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Short Communication

New insights into the phylogeny of glass sponges (Porifera, Hexactinellida): Monophyly of Lyssacinosida and Euplectellinae, and the phylogenetic position of Euretidae

M. Dohrmann [a,c], A.G. Collins [b], G. Wörheide [c,*]

[a] Georg-August-Universität Göttingen, Geowissenschaftliches Zentrum Göttingen (GZG), Abteilung Geobiologie, Goldschmidtstr. 3, 37077 Göttingen, Germany
[b] NMFS, National Systematics Laboratory, National Museum of Natural History, MRC-153, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013-7012, USA
[c] Department für Geo- und Umweltwissenschaften & GeoBioCenter[LMU], Ludwig-Maximilians-Universität München, Richard-Wagner-Str. 10, 80333 München, Germany

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1. Introduction

Glass sponges (Porifera, Hexactinellida) are major components of benthic deep-water communities, and are remarkable for their unique tissue organization, physiology, and aesthetically appealing skeletal morphology (Leys et al., 2007). Leys et al. (2007, p. 117) reported 531 described species, but since then this number has increased to 550 (Lopes et al., 2007; Menshenina et al., 2007a,b; Reiswig et al., 2008; Tabachnick and Collins, 2008; Tabachnick et al., 2008), and description of many more new species and even genera is in progress, suggesting that biodiversity of glass sponges is much higher than currently appreciated. A well-resolved phylogeny of this important yet understudied group of sponges is highly desirable in order to understand how this diversity evolved.

The first molecular phylogeny of Hexactinellida (based on three ribosomal DNA markers) has only recently been published, and revealed a surprisingly high level of congruence with morphology-based systems (Dohrmann et al., 2008). However, monophyly of the most species-rich order, the Lyssacinosida, remained ambiguous, being model dependent. Furthermore, limited taxon sampling prevented resolution of subfamily-level relationships among the Euplectellidae (the 'venus-flower basket' family). Finally, the accuracy of the placement of Farreidae (Sceptrulophora) was also questionable because this taxon was only represented by a single erroneous or possibly pseudogenic 18S rDNA sequence from GenBank (see also Voigt et al., 2008). This same sequence may also have had an adverse effect on the rest of the phylogeny.

Here, we have addressed these issues by including 10 additional species that were previously unavailable to us (i.e., Dohrmann et al., 2008). Among them was a *Farrea* species that yielded high-quality sequences of all three markers, and a representative of the most species-rich family of Sceptrulophora, the Euretidae. Whereas the position of *Farrea* did not change, we find that Lyssacinosida is monophyletic but two of the three subfamilies of Euplectellidae are not. Implications of these results for evolution of morphological characters are discussed. We also elaborate further on comparison of RNA (paired-sites) substitution models (see Savill et al., 2001; Dohrmann et al., 2008) and highlight the non-trivial relationship of taxon sampling and model choice in deep metazoan phylogenies inferred from rDNA data.

2. Materials and methods

2.1. New specimens and sequences

Taxonomic and collection information of the new specimens, and sequence accession numbers, are given in Table 1. Full-length 18S, and partial 28S and mitochondrial 16S rDNA sequences were obtained as described, and added to the previously reported alignments (see Dohrmann et al., 2008). A few additional sites (9 bp overall) had to be excluded due to further ambiguities regarding positional homology introduced by the new sequences. The final concatenated alignment [TreeBase (www.treebase.org) matrix accession number M4266] consisted of 3426 bp for 60 taxa, including the 17 outgroup species (from Choanoflagellata, Demospongiae, Homoscleromorpha, Calcarea, Placozoa, and Cnidaria) used in our previous study (see Dohrmann et al., 2008). The total amount of missing data decreased from 18.75% to 16.82% because of the more complete sequencing of *Farrea* and one *Hyalonema* species (see Table 1).

* Corresponding author. Fax: 49 89 21806602.
E-mail address: woerheide@lmu.de (G. Wörheide).

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Table 1
New hexactinellids sampled for this study. GW, collection of G.W.; HBOI, Harbor Branch Oceanographic Institution; MBARI, Monterey Bay Aquarium Research Institute; USNM, National Museum of Natural History, Smithsonian Institution; ZMA, Zoölogisch Museum Amsterdam.

Family	ID	Collection region	Voucher-No./source	Acc.-Nos. (18S, 28S, 16S)
Hyalonematidae	*Hyalonema* sp.3[a]	Bahamas	GW5454/Deep Scope 3	FM946129, FM946128, FM946109
	Hyalonema sp.4	Gulf of Mexico	USNM 1122180	FM946130, FM946131, FM946108
Euplectellidae	*Docosaccus* n. sp.	California	GW5429/MBARI	FM946116, FM946115, FM946105
	Hertwigia sp.	Florida	USNM 1122181	FM946121, FM946120, FM946104
	Saccocalyx sp.[*]	Hawaii	USNM 1097540	–, FM946119, FM946103
	Bolosoma n. sp.	Hawaii	USNM 1097546	FM946118, FM946117, FM946102
Rossellidae	*Rossella* sp.[*,b]	Antarctica	ZMA POR16769	–, FM946112, FM946107
	Bathydorus n. sp.	California	GW5428/MBARI	FM946114, FM946113, FM946106
Aphrocallistidae	*Aphrocallistes beatrix*	Florida	USNM 1122182	FM946127, FM946126, FM946110
Euretidae	n. gen. n. sp.	Bahamas	HBOI 16-XI-02-1-001/H.M. Reiswig	FM946125, FM946124, FM946101
Farreidae	*Farrea* sp.[c]	Florida	USNM 1122183	FM946123, FM946122, FM946111

[*] Only sequenced for 16S and 3′-half of 28S partition.
[a] Probably the same species as "*Hyalonema* sp.2" used in Dohrmann et al. (2008), but sequenced for all three partitions.
[b] Originally identified as *Anoxycalyx joubini*; re-investigation of this specimen revealed the presence of calycocomes, which are diagnostic/apomorphic for *Rossella*.
[c] Sequenced for all three partitions; the erroneous 18S sequence from *Farrea occa* (see Dohrmann et al., 2008; Voigt et al., 2008) was not included in this study.

2.2. Phylogenetic analyses

Models for the loop partitions and 16S were selected based on the Akaike Information Criterion (AIC; Akaike, 1974) as described (Dohrmann et al., 2008). Results were the same as with the previous alignments, except that the inclusion of a proportion of invariable sites (+I) was now favored for the 16S partition. For stem regions, we employed the four paired-sites models (RNA6A, -6B, -7A, and -7D; see Savill et al., 2001) investigated previously and assessed their fit to our data with Bayes factors (Kass and Raftery, 1995; see Dohrmann et al., 2008 for details). In addition, we also ran an analysis under a 16-state model to assess whether discriminating between all possible base pairings could improve model fit (in 6- and 7-state models, mismatch base pairings are ignored or lumped into a single state, respectively; see Savill et al., 2001). We chose the RNA16C model because it is equivalent to models 7D and 6B (Savill et al., 2001); more general variants (16A, 16D) would have probably resulted in over-parameterization as this was already the case with the most general 6- and 7-state models 6A and 7A (see Results and Dohrmann et al., 2008). Phylogenetic analyses were performed with PHASE v2.0 (http://www.bio-inf.manchester.ac.uk/resources/phase/) essentially as in Dohrmann et al. (2008), except that chains were run for 5×10^7 post-burnin generations and sampled every 10^3 generations. Because currently available Bayesian Markov Chain Monte Carlo (MCMC) implementations might not be able to accurately infer branch lengths under certain conditions (e.g., Kolaczkowski and Thornton, 2007; Yang and Rannala, 2005; Yang, 2007), we re-estimated branch lengths of the consensus phylograms with the maximum likelihood (ML) program *optimizer* of the PHASE package, using exactly the same models as in the Bayesian analyses.

3. Results

Results of Bayes factor comparisons between 6- and 7-state models were the same as in Dohrmann et al. (2008), i.e., 6B > 6A >> 7D > 7A. We only present results obtained under 7D and 6B (Fig. 1), because Markov chains employing 6A and 7A had not converged for many parameters, making the results untrustworthy. Several considerations lead us to conclude that the phylogeny obtained under 7D likely provides the best estimate (Fig. 1A). First, under 6B *Aphrocallistes* and *Heterochone* (Aphrocallistidae) were not monophyletic; instead the two species with the longer terminal branches (*A. beatrix* and *Heterochone* sp.) grouped together (Fig. 1B), potentially indicating long-branch attraction (LBA; Felsenstein, 1978). In addition, the phylogeny obtained under 7D has generally more robust support values than those obtained under 6B (Fig. 1). RNA16C performed worst of all five models (2lnBF = −3018 compared to 7A), and also did not recover monophyly of the aphrocallistid genera (although the branching order was different than under 6B; results not shown).

Overall, the phylogeny is congruent with previous results (Dohrmann et al., 2008): both subclasses (Amphidiscophora, Hexasterophora) and all families as well as most genera are monophyletic, and all sceptrule-bearing taxa (Hexactinosida part.) form a highly supported clade (Sceptrulophora; see Mehl, 1992) to the exclusion of *Iphiteon panicea* (Hexactinosida, Dactylocalycidae). However, Lyssacinosida is recovered as monophyletic under both 6B and 7D (Fig. 1) [and also 16C (not shown)], due to a more stable position of *I. panicea*, which was nested within Lyssacinosida in the previously reported phylogeny obtained under 6B (see Dohrmann et al., 2008). Furthermore, the euplectellid subfamily Euplectellinae is monophyletic, due to a change in position of *Walteria leuckarti* (Corbitellinae) from within Euplectellinae (Dohrmann et al., 2008) to sister of *Hertwigia* sp. + *Saccocalyx* sp. The grouping of the latter two species implies paraphyly of the other two subfamilies, Corbitellinae (*Hertwigia* and *Walteria*) and Bolosominae (*Rhabdopectella*, *Bolosoma*, and *Saccocalyx*). The position of *Farrea* remains the same as in Dohrmann et al. (2008), but the terminal branch leading to it is much shorter here. The representative of the sceptrulophoran family Euretidae is more closely related to *Farrea* + Aphrocallistidae than to Tretodictyidae. Monophyly of *Hyalonema* (Hyalonematidae), *Bathydorus* (Rossellidae), and the Antarctic *Rossella* species (i.e., excluding the North Atlantic *R. nodastrella*) is further corroborated, while support for the inclusion of *Clathrochone clathroclada* (Lyssacinosida *incertae sedis*) in the Leucopsacidae (Dohrmann et al., 2008) substantially decreased. Under 16C, *C. clathroclada* was sister to Leucopsacidae + Rossellidae, but support for the latter clade was only 54% (not shown).

The branching order of the outgroup taxa (not shown) did not change, but some support values differed (Table 2). Support for monophyly of Porifera was 84% under 7D, compared to 72% obtained with the previous taxon set. Under 6B, sponge monophyly had 59% Bayesian support, not significantly different from the 60% reported previously. Likewise, paraphyly of Demospongiae *sensu stricto* with respect to Hexactinellida (see Dohrmann et al., 2008) remained weakly supported under 6B (73%), but had 92% support under 7D, compared to 79% obtained with the previous taxon set. Under 16C, sponge monophyly and demosponge paraphyly had 98% and 93% support, respectively (not shown).

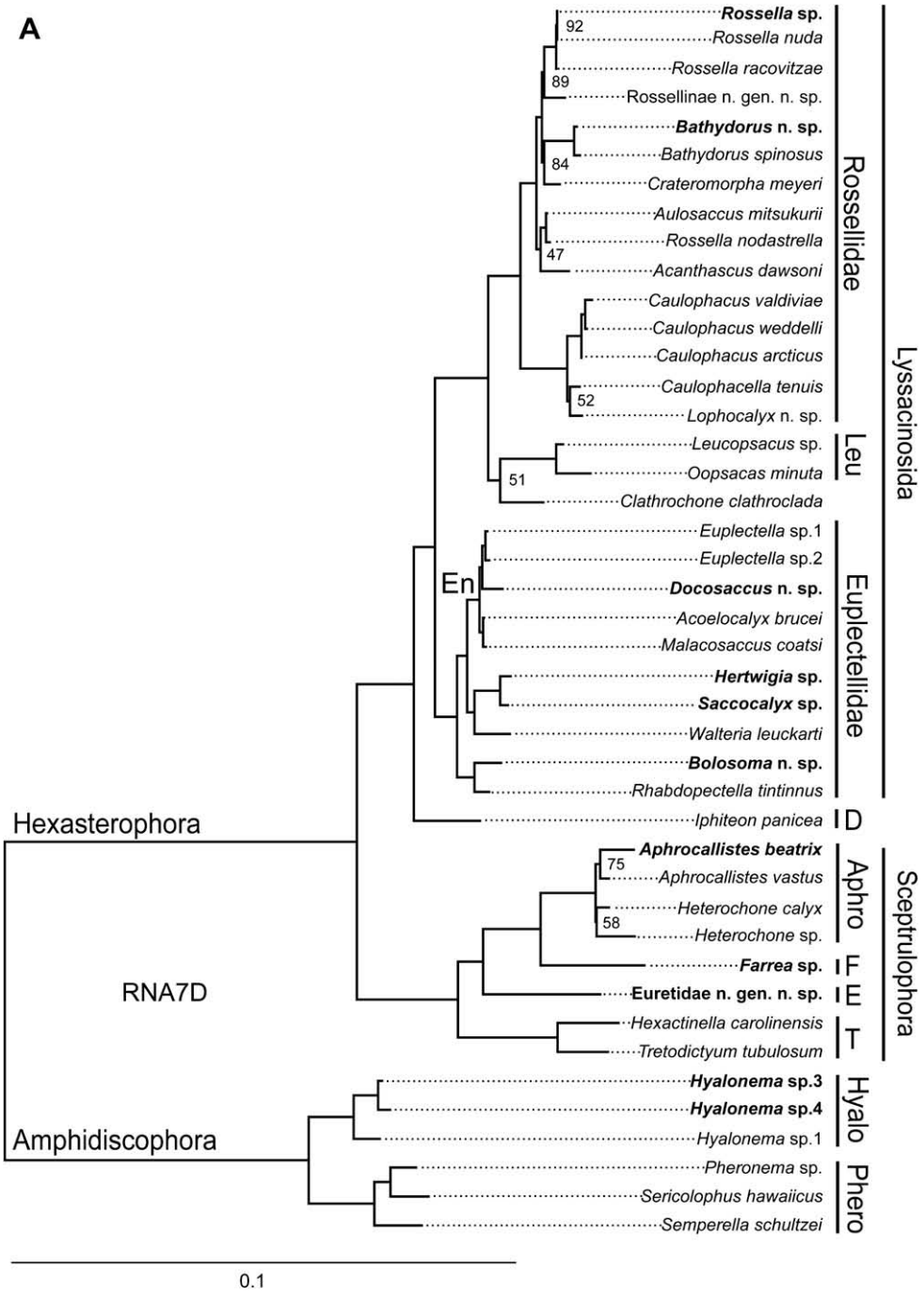

Fig. 1. Ribosomal DNA phylogeny of Hexactinellida (new taxa in bold). Bayesian consensus trees based on 50,000 post-burnin trees; branch lengths re-estimated with ML (see Materials and methods for details). Outgroups not shown. Posterior probabilities only shown where <95%. (A) Phylogeny obtained under RNA7D applied to stem regions. (B) Phylogeny obtained under RNA6B for stem regions. Models for loop regions and 16S were GTR (18S, 16S) and TrN93 (28S). Rate heterogeneity was modeled with a discrete gamma distribution (four categories) and a proportion of invariable sites (+I+G) independently for each partition. Further details can be found in Dohrmann et al. (2008). Aphro, Aphrocallistidae; D, Dactylocalycidae; E, Euretidae; En, Euplectellinae; F, Farreidae; Hyalo, Hyalonematidae; Leu, Leucopsacidae; Phero, Pheronematidae; T, Tretodictyidae. Scale bar, expected number of substitutions per site. The tree in (A), including outgroups, has been deposited in TreeBase (www.treebase.org) under study number S2246.

4. Discussion

4.1. Model comparison and support for outgroup nodes

With our extended dataset, comparison of likelihood-values under the two paired-sites models RNA6B and RNA7D (see Savill et al., 2001) again revealed the former to be higher. However, in the phylogeny obtained under 6B, there is an apparent case of LBA regarding the genera *Heterochone* and *Aphrocallistes*, and the phylogeny is less robust, in terms of clade support, than the 7D phylogeny. Although this has to be further tested with additional data, we therefore suspect that although being preferred by the Bayes factor, the 6B phylogeny is less accurate than that obtained with 7D. This is presumably because mismatch base pairings are treated as missing data in 6-state models, thus potentially decreasing the amount of phylogenetic signal that

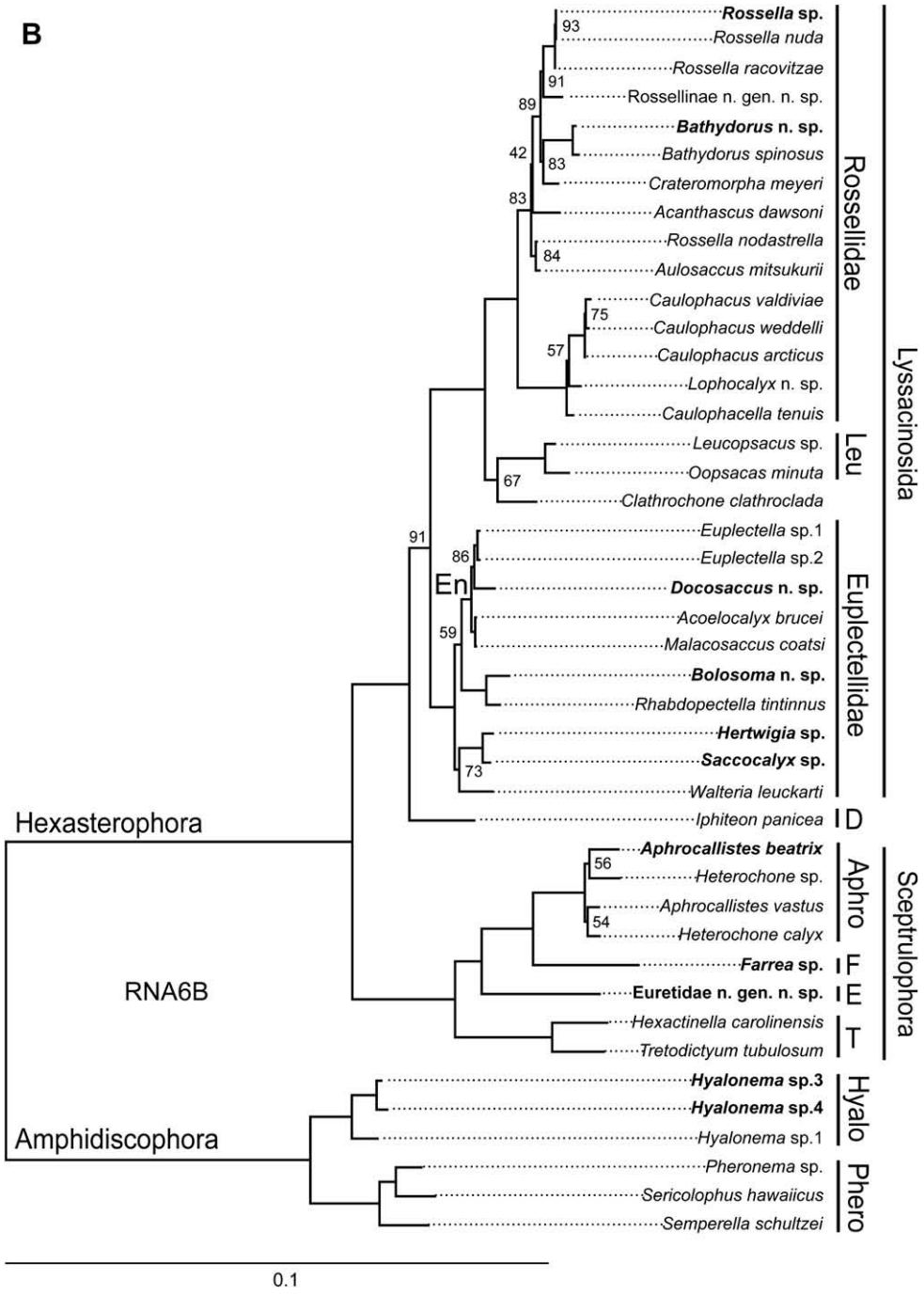

Fig 1. (*continued*)

Table 2
Comparison of Bayesian support for monophyly of Porifera and paraphyly of Demospongiae *sensu stricto*, respectively, obtained with the taxon set used in Dohrmann et al. (2008) and that used in this study. "Demosponge paraphyly" refers to a branching order where the clade (*Spongilla lacustris*(*Mycale fibrexilis*, *Suberites ficus*)) is more closely related to Hexactinellida than to the remaining included Demospongiae *sensu stricto*, (*Dysidea*, *Aplysina fistularis*). With both taxon sets, Demospongiae *sensu stricto* and Hexactinellida form a highly supported clade, whereas the Homoscleromorpha (traditionally assigned to Demospongiae) are the sister group of calcareous sponges (see Dohrmann et al., 2008 for discussion).

Model for stem sites	Posterior probability (%)			
	Sponge monophyly		Demosponge paraphyly	
	Dohrmann et al. (2008) taxon set	This study	Dohrmann et al. (2008) taxon set	This study
RNA6B	60	59	75	73
RNA7D	72[a]	84	79[a]	92

[a] Not reported in Dohrmann et al. (2008).

can be extracted from the alignment. On the other hand, the poor performance of the 16-state model indicates that accounting for all possible mismatches is superfluous in our case, and a single mismatch state is sufficient to describe our data well. These interpretations are also in better agreement with the conclusions of Savill et al. (2001), who gave a general preference to models 7A and 7D.

A finding that deserves further attention is the fact that increased taxon sampling resulted in markedly greater support for monophyly of Porifera and paraphyly of Demospongiae *sensu stricto*, but only in the 7D phylogeny (Table 2). Significant support (>95%) for sponge monophyly was only found with the 16C model (not shown). However, this result has to be interpreted with caution because of the poor performance of this model. Likewise, although receiving >90% Bayesian support under 7D and 16C with the present data set, paraphyly of Demospongiae *s.s.* appears to be an artefact of insufficient taxon sampling (Dohrmann et al., unpublished results). Thus, there appears to be a complex relationship between model choice and taxon sampling in case of rDNA data extracted from early-branching metazoans, suggesting that the influence of both these factors and their interplay need to be thoroughly addressed in studies aiming to resolve deep metazoan relationships from this kind of data.

4.2. Monophyly of Lyssacinosida and hexasterophoran skeletal evolution

In contrast to our previous study (Dohrmann et al., 2008), the most species-rich hexactinellid order, Lyssacinosida, is now recovered as monophyletic, independent of model choice, re-emphasizing the importance of taxon sampling for phylogenetic inference (e.g., Zwickl and Hillis, 2002). Another factor that might have contributed to this result is the replacement of the erroneous or pseudogenic 18S sequence of *Farrea occa* (see Voigt et al., 2008) with new sequences from *Farrea* sp. Exclusion of *F. occa* in our previous study (Dohrmann et al., 2008) resulted in substantially decreased support for the position of *I. panicea* as sister to Euplectellidae. Thus, replacement of the *F. occa* sequence had an overall beneficial effect on tree reconstruction.

Lyssacinosida is a well-established taxon (Reiswig, 2002a), and corroboration of its monophyly with molecular data further increases the high congruence of molecular and morphological systems in Hexactinellida (compared to other sponge groups; see Erpenbeck and Wörheide, 2007). It is noteworthy, however, that no morphological autapomorphies are known for Lyssacinosida (Mehl, 1992); the taxon is basically defined by a skeletal organization of mainly unfused spicules (a plesiomorphy that also characterizes Amphidiscophora), combined with hexasters as microscleres (the defining autapomorphy of Hexasterophora) (Mehl, 1992). In contrast, members of "Hexactinosida" (here represented by Sceptrulophora and *Iphiteon panicea*) possess rigid skeletons composed of fused hexactine megascleres (dictyonal frameworks) in addition to loose spiculation (see Leys et al., 2007). The position of *I. panicea* as the sister taxon to Lyssacinosida raises the possibility that dictyonal frameworks were inherited from the last common ancestor of Hexasterophora and subsequently lost in the lineage leading to Lyssacinosida. Although the occurrence of "basidictyonal frameworks" as attachment structures in many lyssacinosidans (see Leys et al., 2007) might provide some support for this idea, homology of these structures to true dictyonal frameworks is questionable, and reasons for a reversal to the ancestral type of skeletal organization are hard to imagine. It is indispensable to determine the phylogenetic positions of additional non-sceptrulophoran dictyonal taxa such as Aulocalycoida, Lychniscosida, and *Dactylocalyx* in order to reconstruct the evolution of hexasterophoran skeletal organization.

4.3. Position of Farreidae and Euretidae

In contrast to all other sceptrulophoran taxa, whose sceptrules are of the scopule-variant, Farreidae possess clavules (see Reiswig, 2002b). Thus, the nested position of *Farrea* suggests that the division of Sceptrulophora into Scopularia and Clavularia (Schulze, 1886; Mehl, 1992) is artificial, because Scopularia is paraphyletic. Our results imply that scopules belong to the groundplan of Sceptrulophora and were replaced by clavules in Farreidae. The occurrence of "intermediate" forms of sceptrules (aspidoscopules, sarules) in Farreidae (see Reiswig, 2002b) lends some support to this idea.

We also provide the first estimate of the phylogenetic position of Euretidae (Sceptrulophora) with molecular data. Its position (see Fig. 1) does not conflict with the Linnean system, simply because no statements about interrelationships of the families of "Hexactinosida" are made in the current classification (see Hooper and van Soest, 2002, p. 1281 ff). Since Euretidae is the most species-rich family of Sceptrulophora, and its taxonomic definition is weak, it might be suspected that this taxon is paraphyletic. This hypothesis was not tested here and awaits sampling of additional species.

4.4. Phylogeny and evolution of Euplectellidae

In our previous study, we only included one species each of the euplectellid subfamilies Bolosominae (*Rhabdopectella tintinnus*) and Corbitellinae (*Walteria leuckarti*), and Euplectellinae was recovered as paraphyletic (Dohrmann et al., 2008). Here, monophyly of Euplectellinae is highly supported, whereas the other two subfamilies appear to be non-monophyletic since *Saccocalyx* sp. (Bolosominae) groups with *Hertwigia* sp. (Corbitellinae). Although these two genera have extremely different body shapes, their spicule compositions are very similar (see Tabachnick, 2002), so this grouping gains some support from morphology. The topologies reconstructed here further imply that a) attachment to substrate by means of spicule tufts (lophophytous mode), which distinguishes Euplectellinae from the other subfamilies (Tabachnick, 2002), was derived from the basiphytous condition (attachment via basidictyonal frameworks; see above) in Euplectellidae, and b) tubular peduncles (stalks), the main character defining Bolosominae (Tabachnick, 2002), evolved at least twice in this family. The latter finding mirrors the situation in Rossellidae, where the stalked genera *Crateromorpha* and *Caulophacus* are not closely related (see Fig. 1 and Dohrmann et al., 2008). These results highlight the susceptibility of poriferan body shape features to homoplasy. We suggest that a more stable system of Euplectellidae (and also Rossellidae) requires thorough revision of morphology-based taxonomy, combined with increased taxon sampling of molecular markers.

4.5. Further results

In addition to the above findings, this study further corroborates monophyly of *Hyalonema*, *Bathydorus*, and the Antarctic *Rossella* species. Although monophyly of *Aphrocallistes* is also recovered (in the 7D phylogeny), this remains poorly supported. However, given that Aphrocallistidae contains only seven species, complete sampling of this family's diversity in order to robustly resolve its phylogeny appears to be an attainable goal.

Reasons for the decreased support for inclusion of *Clathrochone clathroclada* in the Leucopsacidae (Dohrmann et al., 2008) are somewhat unclear, but we suspect that the exclusion of additional alignment positions (see Materials and methods) may be responsible. *C. clathroclada* is only represented by the 16S and one half of the 28S partition, so confident placement of this species awaits collection of additional sequence data.

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