are insufficient to provide a robust and well-resolved phylogeny of these taxa as a whole.

Keywords: Cladobranchia, Nudibranchia, marine slugs, sea slugs, phylogenetics, maximum likelihood, concatenation, 16S, 18S, 28S, COI, H3, Mollusca

Introduction

Cladobranchia is a diverse and charismatic clade of exclusively marine slugs. These organisms live in globally distributed habitats from the intertidal to the deep ocean, and are characterized by having branched digestive glands [1]. Though not as speciose as some other gastropod clades, cladobranchs have developed remarkable biological features that are rare among animals, many of which are related to defensive strategies. As this is a clade within Nudibranchia, which is characterized by the loss of the shell in adult animals [2], selection likely favored the evolution of defense mechanisms to compensate for the loss of a protective shell. The development of many different chemical and physical defense mechanisms has been hypothesized to have led to the large-scale diversification of Nudibranchia, and within it, Cladobranchia [3]. In order to understand this diversity, as well as the evolution of the ecological roles of taxa within Cladobranchia, an accurate phylogenetic framework is needed. However, given the depth of the evolutionary divergences and the diversity within this clade, reconstruction of the phylogenetic relationships among taxa in this group has proven difficult.

Both Cladobranchia (~1000 species) and its sister taxon, Anthobranchia (~2000 species) [4], have been supported as monophyletic by molecular data [1,2,5], but thus far there has been little resolution among the higher-level groups within these two clades. Within Cladobranchia, there are three traditional taxa characterized on the basis of morphology: Dendronotida, Euarminida and Aeolidida [5]. Though a number of studies on the evolutionary history of Cladobranchia have been undertaken, the majority have been limited to specific clades, often at the family or genus level (e.g., Scyllaeidae [6], Aeolidiidae [7],

Tritoniidae [8], and *Babakina* [9]). Due to this focus on more recent divergences within Cladobranchia, there is little data that either support or reject the traditional classification of the three major taxa, making it difficult to understand the deeper evolutionary history within these groups.

To date, there has been only one large-scale phylogeny attempted for Cladobranchia [1], which was based on the three most commonly used genes in nudibranch systematics: mitochondrial 16S rRNA and Cytochrome Oxidase I, and nuclear Histone 3. In this phylogeny, the majority of relationships between higher-level taxa remained unresolved, both between and within the three traditional taxonomic divisions of Cladobranchia. Consequently, the evolution of traits within Cladobranchia remains poorly understood.

A robust phylogeny of Cladobranchia is necessary to provide a framework for our understanding of adaptations within this clade. Here we present the "current state of knowledge": a phylogeny for Cladobranchia as inferred from all publicly available DNA sequence data.

Materials and Methods

Taxon and data selection

The Cladobranchia sequence data used in our analyses (Dendronotina [=Dendronotida], Arminina [=Euarminida], and Aeolidina [=Aeolidida]; taxa in brackets reflect equivalent taxonomic designations in the literature) were downloaded from GenBank [10] in February 2014. These data comprise 297 species and five genes, including the mitochondrial genes coding for cytochrome oxidase I (COI) and 16S rRNA, and nuclear genes coding for Histone 3 (H3), 18S rRNA and 28S rRNA (Appendix A). The two outgroups for this analysis, *Discodoris atromaculata* and *Cadlina laevis*, were selected to maximize the number of genes for each outgroup as well as provide some taxonomic breadth from within Anthobranchia, the sister taxon to Cladobranchia. *D. atromaculata* was the only species in GenBank from Anthobranchia for which sequences were available for all five genes, and *C. laevis* was the only remaining species for which four of the genes were available.

Multiple sequence alignment and data matrix construction

Alignments were generated for each gene using the auto function in MAFFT 7.130 [11]. In each gene alignment, multiple sequences from the same taxon (identified by GenBank taxon ID) were reduced to a single consensus sequence, using nucleotide ambiguity codes [12] as necessary. The GenBank taxon ID number is the most accurate identifier of species in GenBank because it reflects taxonomic rearrangements (e.g., a genus change), and as such was used to identify taxa. Consensus sequences were generated by providing the nucleotide coding sequence alignment as input to the consensus_iupac BioPerl subroutine [13].

There are a few principal motivations for using consensus sequences. The first is a desire to incorporate all information about the variability of specific nucleotide states for positions in each gene, both within species and within individuals. A second motivation is to mitigate the effects of mistaken taxon identification within GenBank and prevent errors resulting from the incorrect choice of a single representative sequence. A major challenge of working with previously published sequences is the lack of access to morphology and other means of confirming the identification. Finally, by utilizing more available sequence data, the consensus procedure yields somewhat longer final sequences for each taxon.

The individual gene alignments were concatenated into a single matrix, and sites containing data for fewer than four taxa were removed. This matrix (ALL_TAXA) contained 297 species. Three additional data matrices were generated using subsets of this data: one that contained only taxa for which two or more genes were present (MIN_TWO_GENES; 271 species), a second that contained only taxa for which three or more genes were present (MIN_THREE_GENES; 196 species), and a third that includes all species for which either COI, H3 or 16S rRNA genes are present, thereby eliminating taxa for which only 18S or 28S were present (THREE_GENES; 290 species). An additional matrix was generated (MIN_149_TAXA; 297 species) to minimize missing data. For this matrix, the five genes were

concatenated and sites containing data for fewer than 149 taxa (~50%) were removed. All five alignments, plus each separate gene consensus alignment (for a total of ten) are available as supplementary files.

Phylogenetic analyses

To complete the phylogenetic analyses we used GARLI 2.0 (Genetic Algorithm for Rapid Likelihood Inference; [14]) through the GARLI web service hosted at molecularevolution.org [15]. We used a general time reversible nucleotide model [16] with a proportion of invariant sites and an among site rate heterogeneity model with a discrete gamma distribution (GTR+I+G) together with GARLI default settings, including stepwise-addition starting trees. Three analyses were run for all matrices except MIN 149 TAXA: one without data partitioning; another with data partitioned into four possible subsets by type of gene: 1) COI mitochondrial, 2) H3 nuclear, 3) 16S mitochondrial rRNA, and 4) 18S and 28S nuclear rRNA, for a total of at most three partitions; and a third, unpartitioned, with all sequences from the genus Melibe removed (due to an extremely long Melibe branch in our analyses). For MIN 149 TAXA, only a full, unpartitioned analysis was run. Two analyses were also run for each gene, one including and one excluding Melibe. For all analyses, non-parametric bootstrap values were determined using 2000 bootstrap replicates with five search replicates per bootstrap replicate. Postprocessing of the phylogenetic inference results was done by the GARLI web service at molecularevolution.org using DendroPy [17] and the R system for statistical computing [18], which includes the construction of a bootstrap consensus tree for each analysis. The estimation of the number of replicates required to recover the "best" topology follows Regier et al. [19].

Results

Data matrix properties

The matrix of five genes containing 297 species (ALL_TAXA) contained 6,475 nucleotide positions and was 26.9% complete, while the MIN_TWO_GENES (271 taxa) and MIN_THREE_GENES (196 taxa) data matrices each contained 6,484 nucleotide positions and were 28.0% and 29.7% complete, respectively. The THREE_GENES data matrix (290 taxa) contained 2,920 sites and was 41.0% complete. Finally, the MIN_149_TAXA data matrix (297 taxa) contained 1,419 sites and was 78.0% complete (Table 1). The full data matrix represented at least 65 genera (62.5%) and 20 families (66.7%) of all known families and genera within Cladobranchia.

		Five	Genes		Three Genes
Matrix name	ALL_TAXA	MIN_2_GENES	MIN_3_GENES	MIN_149_TAXA	THREE_GENES
Number of taxa	297	271	196	297	290
Number of					
nucleotide					
positions	6,475	6,484	6,484	1419	2,920
Number of					
nucleotides					
(non-gap					
characters) in					
alignment	1,923,075	1,757,164	1,270,864	328, 771	846,800
Matrix					
completeness					
(number nt ÷					
number possible					
nt)	26.9%	28.0%	29.7%	78.0%	41.0%
Percentage of					
ambiguous					
nucleotides (non-	0.10%	0.11%	0.13%	0.51%	0.21%

Table 1. Size and completeness of aligned data matrices from GenBank sequences.

gap, non- A/C/G/T chars)					
Percentage of all possible internal nodes with bootstrap ≥ 80 (non-partitioned)	36.4%	40.4%	41.3%	32.4%	38.4%
Percentage of all possible internal nodes with bootstrap ≥ 80 (partitioned)	36.4%	37.4%	39.8%	Not applicable	23.9%

Phylogenetic analyses

We performed two phylogenetic analyses for four of our five data matrices (ALL_TAXA, MIN_TWO_GENES, MIN_THREE_GENES, THREE_GENES). For the MIN_149_TAXA matrix, only an unpartitioned analysis was run (Appendix Figure B20). The MIN_TWO_GENES tree represented the best combination of comprehensive taxon sampling and proportion of well-supported nodes (those with a bootstrap value \geq 80), in which Cladobranchia had high bootstrap support. The ALL_TAXA tree contained a smaller percentage of resolved nodes, and the MIN_THREE_GENES tree contained 75 fewer taxa and only a slightly higher percentage of resolved internal nodes (+0.9%) (Table 1). Therefore, we consider the bootstrap consensus tree from the MIN_TWO_GENES analysis to be the most reliable current inference of relationships within Cladobranchia based on molecular data, and present it in Figure 1. Phylogenetic trees based on the other data sets are presented in Appendix B, and all trees showed a lack of resolution among most branches. The genes that seem to have contributed the most information are 16S and H3, due to a larger amount of resolution in the topology of these gene trees, followed by 18S and 28S, which had low taxon representation but a considerable amount of resolution, and COI, in which the topology was simply poorly resolved.

The tree generated using the MIN_TWO_GENES matrix (Figure 1) supported the monophyly of Cladobranchia (bootstrap value = 97), including *Melibe* (Tethyidae). Relationships within Cladobranchia, however, were still largely unresolved; our tree included a massive polytomy at the base of Cladobranchia consisting of 41 small clades and 40 individual taxa. Many of these taxa and groups form non-monophyletic assemblages of species at all levels, including genus, family, superfamily and infraorder according to current taxonomic divisions. Five families were well supported (bootstrap value \geq 80) as monophyletic: Bornellidae (bootstrap value = 100), Hancockiidae (bootstrap value = 96), Tergipedidae (bootstrap value = 93), Dotidae (bootstrap value = 93) and Dendronotidae (bootstrap value = 93). One family had relatively low support (80 > bootstrap value \geq 70): Lomanotidae (bootstrap value = 76). Two families in the analysis were represented by only one taxon (Dironidae and Charcotiidae), and these were well supported as sister taxa in our analysis (bootstrap value = 97). All other taxa included in this analysis were from families that were not supported as monophyletic, with as yet unresolved evolutionary histories and taxonomic disarray.



Figure 1. The 70% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from five genes (COI, H3, 16S, 18S, 28S) in the MIN_TWO_GENES data matrix. Bootstrap values are provided above each branch.

Discussion

In this section, we review our findings on the bootstrap support for both shallow and deep divergences in Cladobranchia. We then discuss the importance of our results and how they affect the current understanding of the group relationships themselves.

Support levels

In our trees, the bootstrap support values are highly varied. A major point of interest is the high support for the monophyly of Cladobranchia itself, including *Melibe*, a genus excluded from Cladobranchia in Pola & Gosliner [1]. However, the backbone of the tree within the group is rife with polytomies and low bootstrap values. Some genera and a few families are well supported in our analysis, but the majority of support and resolution comes at a very shallow phylogenetic level. Additionally, specific placement of roughly 15% of the taxa had had bootstrap values of less than 50%, thus forming a comb along the backbone of our majority-rule consensus tree.

There are several explanations for this lack of resolution and low support in our analyses. One possibility is that our relatively small amount of data and sparse data matrices (with at most 78.0% completeness) may have prevented our likelihood analyses from performing well [20]. The problems may concern the specific number or type of genes that were sampled for each taxon and included in the analyses. For example, although species of the same genus were included in the analysis, there may be only one gene for one or more of those taxa. If these genes are different, there can be no comparison of similar characters to place them together on the phylogeny. There are a number of cases in our analyses where this could potentially be an issue, including multiple species of *Eubranchus (E. exiguous*, 76182; *Eubranchus* sp., 252571; *E. rustyus*, 763125; and *E. sanjuanensis*, 763126) and one species of *Protaeolidiella (P. atra*, 1154746).

Prior research suggests that this missing data may not be as much of a problem as previously suspected. In Cho et al. [21], a data matrix with 45% intentionally missing data yielded no signs of the contradictory groupings that missing data would supposedly produce. This result is consistent with those of three other studies from across a broad taxonomic range, including frogs [22], angiosperms [23], and an entire phylum of eukaryotes [24]. Other literature has also indicated that missing data is not always a substantial problem [25]. From Wiens and Morrill [25]: "Overall, our results confirm previous simulation and empirical studies showing that taxa with extensive missing data can be accurately placed in phylogenetic analyses and that adding characters with missing data can be beneficial (at least under some conditions)." In support of this, the tree obtained from the analysis of our MIN_149_TAXA matrix (78% complete) is actually less resolved than any of the other analyses (Table 1, Appendix Figure B20). This indicates that missing data are not the major issue, at least in this case, but rather that the available data are insufficient for the problem.

An alternative to the sparse data matrix hypothesis for the lack of resolution in our trees is possible contamination or specimen misidentification. Based on the location of certain taxa in the tree, either some identifications may be incorrect in GenBank, or these taxa may have been routinely placed in the wrong genus or family, including: *Caloria indica* (376200), *Piseinotecus* sp. (797203), *Pinufius rebus* (797256), *Flabellina baetica* (934968), *Calma glaucoides* (1154735), *Flabellina cacaotica* (1287503), *Piseinotecus gabinierei* (1287625), and *Fiona pinnata* (1287638). These taxa can be found in unexpected locations on both the ALL_TAXA and MIN_TWO_GENES phylogenies, often some distance from others within the same genus or family. The exact reasons for these instances of taxonomic discord are unknown, but may be due to misidentifications, contamination, or taxonomic misplacement. One point to note, however, is that not a single taxon on this list is associated with a higher proportion of ambiguous characters. As such, their placements are likely not artifacts of the consensus procedure.

A third possible explanation for a lack of resolution is that conflicting gene tree topologies may be confounding the true species tree in our analyses. This is a common problem in phylogenetic studies [26]. Our individual gene trees (COI, H3, 16S, 18S and 28S) all resolve different topologies (Figures S8-12), which would be consistent with this hypothesis. However, most of our trees are poorly resolved (both

those based on single gene and those based on multiple genes) and include a large number of polytomies. This, in turn, indicates not that the data are necessarily inconsistent, but that they are insufficient to resolve relationships within Cladobranchia.

Another plausible reason for the low bootstrap support and lack of resolution is that certain taxa are particularly troublesome and can negatively affect bootstrap support values [27]. The genus *Melibe* is a possible example, with long branches for COI and 16S and absent sequences for 18S and 28S. Taxa with vastly elevated rates of evolution, such as *Melibe*, tend to move around, eroding support in bootstrap analyses. To address these concerns, analyses were run excluding *Melibe* from all data matrices where it was formerly included. These tended to have slightly higher support values for most nodes as compared to when *Melibe* was included. However, the exclusion of *Melibe* did not affect the overall resolution for each tree (Figures S13-19), and thus inclusion of this taxon is not likely a strong contributing factor to poor resolution.

Alternatively, gene sequences for a few taxa in our analyses contained slightly more ambiguous characters in their consensus sequence compared to other taxa, including those from *Glaucus marginatus* (1154738, 16S and COI), *Doto coronata* (154624, COI), *Aeolidia papillosa* (195873, 16S), *Favorinus elenalexarium* (797222, H3), *Dondice banyulensis* (869980, 16S), *Spurilla neapolitana* (929453, 16S and COI) and *Phyllodesmium macphersonae* (869973, 16S and COI). This could also have an effect on both the resolution and support for phylogenetic trees estimated by likelihood [28]. However, none of these taxa appear to be in an unexpected place on the MIN_TWO_GENES tree. This is most likely because the percentage of ambiguous characters in all of our matrices is extremely small: between 0.1% and 0.51% (Table 1). This indicates that for the majority of our taxa that have multiple sequences, there are few differences between those sequences. Indeed, one thing we note above is that the taxa identified as potential problems are not the same taxa with a larger percentage of ambiguous characters in the full matrix, *Spurilla neapolitana* (9.7%), was still appropriately placed within a clade with other members of the genus *Spurilla* in all analyses, affirming that our consensus procedure had little to no deleterious effects on our results.

As has been suggested in Regier et al. [19], a final possibility is that insufficient search effort on each bootstrap pseudo-replicate may have played a role in the low bootstrap values found in our tree. However, this is unlikely in our case, as our analysis included a total of five GARLI searches on each pseudo-replicate, in contrast to the single search replicate used in the analyses in Regier et al. [19]. As suggested in Debry & Olmstead [29], this type of resampling results in more precise estimates of bootstrap values, likely because insufficient search effort during bootstrapping has been shown to artificially lower bootstrap values.

In summary, we conclude that the most likely reason for our lack of resolution is simply that the data do not have sufficient phylogenetic signal to successfully reconstruct deep phylogenetic relationships. These might be obtained, however, using high-throughput sequencing for greater genomic data sampling; i.e., "phylogenomics." Rather than yielding only a few genes, these sequencing assays often provide hundreds of genes and have been successfully used to resolve relationships within many groups [30–34]. Thus, a phylogenomics study may be more successful at mapping the evolutionary history of Cladobranchia.

Current understanding of the phylogeny of Cladobranchia

Our results indicate that there is presently a severe lack of data useful for addressing deep evolutionary divergences within Cladobranchia. A result novel to this study, however, is the monophyly of Cladobranchia, which was recovered as paraphyletic (if the genus *Melibe* was included) in the only previous molecular phylogeny of this group [1]. Our analyses resolve Cladobranchia (including *Melibe*) as monophyletic, with high bootstrap support (bootstrap value = 97, MIN_TWO_GENES). However, much like the study of Pola & Gosliner [1], we find little resolution of relationships within Cladobranchia.

Six families within Cladobranchia were resolved as monophyletic, including Bornellidae, Hancockiidae, Tergipedidae, Dotidae, Dendronotidae and Lomanotidae. Three of these families (Bornellidae, Hancockiidae and Dendronotidae) are consistent with the results from a previous study [1], while the monophyly of Tergipedidae, Dotidae and Lomanotidae are novel results. However, given the relatively low support of the monophyly of Lomanotidae, greater taxon and or gene sampling within this family is probably necessary to better establish its position and status. The lower bootstrap support for this clade could be the result of including only two species from Lomanotidae in the analysis. The remaining families within Cladobranchia that were included in the analysis appear as non-monophyletic species assemblages. The monophyly of some of these families, such as Aeolidiidae [7,35], was previously determined by morphological and molecular evidence, while the monophyly of other families, such as Arminidae [36] or Scyllaeidae [6], was determined using only morphological characters. Still other families in Cladobranchia have been weakly supported by morphological data, including Tritoniidae [8]. The lack of support for these clades in this analysis could be due to low taxon sampling in some cases. In other cases, the molecular data may have simply revealed paraphyly or polyphyly within groups previously well supported by morphology.

It is abundantly clear that the evolutionary history of Cladobranchia remains to be understood. Our results provided some additional for the relationships in this group, but the majority of the relationships in our trees remain unresolved (Table 1). In order to better understand evolution within this diverse group, as with any group of organisms, a well-resolved and well-supported phylogenetic tree is necessary. The recent advances in phylogenomic approaches may hold the key to our understanding of taxonomic relationships within Cladobranchia.

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Appendix A.

Table of taxa, including GenBank taxon ID number, species name and GenBank accession number for each sequence used in the analyses.

Taxon ID Taxon Name	COI GenBank IDs	H3 GenBank IDs	16S GenBank IDs	18S GenBank IDs	28S GenBank IDs
195873 Aeolidia papillosa	JQ997042.1	JQ996934.1	JX087464.1	GU227371.1	JQ699293.1
	JQ997039.1	JX087596.1	JQ996836.1		
	JX087536.1	JQ996935.1	JQ996834.1		
	JQ699565.1	JX087597.1	JQ996835.1		
	GQ292049.1	JX087598.1	JX087462.1		
	JQ997038.1	JQ996936.1	JQ996833.1		
	JQ997041.1	JQ996937.1	JQ699475.1		
	JX087535.1	JQ699385.1	JX087463.1		
	JX087534.1				
	JQ997040.1				
	AY345028.1				
1290779 Aeolidia sp. A	JX087532.1	JX087593.1	JX087459.1		
	JX087533.1	JQ996933.1	JQ996832.1		
	JQ997037.1	JX087594.1	JX087460.1		
	JX087531.1	JX087595.1	JX087461.1		
1290780 Aeolidia sp. B	JQ997035.1	JQ996931.1	JQ996831.1		
	JQ997036.1	JQ996932.1	JQ996830.1		
1154711 Aeolidiella alba		JQ699386.1			JQ699294.1
934974 Aeolidiella alderi	HQ616766.1	HQ616794.1	HQ616729.1		
	HQ616765.1	HQ616795.1	JQ996811.1		
		JQ996910.1	HQ616728.1		
1287571 Aeolidiella sanguinea	JX087538.1	JX087599.1	JX087465.1		
-	JX087537.1	JX087600.1	JX087466.1		
1287507 Aeolidiella stephanieae	JQ997044.1	JQ996940.1	JQ996839.1		
1288050 Aeolidiidae gen sp 'alba'	JO997016 1	JO996909 1	JO996806 1		
	JO997017.1	JO996908.1	JO996805.1		
	JO997013.1	JO996907.1	JO996810.1		
	JO997015.1	JO996905.1	JO996808.1		
	JO997012.1	JO996906.1	JO996809.1		
	JO997014.1	JO996904.1			
1288051 Aeolidiidae gen. sp. 'japonica'	JQ997033.1	JQ996929.1	JQ996828.1		
1290799 Aeolidiidae gen. sp. A	JO997011.1	JO996902.1	JO996803.1		
		JO996903.1	JO996804.1		
1290800 Aeolidiidae gen. sp. B	JO997022.1	JO996917.1	JO996818.1		
0r	JO997023.1	JO996916.1	JO996817.1		

Appendix A. Table of taxa, including GenBank taxon ID number, species name and GenBank accession number for each sequence used in the analyses.

1394325 Aeolidiidae sp.	KC706903.1				
1287505 Aeolidiopsis ransoni	JQ997043.1	JQ996938.1	JQ996837.1		
		JQ996939.1	JQ996838.1		
1287503 Anteaeolidiella cacaotica	JX087528.1	JQ996926.1	JX087455.1		
	JQ997030.1	JX087590.1	JQ996825.1		
122051(Autor - 1: 1: -11- home	10007027 1	1000/022 1	JX087457.1		
1330516 Anteaeolidiella lurana	JQ997027.1 JQ007021.1	JQ996922.1 JQ006023.1	JQ996822.1		
	3Q997031.1	JQ990925.1 JQ996927 1	JQ990821.1 JQ996826.1		
1287504 Anteaeolidiella oliviae	JQ997034.1	JQ996930.1	JQ996829.1		
1291184 Anteaeolidiella saldanhensis	JQ997032.1	JQ996928.1	JQ996827.1		
1290782 Anteaeolidiella sp. A	JQ997029.1	JQ996924.1	JQ996823.1		
-	JQ997028.1	JQ996925.1	JQ996824.1		
1290783 Anteaeolidiella sp. B	JQ997020.1	JQ996914.1	JQ996815.1		
1330517 Anteaeolidiella takanosimensis	JX087529.1	JX087592.1	JX087458.1		
	JX087530.1	JX087591.1	JX087456.1		
763115 Armina californica	GQ292055.1			GQ326884.1	
71480 Armina lovenii	AF249781.1		AF249243.1	AF249196.1	
1400840 Armina maculata	KF369111.1				
431601 Armina neapolitana		EF133469.1			
797211 Armina semperi	HM162696.1	HM162512.1	HM162606.1		
797168 Armina sp. 3		HM162513.1	HM162607.1		
797169 Armina sp. 9		HM162514.1	HM162608.1		
930957 Armina sp.	HQ010504.1	HQ010473.1	HQ010539.1		
869979 Austraeolis ornata	GQ403774.1		GQ403752.1		
1154718 Austraeolis stearnsi	JQ699571.1	JQ699395.1	JQ699483.1		JQ699303.1
934965 Babakina anadoni	HQ616767.1	HQ616796.1	HQ616710.1		
	HQ616746.1	HQ616776.1	HQ616730.1		
	HQ616747.1	HQ616806.1	HQ616711.1		
	HQ616748.1	HQ616775.1	HQ616742.1		
		HQ616807.1	HQ616743.1		
		HQ616805.1	HQ616744.1		
		HQ616777.1	HQ616709.1		

934966 Babakina festiva		HQ616802.1 HQ616801.1 HQ616803.1	HQ616736.1 HQ616735.1	
797244 Babakina indopacifica	HM162754.1	HM162587.1	HM162678.1	
929452 Baeolidia australis				GU227367.1
1287509 Baeolidia japonica	JO997058 1	JO996954 1	JO996856 1	
	JO997059 1	JO996956 1	JO996855 1	
	JO997057.1	JO996957.1	JO996854.1	
		JO996955.1	JO996853.1	
1287510 Baeolidia moebii	JX087550.1	JX087619.1	JQ996857.1	
	HQ616771.1	JQ996958.1	JQ996858.1	
	JQ997060.1	JX087618.1	HQ616733.1	
	JQ997061.1	JQ996959.1	JX087481.1	
	JX087551.1	HQ616800.1	HQ616734.1	
	HQ616770.1	HQ616799.1	JX087482.1	
934972 Baeolidia nodosa	JQ997080.1	JX087629.1	HQ616731.1	GU339155.1
	JX087560.1	JQ996992.1	JQ996886.1	
	HQ616768.1	JX087630.1	JX087493.1	
	JX087559.1	HQ616797.1	JX087527.1	
	JQ997081.1	JQ996991.1	JX087494.1	
1290784 Baeolidia sp. A	JQ997056.1	JQ996953.1	JQ996851.1	
	JQ997051.1	JQ996948.1	JQ996850.1	
	JQ997054.1	JQ996952.1	JQ996852.1	
	JQ997055.1	JQ996951.1	JQ996847.1	
1290785 Baeolidia sp. B	JQ997046.1	JQ996943.1	JQ996842.1	
1290786 Baeolidia sp. C	JQ997045.1	JQ996941.1	JQ996840.1	
1287537 Berghia cf. salaamica	JQ997048.1	JQ996945.1	JQ996843.1	
-	JQ997047.1	JQ996944.1	JQ996844.1	
1287511 Berghia coerulescens	JQ997049.1	JQ996946.1	JQ996845.1	
		JX087604.1	JX087470.1	
1287631 Berghia columbina	JX087543.1	JX087608.1	JX087473.1	
	JX087545.1	JX087609.1	JX087472.1	
	JX087544.1	JX087605.1	JX087474.1	
	JX087542.1	JX087606.1	JX087471.1	
		JX087607.1		
1287632 Berghia rissodominguezi	JX087552.1	JX087621.1	JX087484.1	
		JX087620.1	JX087483.1	

1287506 Berghia salaamica	JQ997062.1	JQ996962.1 JQ996960.1	JQ996860.1 JQ996859.1 JO996862.1		
1290787 Berghia sp. A	JX087549.1	JX087617.1	JX087480.1		
929456 Berghia verrucicornis	HQ616750.1 JX087553.1 JX087554.1 HQ616749.1	JX087623.1 HQ616779.1 JX087624.1 JX087610.1 JX087622.1 HQ616778.1	HQ616713.1 JX087487.1 JX087486.1 JX087485.1 HQ616712.1 JX087488.1	GU227364.1	
/9/246 Bonisa nakaza	HM162/46.1	HM162579.1	HM162670.1		
1170240 Bornella anguilla		JN869424.1 IN869425.1			
797212 Bornella calcarata	HM162707.1	HM162533.1 JN869427.1	HM162627.1		
797213 Bornella hermanni	JN869448.1	JN869421.1	JN869403.1		
	JN869446.1	JN869422.1	JN869404.1		
	HM162705.1	JN869423.1	JN869402.1		
	JN869447.1	HM162531.1 JN869420.1	HM162625.1		
797214 Bornella johnsonorum	HM162704.1	JN869419.1	HM162624.1		
1170241 D 11	JN869445.1	HM162530.1	JN869401.1		
1170241 Bornella sarape		JN869428.1			
219659 Bornella stellifer	HM162703.1	JN869418.1 JN869417.1 HM162529.1	JN869400.1 HM162623.1	AY165756.1 AY165755.1	
797215 Bornella valdae	JN869449.1 HM162706.1	HM162532.1 JN869426.1	HM162626.1 JN869405.1		
71296 Cadlina laevis	AY345034.1		AY345034.1		
1154735 Calma glaucoides	JQ699567.1	JQ699388.1	JQ699477.1		JQ699296.1
929458 Calmella cavolini	HQ616772.1		HQ616737.1	GU227361.1	
929450 Caloria elegans	HQ616751.1	HQ616780.1	HQ616714.1 HQ616738.1	GU227363.1	
376200 Caloria indica	DQ417325.1	JQ699389.1	DQ417273.1		JQ699297.1
1287538 Caloria sp. 4	JQ997064.1 JQ997063.1	JQ996966.1 JQ996965.1	JQ996865.1 JQ996864.1		

1291185 Catriona sp. A	JQ997021.1	JQ996915.1	JQ996816.1		
1290775 Catriona sp. B	JQ997024.1	JQ996919.1 JQ996918.1	JQ996819.1		
929460 Cerberilla affinis		JQ996964.1	JQ996863.1	GU227366.1	
1287512 Cerberilla annulata		JQ996967.1	JQ996866.1		
1287633 Cerberilla bernadettae	JX087555.1	JX087625.1	JX087489.1		
1287543 Cerberilla cf. affinis	JQ997065.1	JQ996968.1	JQ996867.1		
1287539 Cerberilla sp. 3		JQ996976.1	JQ996873.1		
1290788 Cerberilla sp. A	JQ997069.1 JQ997070.1	JQ996978.1 JQ996975.1 JQ996977.1	JQ996874.1		
1290789 Cerberilla sp. B	JQ997068.1	JQ996973.1	JQ996872.1		
1290790 Cerberilla sp. C		JQ996974.1			
696318 Cf. Tergipes antarcticus			GU227007.1		
763139 Charcotia granulosa	GQ292060.1			GQ326885.1	
154642 Cratena peregrina	AF249786.1 HQ616752.1	HQ616781.1	HQ616715.1	GU339156.1	
763116 Cratena pilata	GQ292053.1 KC785096.1				
1170246 Crosslandia daedali		JN869444.1			
1154713 Cuthona abronia	JQ699568.1	JQ699390.1	JQ699478.1		JQ699298.1
154644 Cuthona caerulea	AF249807.1			AF249199.1	
763117 Cuthona cocoachroma	GQ292071.1			GQ326893.1	
763118 Cuthona concinna	GQ292072.1			GQ326898.1	
1154714 Cuthona divae	JQ699569.1	JQ699391.1	JQ699479.1		JQ699299.1
1154715 Cuthona fulgens		JQ699392.1	JQ699480.1		JQ699300.1
1154716 Cuthona lagunae		JQ699393.1	JQ699481.1		JQ699301.1
219662 Cuthona nana				AY165760.1	AY427448.1
252567 Cuthona ocellata	AY345043.1		AY345043.1		
219663 Cuthona sibogae				AY165761.1	
763533 Cuthona sp. 1	GQ292068.1			GQ326899.1	
763534 Cuthona sp. 2	GQ292078.1			GQ326908.1 GQ326907.1	

763535 Cuthona sp. 3	GQ292066.1			GQ326902.1	
1287545 Cuthona sp. 35	JO997026.1	JO996921.1	JO996820.1	GQ326903.1	
763536 Cuthona sp. 4	GO292069.1			GO326901.1	
763537 Cuthona sp. 5	GO292067.1			GO326900.1	
763538 Cuthona sp. 6	GQ292070.1			GQ326896.1 GQ326895.1 GQ326897.1 GQ326894.1	
763539 Cuthona sp. 7	GQ292074.1			GQ326892.1	
763540 Cuthona sp. 8	GQ292073.1			GQ326891.1	
763541 Cuthona sp. 9	GQ292076.1 GQ292075.1 GQ292077.1			GQ326906.1	
1290791 Cuthona sp. A	JQ997019.1	JQ996913.1	JQ996814.1		
763120 Dendronotus albopunctatus	GQ292064.1			GQ326861.1	
904359 Dendronotus albus		HQ267088.1	GU339186.1 GU339185.1		
154605 Dendronotus dalli	AF249800.1		AF249252.1	AY165757.1	AY427450.1
71302 Dendronotus frondosus	JN869450.1 GQ292063.1 AY345041.1	HQ267089.1 JN869429.1	JN869406.1 AF249251.1 GU339187.1 AY345041.1	GQ326860.1 AF249206.1	
219661 Dendronotus iris	GQ292062.1	HM162537.1 HQ267090.1 JN869431.1	HM162631.1 GU339188.1 GU339189.1 GU339190.1	AY165758.1	
797216 Dendronotus lacteus	HM162710.1	HM162538.1			
1170242 Dendronotus orientalis		JN869432.1			
1054385 Dendronotus patricki	HQ225828.1		HQ225829.1	HQ225830.1	
797217 Dendronotus regius	JN869451.1 HM162708.1	JN869430.1 HM162535.1	HM162629.1 JN869407.1		
904360 Dendronotus rufus		HQ267091.1	GU339191.1		
763135 Dendronotus sp. 1	GQ292061.1				

797218 Dendronotus subramosus		HM162539.1	HM162632.1		
		HQ267092.1	GU339197.1		
			GU339194.1		
			GU339192.1		
			GU339195.1		
			GU339196.1		
			GU339193.1		
797219 Dendronotus venustus	HM162709.1	HQ267093.1	GU339199.1		
		HM162536.1	GU339198.1		
			GU339200.1		
			HM162630.1		
797220 Dermatobranchus pustulosus		HM162516.1	HM162610.1		
154607 Dermatobranchus semistriatus			AF249244.1	AF249195.1	
797170 Dermatobranchus sp. 12		HM162518.1	HM162612.1		
797171 Dermatobranchus sp. 16		HM162519.1	HM162613.1		
797172 Dermatobranchus sp. 17		HM162520.1	HM162614.1		
-		HM162521.1	HM162615.1		
797173 Dermatobranchus sp. 21	HM162698.1	HM162522.1	HM162616.1		
797174 Dermatobranchus sp. 7		HM162517.1	HM162611.1		
797175 Dermatobranchus sp. A	HM162697.1	HM162515.1	HM162609.1		
934976 Dicata odhneri	HQ616773.1		HQ616739.1		
763122 Dirona albolineata	GQ292058.1	HM162577.1	HM162668.1	GQ326888.1	
329893 Dirona picta	DQ026831.1				
120394 Discodoris atromaculata	AF120637.1	DQ280013.1	DQ280054.1	AF120521.1	AF120577.1

1154717 Dondice occidentalis	JQ699570.1	KC526527.1	KC526513.1		JQ699302.1
		KC526536.1	KC526510.1		
		KC526528.1	KC526509.1		
		KC526530.1	KC526517.1		
		KC526533.1	KC526518.1		
		KC526526.1	KC526514.1		
		KC526524.1	KC526512.1		
		KC526529.1	KC526508.1		
		JQ699394.1	JQ699482.1		
		KC526532.1	KC526507.1		
		KC526534.1	KC526506.1		
		KC526531.1	KC526515.1		
		KC526525.1	KC526511.1		
		KC526523.1	KC526519.1		
1252470 D 1		W.050(505.1	KC526516.1		
13534/8 Dondice parguerensis		KC526535.1	KC526521.1		
			KC520522.1		
762122 Data anteration	CO202025 1		KC320320.1	CO326992 1	
	Q292023.1			0Q320882.1	
763124 Doto columbiana	GQ292026.1			GQ326881.1	
154624 Doto coronata	HM162734.1 AF249794.1	HM162566.1	HM162657.1	AF249203.1	
154610 Doto eireana			AF249248.1	AF249204.1	
154645 Doto floridicola	AF249820.1			AY165759.1	
154611 Doto koenneckeri	HM162735.1	HM162567.1	HM162658.1	AF249205.1	
	AF249797.1		AF249249.1		
154612 Doto pinnatifida	AF249793.1		AF249250.1	AF249202.1	
797176 Doto sp. 15	HM162739.1	HM162571.1	HM162662.1		
797177 Doto sp. 2	HM162737.1	HM162569.1	HM162660.1		
797178 Doto sp. 7	HM162738.1	HM162570.1	HM162661.1		
797179 Doto sp. H	HM162740.1	HM162572.1	HM162663.1		
797180 Doto sp. I	HM162741.1	HM162573.1	HM162664.1		
797181 Doto sp. J	HM162742.1	HM162574.1	HM162665.1		
797182 Doto sp. K	HM162743.1	HM162575.1	HM162666.1		
797221 Doto ussi	HM162736.1	HM162568.1	HM162659.1		

76182 Eubranchus exiguus	AF249792.1		AF249246.1		
763125 Eubranchus rustyus	GQ292065.1			GQ326905.1	
763126 Eubranchus sanjuanensis	GQ292079.1			GQ326909.1	
252571 Eubranchus sp. A	AY345046.1		AY345046.1		
76181 Eubranchus sp. B	AF249791.1				
1287513 Facelina annulicornis	JQ997076.1	JQ996986.1 JQ996987.1	JQ996881.1		
219665 Facelina bostoniensis	AY345031.1		AY345031.1	AY165763.1 GU339157.1	
154649 Facelina punctata	AF249816.1				
1291186 Facelina sp. A	JQ997052.1	JQ996949.1	JQ996848.1		
1290792 Facelina sp. B	JQ997066.1 JQ997067.1	JQ996972.1 JQ996971.1 JQ996970.1 JQ996969.1	JQ996868.1 JQ996871.1 JQ996870.1 JQ996869.1 JQ996882.1		
1290793 Facelina sp. C	JQ997072.1 JQ997093.1 JQ997073.1 JQ997092.1	JQ997004.1 JQ996981.1 JQ996982.1 JQ997005.1	JQ996898.1 JQ996877.1 JQ996876.1 JQ996897.1		
1290794 Facelina sp. D	JQ997074.1	JQ996983.1	JQ996878.1		
1287568 Facelinidae sp. 2	JQ997071.1 JQ997075.1	JQ996985.1 JQ996984.1	JQ996880.1 JQ996879.1		
934967 Favorinus brachialis	HQ616761.1 AY345042.1	HQ616790.1	HQ616724.1 HQ616741.1 AV345042 1		
797222 Favorinus elenalexiarum	HM162755.1	JQ699396.1 HM162588.1	HM162679.1 JQ699484.1		JQ699304.1
929454 Favorinus sp.				GU227369.1	
1287638 Fiona pinnata	JX087558.1	JX087628.1	JX087492.1		
154626 Flabellina affinis	HQ616753.1 AF249783.1 AY345055.1	HQ616782.1	HQ616716.1 AY345055.1	AY165767.1	
763127 Flabellina amabilis	GQ292022.1			GQ326912.1	

219672 Flabellina babai	HQ616754.1	HQ616783.1	HQ616717.1	AY165768.1	AY427449.1
934968 Flabellina baetica	HQ616755.1	HQ616784.1	HQ616718.1		
929451 Flabellina bilas				GU227368.1	
1287634 Flabellina confusa	JX087556.1	JX087627.1	JX087490.1		
	JX087557.1	JX087626.1	JX087491.1		
1154719 Flabellina exoptata	JQ699572.1	JQ699397.1	JQ699485.1		JQ699305.1
1154720 Flabellina fusca	JQ699573.1	JQ699398.1	JQ699486.1		JQ699306.1
154627 Flabellina ischitana	HQ616757.1	HQ616785.1	HQ616719.1		
	HQ616756.1	HQ616808.1	HQ616720.1		
	AF249814.1	HQ616786.1	HQ616745.1		
76183 Flabellina pedata	HQ616758.1	HQ616787.1	AF249247.1		
	AF249817.1		HQ616721.1		
219673 Flabellina sp.				AY165769.1	
763128 Flabellina trilineata	GQ292024.1	JQ699399.1	JQ699487.1	GQ326911.1	JQ699307.1
763129 Flabellina trophina	GQ292023.1			GQ326910.1	
154613 Flabellina verrucosa	AF249790.1		AF249245.1	AF249198.1	

1154737 Glaucus atlanticus

JQ699595.1	JQ699403.1	JQ699510.1	JQ699312.1
JQ699590.1	JQ699400.1	JQ699514.1	JQ699314.1
JQ699598.1	JQ699415.1	JQ699511.1	JQ699327.1
JQ699576.1	JQ699414.1	JQ699508.1	JQ699337.1
JQ699594.1	JQ699427.1	JQ699492.1	JQ699336.1
JQ699596.1	JQ699406.1	JQ699500.1	JQ699316.1
JQ699588.1	JQ699416.1	JQ699495.1	JQ699317.1
JQ699586.1	JQ699401.1	JQ699496.1	JQ699326.1
JQ699581.1	JQ699422.1	JQ699499.1	JQ699324.1
JQ699583.1	JQ699409.1	JQ699490.1	JQ699329.1
JQ699575.1	JQ699426.1	JQ699512.1	JQ699318.1
JQ699578.1	JQ699425.1	JQ699489.1	JQ699330.1
JQ699574.1	JQ699412.1	JQ699513.1	JQ699321.1
JQ699585.1	JQ699407.1	JQ699497.1	JQ699335.1
JQ699600.1	JQ699421.1	JQ699506.1	JQ699322.1
JQ699602.1	JQ699405.1	JQ699507.1	JQ699308.1
JQ699601.1	JQ699428.1	JQ699517.1	JQ699333.1
JQ699589.1	JQ699413.1	JQ699491.1	JQ699310.1
JQ699580.1	JQ699410.1	JQ699494.1	JQ699332.1
JQ699587.1	JQ699417.1	JQ699501.1	JQ699315.1
JQ699597.1	JQ699402.1	JQ699505.1	JQ699325.1
JQ699599.1	JQ699419.1	JQ699488.1	JQ699323.1
JQ699603.1	JQ699423.1	JQ699503.1	JQ699334.1
JQ699579.1	JQ699408.1	JQ699498.1	JQ699313.1
JQ699592.1	JQ699429.1	JQ699502.1	JQ699331.1
JQ699584.1	JQ699404.1	JQ699509.1	JQ699311.1
JQ699593.1	JQ699411.1	JQ699516.1	JQ699309.1
JQ699591.1	JQ699418.1	JQ699504.1	JQ699319.1
JQ699577.1	JQ699420.1	JQ699493.1	JQ699320.1
JQ699582.1	JQ699424.1	JQ699515.1	JQ699328.1

1164700	01	• •
115/1748	(+19110110	marginatus
1134/30	Ulaucus	marginatus

869980 Godiva banyulensis

797223 Godiva quadricolor

JQ699607.1	JQ699459.1	JQ699552.1		JQ699339.1
JQ699618.1	JQ699442.1	JQ699519.1		JQ699347.1
JQ699613.1	JQ699446.1	JQ699523.1		JQ699354.1
JQ699616.1	JQ699451.1	JQ699518.1		JQ699342.1
JQ699623.1	JQ699438.1	JQ699551.1		JQ699344.1
JQ699625.1	JQ699450.1	JQ699550.1		JQ699349.1
JQ699605.1	JQ699435.1	JQ699529.1		JQ699370.1
JQ699608.1	JQ699445.1	JQ699533.1		JQ699368.1
JQ699609.1	JQ699441.1	JQ699541.1		JQ699357.1
JQ699604.1	JQ699436.1	JQ699549.1		JQ699338.1
JQ699622.1	JQ699454.1	JQ699544.1		JQ699343.1
JQ699612.1	JQ699457.1	JQ699545.1		JQ699364.1
JQ699610.1	JQ699432.1	JQ699543.1		JQ699346.1
JQ699611.1	JQ699461.1	JQ699548.1		JQ699358.1
JQ699606.1	JQ699448.1	JQ699539.1		JQ699371.1
JQ699627.1	JQ699433.1	JQ699521.1		JQ699345.1
JQ699624.1	JQ699439.1	JQ699540.1		JQ699361.1
JQ699620.1	JQ699465.1	JQ699546.1		JQ699348.1
JQ699619.1	JQ699463.1	JQ699528.1		JQ699362.1
JQ699626.1	JQ699434.1	JQ699542.1		JQ699372.1
JQ699614.1	JQ699460.1	JQ699537.1		JQ699351.1
JQ699615.1	JQ699447.1	JQ699530.1		JQ699366.1
JQ699628.1	JQ699453.1	JQ699522.1		JQ699353.1
JQ699629.1	JQ699458.1	JQ699532.1		JQ699359.1
JQ699617.1	JQ699464.1	JQ699553.1		JQ699341.1
JQ699621.1	JQ699430.1	JQ699535.1		JQ699340.1
	JQ699455.1	JQ699526.1		JQ699373.1
	JQ699440.1	JQ699547.1		JQ699355.1
	JQ699449.1	JQ699524.1		JQ699350.1
	JQ699437.1	JQ699525.1		JQ699369.1
	JQ699462.1	JQ699520.1		JQ699365.1
	JQ699452.1	JQ699527.1		JQ699363.1
	JQ699443.1	JQ699538.1		JQ699360.1
	JQ699431.1	JQ699531.1		JQ699352.1
GQ403773.1	HQ616804.1	GQ403751.1	AY165764.1	
AF249782.1		HQ616740.1		
HM162756.1	HM162589.1	HM162680.1		

797263 Hancockia californica	HM162702.1 JN869452.1	HM162527.1 JN869433.1	JN869408.1 HM162621.1		
797208 Hancockia cf. uncinata		HM162528.1	HM162622.1		
252574 Hancockia uncinata	AY345047.1		AY345047.1		
205593 Hermissenda crassicornis	JQ699630.1 GQ292054.1	JQ699466.1	JQ699554.1		JQ699374.1
1154740 Hermosita hakunamatata	JQ699631.1	JQ699467.1	JQ699555.1		JQ699375.1
797226 Janolus barbarensis	HM162747.1	HM162580.1	HM162671.1		
797227 Janolus capensis	HM162748.1	HM162581.1	HM162672.1		
154651 Janolus cristatus	AF249813.1			AF249194.1	
763130 Janolus fuscus	GQ292048.1			GQ326887.1	
797228 Janolus longidentatus	HM162749.1	HM162582.1	HM162673.1		
797229 Janolus mirabilis	HM162750.1	HM162583.1	HM162674.1		
797183 Janolus sp. 1	HM162751.1	HM162584.1	HM162675.1		
797184 Janolus sp. 2	HM162752.1	HM162585.1	HM162676.1		
797185 Janolus sp. 7	HM162753.1	HM162586.1	HM162677.1		
1154742 Learchis poica	JQ699632.1	JQ699468.1	JQ699556.1		JQ699376.1
797250 Leminda millecra	HM162745.1	HM162578.1	HM162669.1		
1287514 Limenandra fusiformis	JQ997077.1 JO997078.1	JQ996988.1 JO996989.1	JQ996883.1 JO996884.1		
1290776 Limenandra sp. A	JQ997082.1 HQ616769.1	HQ616798.1 JQ996993.1	JQ996887.1 HQ616732.1		
1291187 Limenandra sp. B	JX087540.1 JX087539.1 JX087541.1 JO997050 1	JQ996947.1 JX087601.1 JX087602.1 JX087603 1	JQ996846.1 JX087469.1 JX087468.1 JX087467 1		
1290795 Limenandra sp. C	JQ997079.1	JQ996990.1 JQ996942.1	JQ996841.1 JQ996885.1		
797197 Lomanotus sp. E	HM162715.1	HM162547.1	HM162640.1		
1170243 Lomanotus sp.	JN869453.1	JN869434.1	JN869409.1		
1170244 Lomanotus vermiformis		JN869435.1			
797254 Marianina rosea	HM162733.1	HM162565.1	HM162656.1		
797230 Marionia arborescens	HM162722.1	HM162554.1	HM162646.1		

154647 Marionia blainvillea	AF249812.1 HM162721_1	HM162553.1	HM162645.1		
797231 Marionia distincta	HM162725.1	HM162557.1	HM162648.1		
797232 Marionia elongoviridis	HM162724.1	HM162556.1			
797233 Marionia levis	HM162723.1	HM162555.1	HM162647.1		
797188 Marionia sp. 10	HM162728.1	HM162560.1	HM162651.1		
797189 Marionia sp. 14	HM162729.1	HM162561.1	HM162652.1		
797190 Marionia sp. 5	HM162727.1	HM162559.1	HM162650.1		
904361 Marionia sp. A			GU339201.1		
857010 Marionia sp. B	HM162726.1	HM162558.1	HM162649.1		
1370030 Melibe arianeae	KC992314.1	KC992315.1	KC992313.1		
797234 Melibe digitata	HM162699.1	HM162523.1	JX306061.1		
797235 Melibe engeli	JX306069.1	HM162525.1 IX306077 1	JX306062.1 HM162619.1		
76178 Melibe leonina	GQ292059.1	01100007711	GU339202.1		
797236 Melibe rosea	JX306070.1 JX306071.1 JX306073.1 JX306072.1 JX306074.1 HM162701.1	JX306081.1 JX306082.1 JX306079.1 JX306080.1 JX306078.1 HM162526.1	HM162620.1 JX306063.1 JX306064.1 JX306066.1 JX306065.1		
1239314 Melibe sp.		JX306084.1			
499938 Melibe viridis	HM162700.1 JX306075.1	JX306083.1 HM162524.1	HM162618.1 JX306068.1		
128/51/ Moridilla brockii	JQ997083.1	JQ996994.1	JQ996888.1		10(00277.1
1154/44 Nanuca sebastiani	JQ699633.1	JQ699469.1	JQ699557.1		JQ699377.1
2196/6 Notaeolidia depressa	GQ292057.1			GQ326886.1	
1171428 Notobryon panamica		JN869440.1			
797199 Notobryon sp. B		HM162541.1	HM162634.1		
797200 Notobryon sp. C	HM162712.1	HM162542.1	HM162635.1		
797201 Notobryon sp. D	HM162713.1	HM162543.1	HM162636.1		

1171429 Notobryon thompsoni	JN869455.1	JN869438.1	JN869412.1	
	JN869456.1	JN869439.1	JN869413.1	
797237 Notobryon wardi	JN869454.1	HM162546.1	HM162637.1	
	HM162714.1	JN869436.1	HM162639.1	
		HM162545.1	JN869411.1	
		JN869437.1	JN869410.1	
		HM162544.1	HM162638.1	
1287519 Noumeaella isa	JQ997084.1	JQ996995.1	JQ996889.1	
1290774 Noumeaella rehderi		JQ996961.1	JQ996861.1	
1287556 Noumeaella sp. 3	JQ997087.1	JQ996999.1	JQ996893.1	
	JQ997088.1	JQ996998.1	JQ996892.1	
1287557 Noumeaella sp. 4	JQ997085.1	JQ997003.1	JQ996894.1	
	JQ997090.1	JQ997000.1	JQ996890.1	
	JQ997091.1	JQ997001.1	JQ996891.1	
	JQ997086.1	JQ996997.1	JQ996896.1	
	JQ997089.1	JQ996996.1	JQ996895.1	
		JQ997002.1		
1290796 Noumeaella sp. A	JQ997053.1	JQ996950.1	JQ996849.1	
1290797 Noumeaella sp. B	JX087548.1	JX087616.1	JX087479.1	
376196 Phestilla lugubris	DQ417299.1		DQ417253.1	
	DQ417300.1		DQ417252.1	
	DQ417298.1		DQ417254.1	
376192 Phestilla melanobrachia	DQ417281.1		DQ417228.1	
	DQ417277.1		DQ417233.1	
	DQ417274.1		DQ417231.1	
	DQ417280.1		DQ417236.1	
	DQ417282.1		DQ417235.1	
	DQ417278.1		DQ417230.1	
	DQ417279.1		DQ417232.1	
	DQ417275.1		DQ417229.1	
	DQ417276.1		DQ417234.1	

376197 Phestilla minor	DQ417311.1	DQ417263.1
	DQ417301.1	DQ417257.1
	DQ417307.1	DQ417258.1
	DQ417308.1	DQ417262.1
	DQ417310.1	DQ417264.1
	DQ417305.1	DQ417260.1
	DQ417303.1	DQ417256.1
	DQ417304.1	DQ417261.1
	DQ417313.1	DQ417259.1
	DQ417309.1	DQ417255.1
	DQ417302.1	
	DQ417312.1	
	DQ417306.1	
376195 Phestilla sibogae	DQ417297.1	DQ417245.1
-	DQ417292.1	DQ417249.1
	DQ417293.1	DQ417242.1
	DQ417296.1	DQ417251.1
	DQ417288.1	DQ417248.1
	DQ417287.1	DQ417241.1
	DQ417294.1	DQ417246.1
	DQ417291.1	DQ417247.1
	DQ417290.1	DQ417244.1
	DQ417295.1	DQ417250.1
	DQ417289.1	DQ417243.1
376198 Phestilla sp. 1	DQ417320.1	DQ417272.1
	DQ417324.1	DQ417270.1
	DQ417322.1	DQ417269.1
	DQ417314.1	DQ417266.1
	DQ417316.1	DQ417268.1
	DQ417315.1	DQ417267.1
	DQ417319.1	DQ417271.1
	DQ417323.1	DQ417265.1
	DQ417318.1	
	DQ417317.1	
	DQ417321.1	

376194 Phestilla sp. 2	DQ417286.1 DQ417285.1 DQ417284.1 DQ417283.1		DQ417238.1 DQ417237.1 DQ417239.1 DQ417240.1		
1154721 Phidiana hiltoni	DQ417283.1	JQ699470.1	JQ699558.1		JQ699378.1
219669 Phidiana lynceus	JX087562.1 JX087563.1	JX087633.1 JX087634.1	JX087497.1 JX087498.1	AY165765.1	
1287508 Phidiana militaris		JQ996979.1	JQ996875.1		
219671 Phyllodesmium briareum	HQ010492.1	HQ010442.1	HQ010510.1	GU339158.1	
	HQ010480.1	HQ010459.1	HQ010528.1		
	GQ403775.1	HQ010460.1	GQ403753.1		
	HQ010491.1		HQ010527.1		
869976 Phyllodesmium cf. magnum	GQ403785.1		GQ403762.1		
	GQ403784.1		GQ403763.1		
869965 Phyllodesmium colemani	HQ010499.1	HQ010466.1	GQ403755.1	GU339159.1	
	GQ403777.1	HQ010467.1	GQ403754.1		
	HQ010498.1		HQ010534.1		
	GQ403776.1				
869966 Phyllodesmium crypticum	HQ010507.1	HQ010477.1	HQ010537.1	GU339160.1	
	HQ010502.1	HQ010470.1	GQ403770.1		
		HQ010471.1	HQ010536.1		
			HQ010543.1		
797238 Phyllodesmium horridum	HM162757.1	HQ010445.1	HQ010513.1		
		HM162590.1	HM162681.1		
			HQ010514.1		
869967 Phyllodesmium hyalinum	GQ403778.1		GQ403756.1		
869968 Phyllodesmium jakobsenae	HQ010488.1	HQ010455.1	GQ403757.1	GU339162.1	
	HQ010489.1	HQ010456.1	GQ403759.1		
	GQ403779.1		HQ010524.1		
	GQ403781.1				
869969 Phyllodesmium kabiranum		HQ010454.1	HQ010512.1		
		HQ010444.1	HQ010523.1		
			GQ403766.1		
			GQ403767.1		
930959 Phyllodesmium karenae	HQ010483.1	HQ010478.1	HQ010544.1		
	HQ010508.1	HQ010448.1	HQ010517.1		
869970 Phyllodesmium koehleri	HQ010494.1	HQ010462.1	GQ403760.1		
	GQ403782.1		HQ010530.1		

869971 Phyllodesmium lembehensis	GQ403780.1		GQ403758.1		
			GQ403771.1		
674072 Phyllodesmium lizardensis	HQ010505.1	HQ010464.1	GQ403772.1		
	HQ010496.1	HQ010474.1	HQ010540.1		
			HQ010532.1		
869972 Phyllodesmium longicirrum	JQ699634.1	JQ699471.1	GQ403761.1	GU339161.1	JQ699379.1
	GQ403783.1		JQ699559.1		
869973 Phyllodesmium macphersonae	HQ010487.1	HQ010446.1	GQ403769.1		
	HQ010479.1	HQ010453.1	HQ010522.1		
	HQ010482.1	HQ010441.1	HQ010509.1		
			HQ010515.1		
			GQ403768.1		
869964 Phyllodesmium magnum	HQ010500.1	HQ010443.1	HQ010511.1		
	HQ010481.1	HQ010468.1			
930960 Phyllodesmium opalescens	HQ010484.1	HQ010450.1	HQ010519.1		
	HQ010485.1	HQ010449.1	HQ010518.1		
0200/1 DI 11 1	110010501 1	HQ010451.1	HQ010520.1		10(00200.1
930961 Phyllodesmium parangatum	HQ010501.1	JQ6994/2.1	JQ699560.1		JQ699380.1
	HQ010506.1	HQ0104/5.1	HQ010542.1		
	JQ699635.1	HQ010469.1	HQ010535.1		
0200(2 D L-11, 1,		HQ010476.1	HQ010541.1		
930962 Phyliodesmium pinnatum		HQ010458.1	HQ010526.1		
869974 Phyllodesmium poindimiei	GQ403786.1	HQ010452.1	HQ010531.1		
	HQ010495.1	HQ010463.1	GQ403764.1		
	HQ010486.1		HQ010521.1		
869975 Phyllodesmium rudmani	GQ403787.1	HQ010461.1	HQ010529.1		
	HQ010493.1		GQ403765.1		
930958 Phyllodesmium sp. 2		HQ010447.1	HQ010516.1		
930963 Phyllodesmium tuberculatum	HQ010490.1	HQ010465.1	HQ010525.1		
	HQ010497.1	HQ010457.1	HQ010533.1		
797256 Pinufius rebus	HM162744.1	HM162576.1	HM162667.1		
1287625 Piseinotecus gabinierei	JX087561.1	JX087632.1	JX087496.1		
C		JX087631.1	JX087495.1		
934969 Piseinotecus gaditanus	HQ616759.1	HQ616788.1	HQ616722.1		
797203 Piseinotecus sp.	HM162694.1	HM162510.1	HM162604.1		
1154746 Protaeolidiella atra			JQ699561.1		JQ699381.1
1287515 Protaeolidiella juliae	JQ997094.1	JQ997007.1	JQ996899.1		

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934978 Pruvotiolia longicirrha	HQ616/60.1	HQ616/89.1	HQ616/23.1		
934979 Pruvotfolia pselliotes	HQ616762.1	HQ616791.1	HQ616725.1		
1290777 Pruvotfolia sp. A		JQ997008.1			
1290778 Pruvotfolia sp. B		JQ996980.1			
797258 Pseudobornella orientalis		HM162534.1	HM162628.1		
929462 Pteraeolidia ianthina		JQ699473.1	JQ699562.1	GU227370.1	JQ699382.1
		JQ997006.1			
797260 Sakuraeolis enosimensis	HQ010503.1	HQ010472.1	HQ010538.1		
	HM162758.1	HM162591.1	HM162682.1		
797262 Scyllaea pelagica	HM162711.1	HM162540.1	JN869415.1		
	JN869458.1	JN869441.1	JN869414.1		
	JN869459.1	JN869442.1	HM162633.1		
	JN869457.1	JN869443.1	JN869416.1		
1449875 Spurilla braziliana	JX087575.1	JQ997009.1	JX087503.1		
	JX087568.1	JX087639.1	JQ996900.1		
	JQ997095.1	JX087638.1	JX087508.1		
	JQ997097.1	JX114844.1	JX087511.1		
	JX087567.1	JX087644.1			
	JX087578.1	JX087647.1			
	JQ997096.1				
1154712 Spurilla chromosoma	JQ699566.1	JQ996912.1	JQ996812.1		JQ699295.1
	JQ997018.1	JQ699387.1	JQ699476.1		
		JQ996911.1	JQ996813.1		
1287630 Spurilla creutzbergi	JX087547.1	JX087614.1	JX087475.1		
	JX087546.1	JX087613.1	JX087477.1		
		JX087615.1	JX087478.1		
		JX087612.1	JX087476.1		
910326 Spurilla major				GU227365.1	

929453 Spurilla neapolitana	JX087574.1	JX087655.1	JX087509.1	GU227362.1	JQ699383.1
1 1	JX087583.1	JX087656.1	HQ616726.1		
	JX087586.1	JX087646.1	JX087502.1		
	JX087566.1	JX087643.1	HQ616727.1		
	JX087576.1	JX087645.1	JX087517.1		
	JX087570.1	JX087640.1	JX087521.1		
	JQ699636.1	JX087661.1	JX087523.1		
	JX087569.1	JX087651.1	JX087520.1		
	HQ616764.1	JX087642.1	JX087504.1		
	JX087572.1	HQ616792.1	JX087519.1		
	JX087571.1	JX087652.1	JX087518.1		
	JX087581.1	JX087658.1	JX087506.1		
	JX087577.1	JX087635.1	JX087499.1		
	HQ616763.1	JX087650.1	JX087516.1		
	JX087564.1	JX114845.1	JX087510.1		
	JX087585.1	JX087654.1	JX087524.1		
	JX087584.1	JX087660.1	JX114843.1		
	JX087582.1	JX087637.1	JX087507.1		
	JX087587.1	JX087641.1	JX087522.1		
	JX087573.1	JX087659.1	JX087514.1		
		JX087657.1	JX087515.1		
		JQ699474.1	JQ699563.1		
		JX087662.1	JX087500.1		
		JX087653.1	JX087505.1		
		HQ616793.1	JX114842.1		
1154722 Spurilla sargassicola	JX087589.1	JX087663.1	JQ996901.1		JQ699384.1
	JX087588.1	JX087664.1	JX087525.1		
	JQ997098.1	JQ997010.1	JQ699564.1		
		JX087665.1	JX087526.1		
1290798 Spurilla sp. A	JX087565.1	JX087649.1	JX087501.1		
	JX087580.1	JX087636.1	JX087513.1		
	JX087579.1	JX087648.1	JX087512.1		
530585 Tergipes antarcticus	EU727251.1		KF713480.1		
	EU727252.1				
	EU727253.1				
	GU227106.1				
	EU727250.1				
157144 Tergipes tergipes	AY345032.1		AY345032.1	AF249197.1	

252556 Tethys fimbria		EF133468.1		
797240 Tritonia antarctica	HM162718.1	HM162550.1	HM162643.1	
763132 Tritonia challengeriana	GQ292052.1			GQ326904.1
70853 Tritonia diomedea	GQ292050.1		GU339203.1	GQ326890.1
763133 Tritonia festiva	GQ292051.1 HM162719 1	HM162551.1		GQ326889.1
157146 Tritonia nilsodhneri	HM162716.1	HM162548.1	HM162641.1	AF249200.1
797241 Tritonia pickensi	HM162717.1	HM162549.1	HM162642.1	
797192 Tritonia sp. 3	HM162731.1	HM162563.1	HM162654.1	
797193 Tritonia sp. 4	HM162732.1	HM162564.1	HM162655.1	
797194 Tritonia sp. F	HM162720.1	HM162552.1	HM162644.1	
797195 Tritonia sp. G	HM162730.1	HM162562.1	HM162653.1	
157148 Tritoniella belli	GQ292056.1		GU227002.1	AF249201.1
	GU227111.1			GQ326883.1

Appendix B.

This appendix contains the legends for 20 additional tree figures, as cited in the text.

Figure B1.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from five genes (COI, H3, 16S, 18S, 28S) in the ALL_TAXA data matrix. The outgroup is the clade containing *Discodoris atromaculata* and *Cadlina laevis*.

Figure B2.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from five genes (COI, H3, 16S, 18S, 28S), partitioned, in the ALL_TAXA data matrix. The outgroup is the clade containing *Discodoris atromaculata* and *Cadlina laevis*.

Figure B3.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from five genes (COI, H3, 16S, 18S, 28S), partitioned, in the MIN_TWO_GENES data matrix. The outgroup is the clade containing *Discodoris atromaculata* and *Cadlina laevis*.

Figure B4.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from five genes (COI, H3, 16S, 18S, 28S) in the MIN_THREE_GENES data matrix. The outgroup is *Discodoris atromaculata*.

Figure B5.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from five genes (COI, H3, 16S, 18S, 28S), partitioned, in the MIN_THREE_GENES data matrix. The outgroup is *Discodoris atromaculata*.

Figure B6.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from three genes (COI, H3, 16S) in the THREE_GENES data matrix. The outgroup is the clade containing *Discodoris atromaculata* and *Cadlina laevis*.

Figure B7.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from three genes (COI, H3, 16S), partitioned, in the THREE_GENES data matrix. The outgroup is containing *Discodoris atromaculata*.

Figure B8.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from the mitochondrial Cytochrome Oxidase I (COI) gene. The outgroup is *Discodoris atromaculata*.

Figure B9.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from the nuclear Histone 3 (H3) gene. The outgroup is *Discodoris atromaculata*.

Figure B10.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from the mitochondrial 16S rRNA gene. The outgroup is the clade containing *Discodoris atromaculata* and *Cadlina laevis*.

Figure B11.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from the nuclear 28S rRNA gene. The outgroup is *Discodoris atromaculata*.

Figure B12.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from the nuclear 18S rRNA gene. The outgroup is *Discodoris atromaculata*.

Figure B13.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from five genes (COI, H3, 16S, 18S, 28S) in the ALL_TAXA data matrix, excluding all sequences from the genus *Melibe*. The outgroup is the clade containing *Discodoris atromaculata* and *Cadlina laevis*.

Figure B14.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from five genes (COI, H3, 16S, 18S, 28S) in the MIN_TWO_GENES data matrix, excluding all sequences from the genus *Melibe*. Bootstrap values are provided above each branch.

Figure B15.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from five genes (COI, H3, 16S, 18S, 28S) in the MIN_THREE_GENES data matrix, excluding all sequences from the genus *Melibe*. The outgroup is *Discodoris atromaculata*.

Figure B16.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from three genes (COI, H3, 16S) in the THREE_GENES data matrix, excluding all sequences from the genus *Melibe*. The outgroup is the clade containing *Discodoris atromaculata* and *Cadlina laevis*.

Figure B17.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from the mitochondrial Cytochrome Oxidase I (COI) gene, excluding all sequences from the genus *Melibe*. The outgroup is *Discodoris atromaculata*.

Figure B18.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from the nuclear Histone 3 (H3) gene, excluding all sequences from the genus *Melibe*. The outgroup is *Discodoris atromaculata*.

Figure B19.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from the mitochondrial 16S rRNA gene, excluding all sequences from the genus *Melibe*. The outgroup is the clade containing *Discodoris atromaculata* and *Cadlina laevis*.

Figure B20.

The 50% majority-rule bootstrap consensus tree of Cladobranchia using sequence data from five genes (COI, H3, 16S, 18S, 28S) in the MIN_149_TAXA data matrix. The outgroup is the clade containing *Discodoris atromaculata* and *Cadlina laevis*.