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PHYLOGENETIC ANALYSIS AND SYSTEMATIC REVISION OF REMIPEDIA (NECTIOPODA) FROM BAYESIAN ANALYSIS OF MOLECULAR DATA

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ABSTRACT

We performed a phylogenetic analysis of the crustacean class Remipedia. For this purpose, we generated sequences of three different molecular markers, 16S rRNA (16S), histone 3 (H3), and cytochrome c oxidase subunit I (COI). The analyses included sequences from 20 of the 27 recent species of Remipedia, plus four still-undescribed species. The data matrix was complemented with sequences from online databases (The European Molecular Biology Laboratory and GenBank®). *Campodea tillyardi* (Diplura), *Hutchinsoniella macracantha* (Cephalocarida), *Penaeus monodon* (Malacostraca) and *Branchinella occidentalis* (Branchiopoda) served as out-groups. In addition to the classic computer-based alignment methods used for protein-coding markers (H3 and COI), an alternative approach combining structural alignment and manual optimization was used for 16S. The results of our analyses uncovered several inconsistencies with the current taxonomic classification of Remipedia. Godzilliidae and the genera *Speleonectes* and *Lasionectes* are polyphyletic, while Speleonectidae emerges as a paraphyletic group. We discuss current taxonomic diagnoses based on morphologic characters, and suggest a taxonomic revision that accords with the topologies of the phylogenetic analyses. Three new families (Kumongidae, Pleomothridae, and Cryptocorynetidae) as well as three new genera (*Kumonga*, *Angirasu*, and *Xibalbanus*) are erected. The family Morlockiidae and the genus *Morlockia* are removed from synonymy and returned to separate status.

KEY WORDS: Bayesian phylogeny, molecular taxonomy, structural alignment

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INTRODUCTION

The comparatively small crustacean class Remipedia Yager, 1981 currently encompasses 27 described species. Nearly all the extant representatives of this taxon inhabit subterranean sections of anchialine caves in coastal regions. The only known species found in a fully marine, sub-seafloor cave is *Speleonectes kakuki* Daenekas et al., 2009. Another exception to the general ecological profile is *Speleonectes epilimnius* Yager and Carpenter, 1999, collected from the highly oxygenated surface water of an anchialine cave on San Salvador (Carpenter, 1999).

Remipedes live generally in salinity ranges from 18 to 35 ppt and temperature from 22 to 26°C. These crustaceans are thought to be scavengers and top predators in the ecosystems they inhabit, but evidence exists that they probably feed on detritus as well (Koenemann et al., 2007d). Although our knowledge of remipedes has increased greatly in the last dozen years, there are still large gaps in our understanding of their ecology, ethology, and evolutionary history.

The distinctive body plan of the class, composed of a head with six fused, appendage-bearing somites and an undivided, homonomously segmented trunk, cause remipedes to stand out among the disparity of crustacean shapes and forms. Because of the homonomous trunk, remipedes initially were regarded as "primitive" crustaceans (Fig. 1).

Early phylogenetic analyses based on morphological data sets supported a presumed basal position with different assemblages of crustaceans (Schram and Hof, 1997; Wills, 1997; Lange and Schram, 1999). However, the results of more recent studies of cerebral structures, DNA sequences, and larval embryology suggest that Remipedia represents a derived, rather than a primitive group (Fanenbruck et al., 2004; Harzsch, 2004; Koenemann et al., 2007b, 2009b; Ertas et al., 2009; Stemme et al., 2012). These hypotheses have variously placed remipedes as a sister group to:
  – all other crustaceans (Schram, 1986; Wheeler et al., 2004);

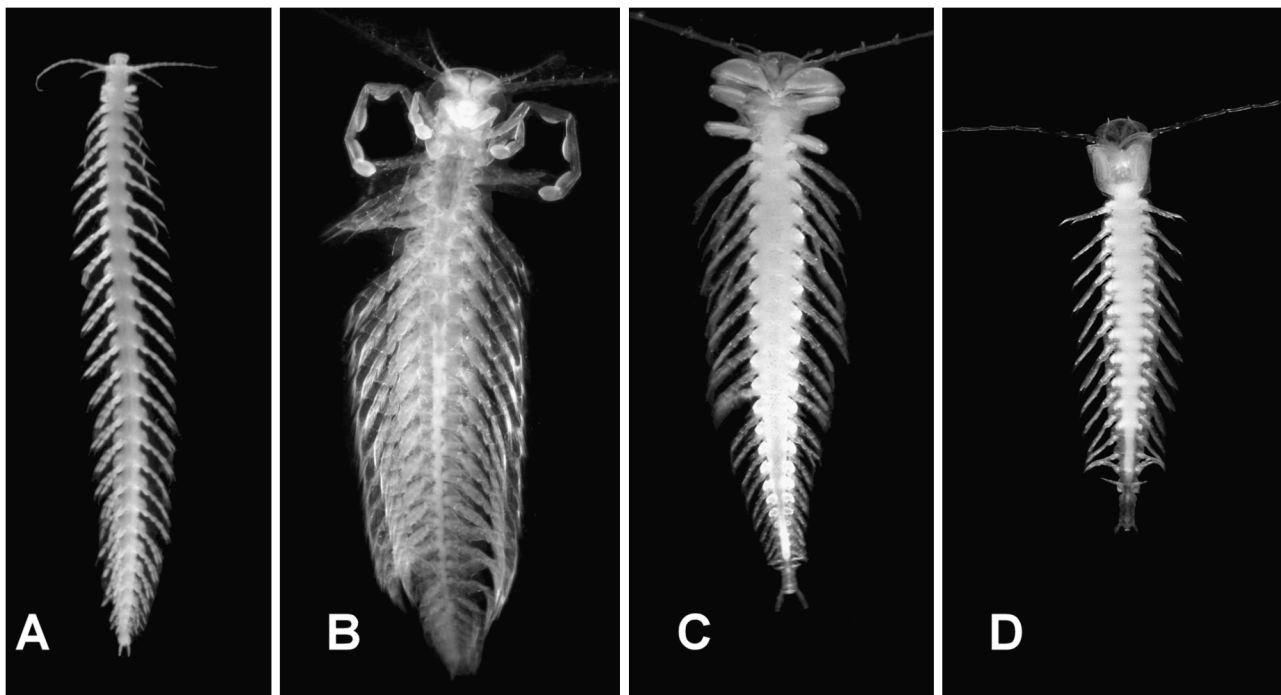* Corresponding author; e-mail: mario.hoenemann@gmx.de

Fig. 1.   Photographs of four species of Remipedia (not shown at same scale). A, *Speleonectes tanumekes* Koenemann et al., 2003 (dorsal view; photo by J. L. van der Ham); B, living specimen of *Cryptocorynetes elmorei* Hazerli et al., 2009 (ventral view; body length 11 mm; modified from Hazerli et al., 2009); C, living specimen of *Pleomothra fragilis* Koenemann et al., 2008 (body length not known; modified from Koenemann et al., 2008). D, *Godzilliognomus frondosus* Yager, 1989 (body length approximately 8 mm). A: dorsal view, B-D: ventral views.

– cephalocarids (Spears and Abele, 1997; Giribet et al., 2001; Regier et al., 2005, 2010; Koenemann et al., 2010);
– cirripedes (Lavrov et al., 2004; Carapelli et al., 2007);
– malacostracans (Fanenbruck et al., 2004; Harzsch, 2004; Koenemann et al., 2010; Stemme et al., 2012).

In addition, several analyses also place remipedes, in some cases together with cephalocarids, in various relationships to hexapods, including collembolans (Cook et al., 2005), diplurans (Carapelli et al., 2007; Koenemann et al., 2010), and all Hexapoda (Regier et al., 2010; Stemme et al., 2012; von Reumont et al., 2012) (for a detailed overview see Jenner, 2010).

At present, Remipedia includes two orders. The extinct Enantiopoda Birshtein, 1960 contains the fossil species *Tesnusocaris goldichi* Brooks, 1955 and *Cryptocaris hootchi* Schram, 1974 (see Emerson and Schram, 1991; Neiber et al., 2012), while Nectiopoda Schram, 1986 encompasses all extant species divided up until now amongst three families: Speleonectidae Yager, 1981, Godzilliidae Schram et al., 1986, and Micropacteridae Koenemann et al., 2007a.

Extant remipedes exhibit a disjunct geographic distribution (Fig. 2). The highest abundance and diversity is in the greater Caribbean region including the Bahamas, the Yucatán Peninsula, Cuba, the Dominican Republic, and the Turks and Caicos Islands. As the center of biodiversity, the Bahamas and the Turks and Caicos Islands have two endemic families according to the currently accepted systematics of the group: (1) Godzilliidae, composed of three genera and six species (*Godzillius robustus* Schram et al., 1986; *Godzillius fuchsi* Gonzalez et al., 2013; *Godzilliognomus*

frondosus Yager, 1989; *Godzilliognomus schrami* Iliffe et al., 2010; *Pleomothra apletocheles* Yager, 1989; and *Pleomothra fragilis* Koenemann et al., 2008); and (2) the monotypic Micropacteridae with *Micropacter yagerae* Koenemann et al., 2007a from the Turks and Caicos.

Within Speleonectidae, *Cryptocorynetes* Yager, 1987a (*C. haptodiscus* Yager, 1987a; *C. longulus* Wollermann et al., 2007; and *C. elmorei* Hazerli et al., 2009) is known from the Bahamas Islands, while the monotypic genus *Kaloketos* Koenemann et al., 2004 occurs in the Turks and Caicos Islands. Of the remaining speleonectid genera, *Speleonectes* Yager, 1981 (as currently accepted) has an amphi-Atlantic distribution, with many species from the Caribbean area and two species known from Lanzarote (Canary Islands) in the eastern Atlantic; *Lasionectes* Yager and Schram, 1986 shows a greater disjunction, with *Lasionectes entrichoma* Yager and Schram, 1986 in the Bahamas and *Lasionectes exleyi* Yager and Humphreys, 1996 from Bundera Sinkhole in Western Australia.

We have yet to achieve a consensus on classification and phylogenetic relationships within Remipedia. Koenemann et al. (2007c) presented a morphological cladistic analysis of 17 extant species of Nectiopoda, in which different methodological approaches were applied. It supported monophyly of Godzilliidae, confirmed the familial status of Micropacteridae, and revealed Speleonectidae as paraphyletic. In the first comprehensive molecular analysis, based on COI from some 22 remipede taxa, Godzilliidae and Speleonectidae emerged as paraphyletic assemblages, but no molecular data were available at that time from Micropacteridae (Neiber et al., 2011).
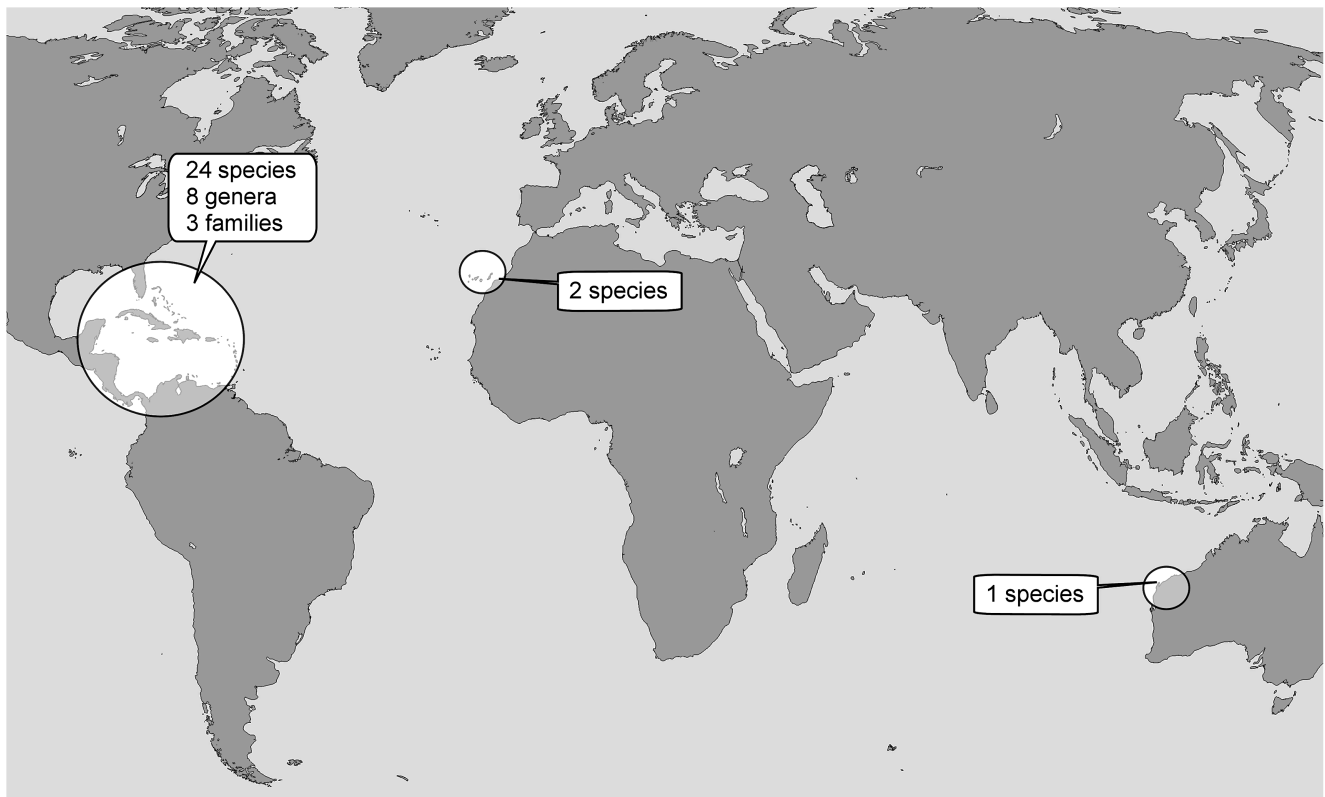
Fig. 2. Global distribution of extant Remipedia, including a total of 27 described species, 8 genera and 3 families (according to taxonomy prior to our revision).

In this study, we examine the phylogenetic relationships among Remipedia using molecular sequence data from COI, H3 and 16S.

MATERIAL AND METHODS

Taxon Sampling and Preservation

All animals were preserved in 70% to 96% ethanol immediately after collection; for DNA extraction, samples were stored at −20°C. See Table S1 in the online Supplementary material for a detailed list of sampled specimens.

Out-Group Selection

We selected four out-group taxa as representatives of crustacean and hexapod lineages to effectively polarize the data from Remipedia; these taxa include *Penaeus monodon* Fabricius, 1798 (Malacostraca), *Branchinella occidentalis* Dakin, 1914 (Branchiopoda), *Hutchinsoniella macracantha* Sanders, 1955 (Cephalocarida) and *Campodea tillyardi* Silvestri, 1931 (Hexapoda) (see Table S4 in the online Supplementary material).

Newly Generated Sequence Data

Total genomic DNA was extracted either from trunk segments or trunk limbs of our remipedes using the DNeasy® Blood & Tissue Kit (Qiagen, Hilden, Germany). To ensure success of the DNA extraction, purified isolates were run on 0.8% agarose gels, and stained with ethidium bromide. A fragment of 709 base pairs (bp) or 1096 bp including primers of the mitochondrial marker COI was amplified by polymerase chain reaction (PCR) with the universal primers LCO-1490 and HCO-2198 (Folmer et al., 1994) or the primers COI as and COI s, respectively (see Table S3 in the online Supplementary material). Using the universal primer pair 16Sar and 16Sbr (Palumbi, 1996) or the crustacean specific primer pair CRUST16SF and CRUST16SR (Ivey and Santos, 2007), fragments of 581 bp or 1047 bp including primers of the mitochondrial 16S rRNA gene were amplified. Partial sequences of the nuclear H3 gene (374 bp including primers) were generated with the primer pair H3 AF and H3 AR (Folmer et al., 1994, Table S3 in the online Supplementary material).

PCRs were performed with 1 μl of each DNA sample in a 25 μl volume: 1 μl of 10 mM dNTP (deoxyribonucleoside triphosphate), 2 μl of 50 mM MgCl$_2$, 2.5 μl of 10× NH$_4$-Reaction-Buffer (Bioline, Luckenwalde, Germany), 1 μl of each primer (10 pM), 16.3 μl H$_2$O and 0.2 μl (=1 unit) of BIOTAQ™ DNA polymerase (Bioline) in a Mastercycler® ep gradient thermal cycler (Eppendorf, Wesseling-Berzdorf, Germany). The reactions were initiated by a denaturation step of 2 minutes at 93°C, followed by 40 cycles of denaturation (45 seconds, 93°C), annealing (1 minute, primer pair-specific annealing temperature, see Table S3 in the online Supplementary material) and elongation (1 minute, 72°C). Cycling was terminated with a 7 minute elongation step at 72°C. Purification of PCR products was carried out using the NucleoSpin® Extract II kit (Macherey-Nagel, Düren, Germany). DNA sequences for the COI, 16S rRNA, and H3 gene fragments were obtained through Macrogen Sequencing Service (Macrogen, Seoul, South Korea), and assembled using the SeqMan™ II software package (DNASTAR, Madison, WI, USA, Swindell and Plasterer, 1997). All new sequences were deposited in the GenBank® database after removing primers (see Table S2 in the online Supplementary material for GenBank® accession numbers). Additional remipede sequences were downloaded from GenBank®, and added to our data sets.

Alignments

Prior to alignment, we carried out BLASTN and MEGABLAST (Altschul et al., 1990) searches for each sequence, including both newly generated and published (GenBank®) sequences, to identify possible contamination. Ambiguous sequences were excluded from the analyses. In addition, we verified that the COI data did not contain any nuclear copies of mitochondrial-derived genes (NUMTs) according to the procedure described in Buhay (2009).

The protein coding genes COI and H3 were aligned with MUSCLE (Edgar, 2004) using default parameters. For the 16S dataset, we followed an alternative approach by considering secondary structure information. First, the 16S sequence from *Artemia franciscana* Kellogg, 1906 was added

to the matrix to serve as a leading sequence for structural alignment. Secondly, we performed a pre-alignment with MUSCLE (Edgar, 2004) with default parameters. Subsequently, the pre-aligned 16S matrix was realigned manually based on the information for secondary structure of *A. franciscana* from the European ribosomal RNA database (Wuyts et al., 2004) (for descriptions and discussions of methods see Kjer, 1995; Kjer et al., 2007; Koenemann et al., 2010). Finally, the 16S sequence of *A. franciscana* was removed again from the alignment before analyzing the data. Both terminal regions were excluded from the pre-aligned data set, because these regions appeared to contain erroneous or doubtful sequence fragments for a number of taxa.

Data Sets

Because for some species DNA had been extracted from different samples, in some instances also from different locations, there was more than one sequence per taxon available. For taxa with multiple sequences, we chose a representative sequence for each taxon, based on the length and quality of the electropherograms. For our analyses we used a total of 37 COI sequences, 26 H3 sequences, and 30 16S sequences (for details see Supplementary on-line file, Tables 1 and 2). Since each of the three markers covered slightly different sets of taxa, we conducted separate runs for each marker, and an additional run with all three markers combined as follows: COI (Run 1), 16S (Run 2), H3 (Run 3), COI + 16S + H3 (Run 4). For Run 5, we included all COI sequences available, so that some species are represented by two or more specimens. The matrices of Runs 6 and 7 were identical with the matrix of Run 4, except for the following modifications: (1) in Run 6, the 16S sequence of *S. gironensis* Yager, 1994 was excluded, and (2) in Run 7, we omitted the 16S sequence of *S. gironensis* as well as the

COI sequence of *P. fragilis*. The 16S sequence of *S. gironensis* was excluded because it differed in some parts markedly from all other 16S sequences of Remipedia, and it therefore was difficult to align. The COI sequence of *P. fragilis* was excluded because it was almost identical to sequences of *P. apletocheles* indicating either a possible contamination or, e.g., a very young split between *P. apletocheles* and *P. fragilis* resulting in incomplete sorting of lineages.

When we began our analyses, *S. tulumensis* and *S.* cf. *tulumensis* were suspected of being different species, but recently Neiber et al. (2012) showed that *S. tulumensis* and *S.* cf. *tulumensis* are the same taxon.

Phylogenetic Analysis

Bayesian inferences (BI) of phylogeny were performed using MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). For each single marker, we conducted an extensive set of pre-tests on the preliminary data matrices in order to assess the effects of varying the analysis parameters. As a result, we assumed that different models of evolution apply for the first, second, and third codon positions in the COI data set, whereas the 16S and H3 data sets were not further subdivided into smaller partitions. Models of sequence evolution were selected using the Akaike information criterion (AIC, see Akaike, 1974; implemented in MrModeltest 2.3, Nylander, 2004) for each data set separately with a random neighbor-joining tree (Saitou and Nei, 1987) as starting tree, and model scores were computed in PAUP* Version 4.0b10 (Swofford, 2003). Two different types of evolution models were selected: (1) the Hasegawa-Kishino-Yano model (HKY, Hasegawa et al., 1985) for the second codon positions in the COI data set, and (2) the general time reversible model (GTR, Rodriguez et al., 1990, Yang, 1993) for the remaining partitions.

Table 1.   Shape of sternal bars and sternal plates of remipede taxa.

Taxon	Sternal bars 1-13	Sternal bar 14	Sternal bars from segment 15 onwards	Sternal plates
Micropacteridae				
Micropacter	greatly reduced	convex flap	absent	rounded
Gozilliidae				
Godzillius	isomorphic	isomorphic	isomorphic	rounded
Godzilliognomus	isomorphic	isomorphic	isomorphic	rounded
Pleomothridae				
Pleomothra	isomorphic	isomorphic	isomorphic	rounded
Kumongidae				
Kumonga	long, straight	large, triangular	15 + 16 slightly convex, then becoming triangular	rounded
Speleonectidae				
S. lucayensis	narrow, sublinear	large, concave	15-23 slightly concave, 24-convex flaps	rounded
S. kakuki	narrow, sublinear	large, concave	15-20 sublinear, 21-30 triangular flaps	rounded
S. minnsi	isomorphic	isomorphic	isomorphic	rounded
Lasionectes	narrow, slightly concave	large, concave	distinctly concave	rounded
Morlockiidae				
Morlockia	isomorphic	isomorphic	isomorphic	rounded
Cryptocorynetidae				
Cryptocorynetes	concave	large, convex (triangular)	15: concave, then straight, 19: convex flap	with pointed corners
Angirasu	long, slightly concave	large, convex	convex flap	with pointed corners
Kaloketos	concave	large, convex	concave	with pointed corners
Incertae familiae				
Xibalbanus	isomorphic	isomorphic	isomorphic	rounded
Incertae familiae and incerti generis				
"*S.*" *gironensis*	isomorphic	isomorphic	isomorphic	rounded
"*S.*" *epilimnius*	isomorphic	isomorphic	isomorphic	rounded
"*S.*" *tanumekes*	isomorphic	isomorphic	isomorphic	rounded

Table 2. Shape of terminal claw complexes of maxillae (Mx2) and maxillipeds (Mxp) of remipede taxa.

Taxon	Description of claw complexes
Micropacteridae	
Micropacter	Mx2 and Mxp different. Mx2: longfinger-type, 1 long denticle flanked by 4 shorter denticles; Mxp: horseshoe-type with 9-10 fused denticles.
Godzilliidae	
Godzillius	Mx2 + Mxp subequal or slightly different. Grappling hook-type: Mx2 with 7-10 prongs; Mxp with 10 prongs or with about 6 denticles flanked by 3 prongs on each side.
Godzilliognomus	Mx2 + Mxp subequal. Grappling hook-type with 5 prongs.
Pleomothridae	
Pleomothra	Mx2 + Mxp subequal. Longfinger-type: 1 long flanked by several shorter denticles.
Kumongidae	
Kumonga	Mx2 + Mxp subequal. Longfinger-type: 1 long spine flanked by 2 shorter stout spines and Posterior arc of 5-6 less robust spines.
Speleonectidae	
Speleonectes	Mx2 + Mxp subequal. Horseshoe-type: 1 separate arcuate spine and an arc of 7-15 smaller denticles flanked by 2 somewhat stouter denticles.
Lasionectes	Mx2 + Mxp subequal. Longfinger-type: trifid structure of three spines, the central one being the longest. Between the central and anterior spine is a comb-like row of about 5-6 short, delicate denticles.
Morlockiidae	
Morlockia	Mx2 + Mxp subequal. Horseshoe-type: 1 free arcuate spine and an arc of 7-14 denticles, the lateral ones slightly more robust.
Cryptocorynetidae	
Cryptocorynetes	Mx2 + Mxp subequal, small in relation to penultimate maxillary and maxillipedal segments. Horseshoe-type: composed of a free spine and an arc of 8-14 deeply incised denticles.
Angirasu	Mx2 + Mxp subequal. Horseshoe-type: arc of 7-8 small denticles flanked by 2 stronger, separate spines.
Kaloketos	Mx2 + Mxp subequal. Horseshoe-type: arc composed of 17-19 fine denticles flanked by stouter, somewhat more separated denticles on each side.
Incertae familiae	
Xibalbanus	Mx2 + Mxp subequal. Horseshoe-type: arc of small denticles flanked posteriorly by 1 robust, separate spine.
Incertae familiae and incerti generis	
"*S.*" *gironensis*	Mx2 + Mxp subequal. Horseshoe-type: arc of about 13 denticles flanked by a very large anterior spine and a somewhat smaller separated spine.
"*S.*" *epilimnius*	Mx2 + Mxp subequal. Horseshoe-type: 1 robust, subterminal anterior spine and posterior arch of numerous fused denticles, anteriormost denticle elongate, more robust.
"*S.*" *tanumekes*	Mx2 + Mxp subequal. Horseshoe-type: arc of 17-20 fine denticles flanked by 2 stouter, separate denticles.

MrModeltest 2.3 analyses also indicated that among-site variation in the different partitions is best modeled assuming a proportion of invariable sites (I) in combination with a discrete gamma-distributed among-site variation of substitutions (G). For the combined data set comprising COI, 16S rDNA, and H3 sequences, the same models of sequence evolution as in the data sets for the single gene fragments were used. In an additional analysis, we applied a codon model (invertebrate mitochondrial genetic code) implemented in MrBayes 3.1.2, based on the formulations outlined in Goldman and Yang (1994) and Muse and Gaut (1994) in combination with the GTR + G + I model to all available COI sequences of Remipedia and the selected out-groups.

Metropolis-coupled Markov-chain Monte Carlo (MCMCMC) searches in MrBayes Version 3.1.2 were run with ten chains in two separate runs for 20 000 000 generations (Runs 1-4, 6 + 7), or with four chains and 10 000 000 generations in two separate runs (Run 5) with default priors, trees sampled every 1000th generation, and separate estimation of parameters for individual partitions.

In addition to plotting the negative logarithmic likelihoods against sampled generations, potential scale reduction factors (PSRF, Gelman and Rubin, 1992) provided in MrBayes 3.1.2, and the AWTY software (Nylander et al., 2008) were used to ensure that the MCMCMC searches had reached stability. The first 25% of the generations were discarded as burn-in period. Majority-rule consensus trees with average branch lengths and posterior probabilities (pp) as node support values were calculated in MrBayes 3.1.2. Posterior probability values of more than 0.95 were considered as strong support.

RESULTS

The COI p-distances ranged from 0.000 to 0.234 in H3, 0.000 to 0.403 in COI and 0.000 to 0.379 in 16S among in-group species.

COI, H3, 16S

Remipedia emerges as a monophyletic group, although internal poly- and paraphyly is noted for formerly-recognized clades within Nectiopoda (Fig. 3). In this group, Micropacteridae is the most basal family of Remipedia, but the posterior probability value is low (0.62). Godzilliidae sensu lato are polyphyletic with a maximally supported clade (clade A), consisting only of *Godzillius robustus*, *Godzil-*
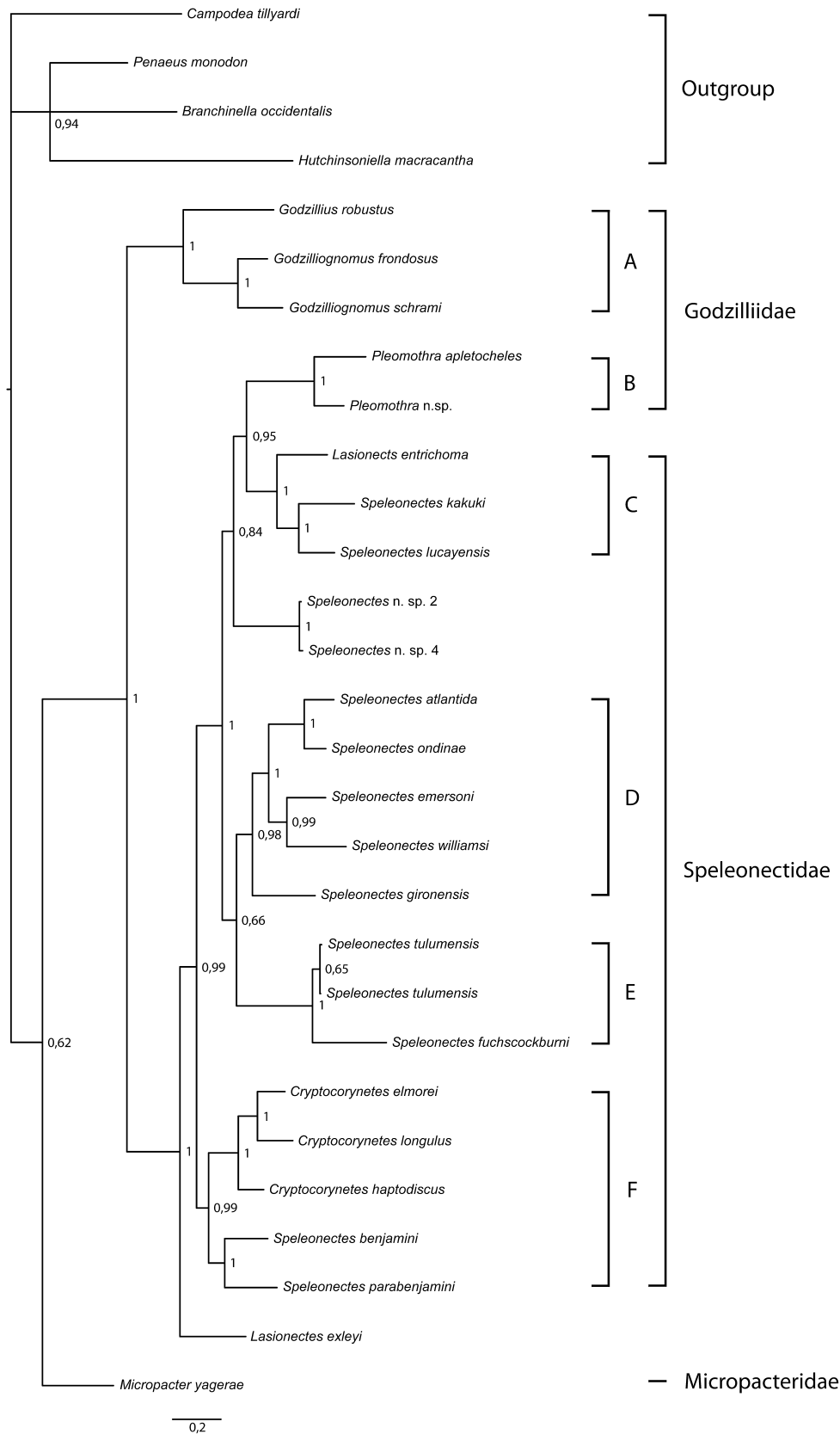
Fig. 3.   Bayesian consensus tree of Run 7 (Combined analysis with all three markers COI, 16S and H3). Numbers on nodes represent posterior probability values. Neiber et al. (2012) concluded that the specimens from Cenote Crustacea, which were assumed to represent a new, undescribed species (*Speleonectes* cf. *tulumensis*) when starting the analyses, are conspecific with *Speleonectes tulumensis* Yager, 1987b. Therefore, two samples of *S. tulumensis* are present in our analyses.

lius fuchsi, Godzilliognomus frondosus, and *Godzilliognomus schrami* appear close to the base of the Remipedia clade, whereas the other three supposed godzilliids (*P. apletocheles*, *P. fragilis*, and a new, still undescribed, species of *Pleomothra* Yager, 1989) emerge among taxa that are currently classified as Speleonectidae.

The pattern of relationships we recovered for Speleonectidae shows several inconsistencies with the current taxonomy. *Lasionectes* is polyphyletic; *L. exleyi* has a singular position outside the other speleonectids, whereas *L. entrichoma* is a sister taxon to a clade containing *Speleonectes lucayensis* Yager, 1981 and *S. kakuki* nested deep inside the Speleonectidae sensu lato. The two Canary Island species are in a sister group relation to *S. emersoni* Lorentzen et al., 2007 and *S. williamsi* Hartke et al., 2011, while *S. gironensis* emerges as sister group to these taxa (clade D). The two species from the Yucatán Peninsula form a monophyletic group (clade E).

The genus *Cryptocorynetes* is monophyletic and forms a sister group to another species pair, *Speleonectes benjamini* Yager, 1987a and *Speleonectes parabenjamini* Koenemann et al., 2003. The clades of these clusters have high support values. Thus, the genus *Speleonectes* is polyphyletic, with *S. parabenjamini* and *S. benjamini* as sisters to *Cryptocorynetes*, while the remaining speleonectids form a large clade that also contains *L. entrichoma* and *Pleomothra*.

The clades A to F show high to very high pp-values, while some of the nodes basal to them have low support values. For example, the node giving rise to clade B + C and a small clade with the two undescribed speleonectids *S.* n. sp. 2 and *S.* n. sp. 4, has a pp-value of 0.84. The lowest support values are found for the basal split into *M. yagerae* and all remaining Remipedia (0.66), and the split into clades D and E.

COI

In addition to the combined data matrix, we prepared a matrix with all available COI sequences, comprising specimens that represent species from additional, geographically separated localities (Run 5). The overall topology of its consensus tree is similar to the one of the combined analysis. However, there are some interesting differences. The position of *Speleonectes gironensis* shifts to become a sister taxon of the clade containing [*L. entrichoma*, [*S. kakuki*, *S. lucayensis*]] and the species of *Pleomothra* appear to emerge as a sister group of two still undescribed speleonectids (*S.* n. sp. 2, *S.* n. sp. 4). The posterior probability (pp) values are very high in the Remipedia clade, only the split between *Cryptocorynetes* and *S. benjamini* shows low pp-value (0.59). *Micropacter yagerae* and *S. parabenjamini* are not represented (Fig. 4).

16S

Although the topology of the 16S tree (not shown) resembles the topology of the combined tree (Fig. 3), some distinct differences exist. The most prominent one concerns the position of *L. exleyi* and its support values. *Lasionectes exleyi* is placed inside the clade comprising [*Cryptocorynetes*, [*S. benjamini*, *S. parabenjamini*]], but the pp value is very low. *Cryptocorynetes longulus, M. yagerae, S. fuchscockburni* Neiber et al., 2012, and *S. gironensis* are missing from the 16S data set.

DISCUSSION

Taken together, the results of our new molecular phylogenetic analyses stand in opposition to the current taxonomy of Remipedia. Speleonectidae, Godzilliidae, and the genera *Speleonectes* and *Lasionectes* are either para- or polyphyletic assemblages, whereas the genera *Cryptocorynetes*, *Pleomothra*, and *Godzilliognomus* Yager, 1989 appear as monophyletic groups in all analyses conducted (Fig. 5). The labeling of the clades in this section refers to Fig. 3.

Micropacteridae

In our analyses, *M. yagerae* is only represented by a single marker (H3); therefore, the support for its position at the base of the remipedian clade might be considered weak. While the phylogenetic position of Micropacteridae within Nectiopoda needs further evaluation, we nonetheless believe that their familial status is justified. Below, we provide a morphologic diagnosis of the family that includes several distinct autapomorphies.

Clade A (Godzilliidae)

In all analyses we performed, Godzilliidae, as previously understood, emerge as a polyphyletic group. While *Godzilliognomus* and *Godzillius* form a very highly supported monophyletic clade, the genus *Pleomothra* appears within the "speleonectids," likewise with high support values. Hence, the current structure of the godzilliids is not tenable.

Therefore, we redefine Godzilliidae sensu stricto to take into account this new information (see below).

Clade B (*Pleomothra*)

Yager (1989) assigned *P. apletocheles* to Godzilliidae (together with *Godzillius robustus* and *Godzilliognomus frondosus*) predominantly based on the morphology of the three post-mandibular prehensile limbs. Both species are equipped with robust sub-triangular third maxillulary segments that lack endites, and highly similar modifications and setal patterns in maxillae and maxillipeds. Like in *Godzillius* and *Godzilliognomus*, the maxillary and maxillipedal segments in *Pleomothra* are long and narrow, and fused beyond the elbow. Based on the results of our analyses, however, it appears that these features evolved independently in *Pleomothra* and *Godzilliognomus/Godzillius*.

The genus *Pleomothra* possesses some remarkable autapomorphies. The most striking features are the morphology of the maxillules and the head shield. The massive fourth segments of the maxillules bear a prominent, presumably enditic process, forming a subchelate unit with the distal segments. Moreover, Koenemann et al. (2007c) suggest the presence of a secondarily derived joint between maxillulary segments three and four. The maxillulary termini are subchelate, i.e., not bearing the distinctive remipede fangs. The head shield of *Pleomothra* is equipped with unique posterolateral projections.

If we ignored the morphology of the maxillae and the maxillipeds, then an assignment of this genus to Speleonectidae might be conceivable. However, because of the very distinct autapomorphies of the second maxillae and the maxillipeds, we believe that it is necessary to erect a separate family for the genus *Pleomothra* (see below).
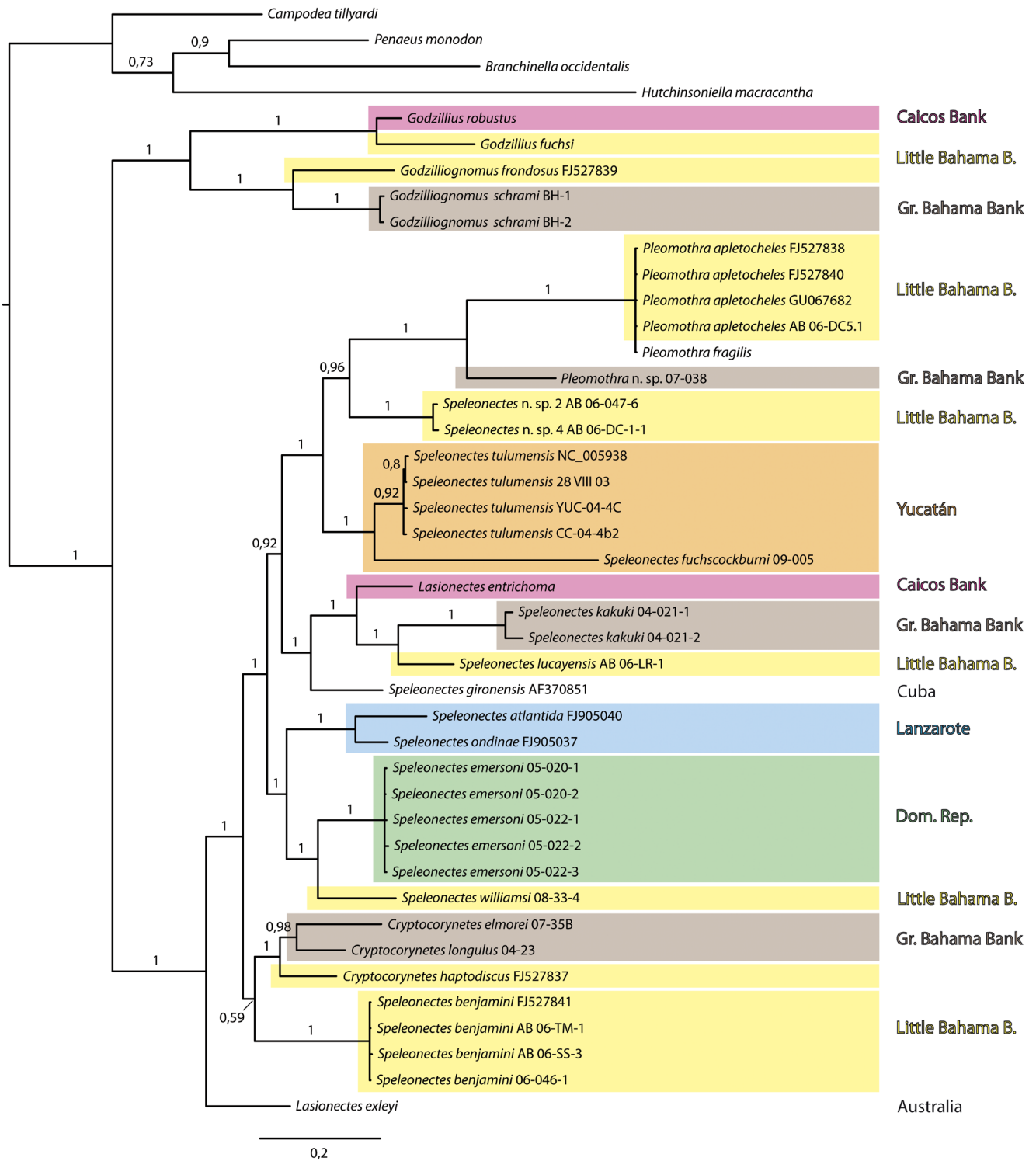
Fig. 4. Consensus tree of COI data set (Run 5). Numbers on nodes represent posterior probability values. The colored rectangles indicate the geographic region in which the samples were collected (Little Bahama B. = Little Bahama Bank; Gr. Bahama Bank = Great Bahama Bank; Yucatán = Yucatán Peninsula; Dom. Rep. = Dominican Republic).

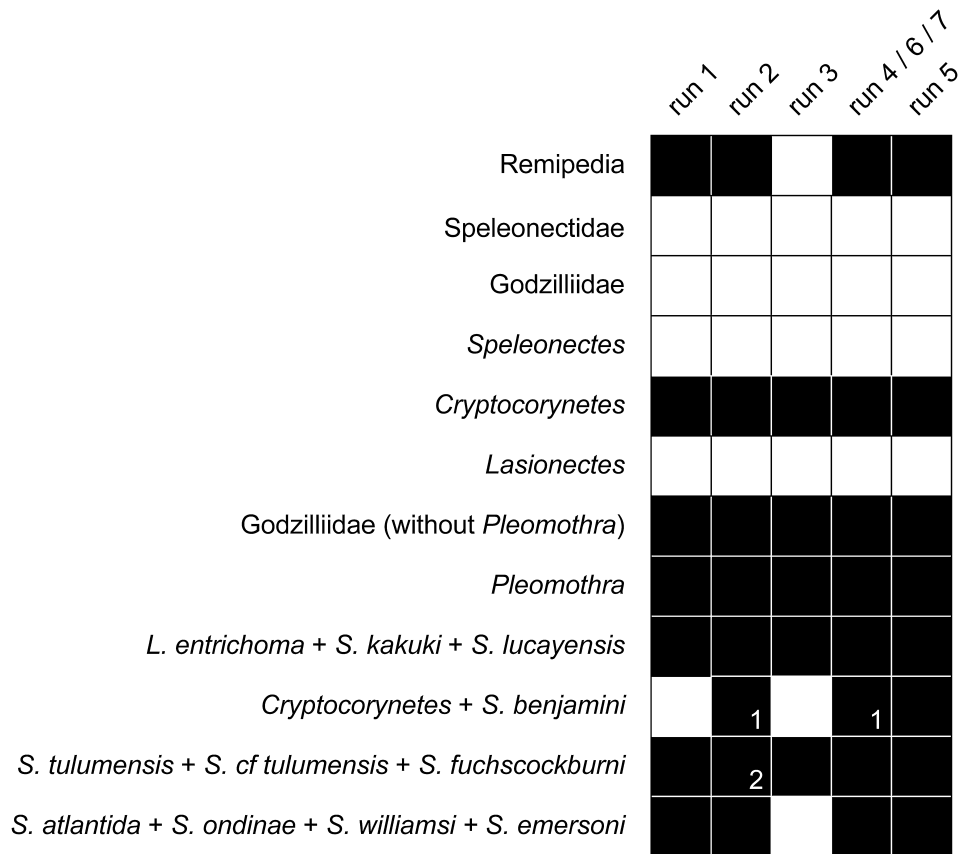|	run 1	run 2	run 3	run 4/6/7	run 5
Remipedia	■	■	□	■	■
Speleonectidae	□	□	□	□	□
Godzilliidae	□	□	□	□	□
Speleonectes	□	□	□	□	□
Cryptocorynetes	■	■	■	■	■
Lasionectes	□	□	□	□	□
Godzilliidae (without *Pleomothra*)	■	■	■	■	■
Pleomothra	■	■	■	■	■
L. entrichoma + *S. kakuki* + *S. lucayensis*	■	■	■	■	■
Cryptocorynetes + *S. benjamini*	□	■ (1)	□	■ (1)	■
S. tulumensis + *S. cf tulumensis* + *S. fuchscockburni*	■	■ (2)	■	■	■
S. atlantida + *S. ondinae* + *S. williamsi* + *S. emersoni*	■	■	□	■	■

Fig. 5. Navajo rugs showing the distribution of Remipedia clades for all seven analyses presented in this study (top row). Black squares indicate monophyly, white squares non-monophyly. 1 = plus *S. parabenjamini* Koenemann et al., 2003; 2 = without *S. fuchscockburni* Neiber et al., 2012.

Clades B-F (Speleonectidae *sensu* Yager, 1981)

The large clade (B-F), including members until now placed in Speleonectidae, shows the most inconsistencies with the current taxonomy.

Clade C

The results of our analyses challenge the status of a monophyletic genus *Lasionectes*. It seems that *L. entrichoma* from the Caribbean and *L. exleyi* from Western Australia are not only separated from each other geographically, but phylogenetically as well. The isolated status of *L. exleyi* requires a separate genus for this species. We herein propose *Kumonga* n. gen. as the type genus for a new, monotypic Kumongidae n. fam. (see below).

The phylogenetic position of *Kumonga exleyi* close to the base of a "speleonectid" clade suggests an ancient split, and perhaps also a global distribution range of remipedes. We predict that there will indeed be more discoveries of remipedes between Australia and the Caribbean, supporting a Tethyan origin of Remipedia.

Our analyses retrieved *L. entrichoma* in a highly supported clade with *S. kakuki* and *S. lucayensis*. This clade, which we can conceive of as representing the core Speleonectidae, can be distinguished by some well-defined synapomorphies (Fig. 6) (see Systematics).

Clades D and E

Our analyses reveal ambiguous results concerning the position of the species from the Yucatán Peninsula, viz., *Speleonectes tulumensis* Yager, 1987b and *S. fuchscockburni*. In the COI tree, these three species are the sister group of the clade with [*Pleomothra* [*S.* n. sp. 2, *S.* n. sp. 4]]. In contrast to this arrangement, in the combined analysis, these three species appear as the sister group to the clade containing *S. ondinae* (García-Valdecasas, 1984); *S. atlantida* Koenemann et al., 2009a, *S. emersoni*, and *S. williamsi*. Hence, based on the molecular analyses alone, an unambiguous assignment of the Yucatán species is not possible at this time.

However, we recognize a number of synapomorphies for a clade consisting of the subclades [[*S. ondinae*, *S. atlantida*], [*S. emersoni*, *S. williamsi*]] and [[*S. tulumensis*, *S.* cf. *tulumensis*] *S. fuchscockburni*]]. These synapomorphies could serve to unite all these taxa into a single family: maxillulary endites of segments 4 small and conical; maxillary and maxillipedal third segments weakly expanded, medial margins with few simple setae or small clusters with few setae; segments proximal and distal from elbows equally long; sternal bars isomorphic; caudal rami longer than anal segment (Fig. 7).

Of greater interest, however, is the clade with [[*S. ondinae*, *S. atlantida*], [*S. emersoni*, *S. williamsi*]]; the taxa appear morphologically clearly related, which harkens back to the original description of *S. ondinae* (see García-Valdecasas,
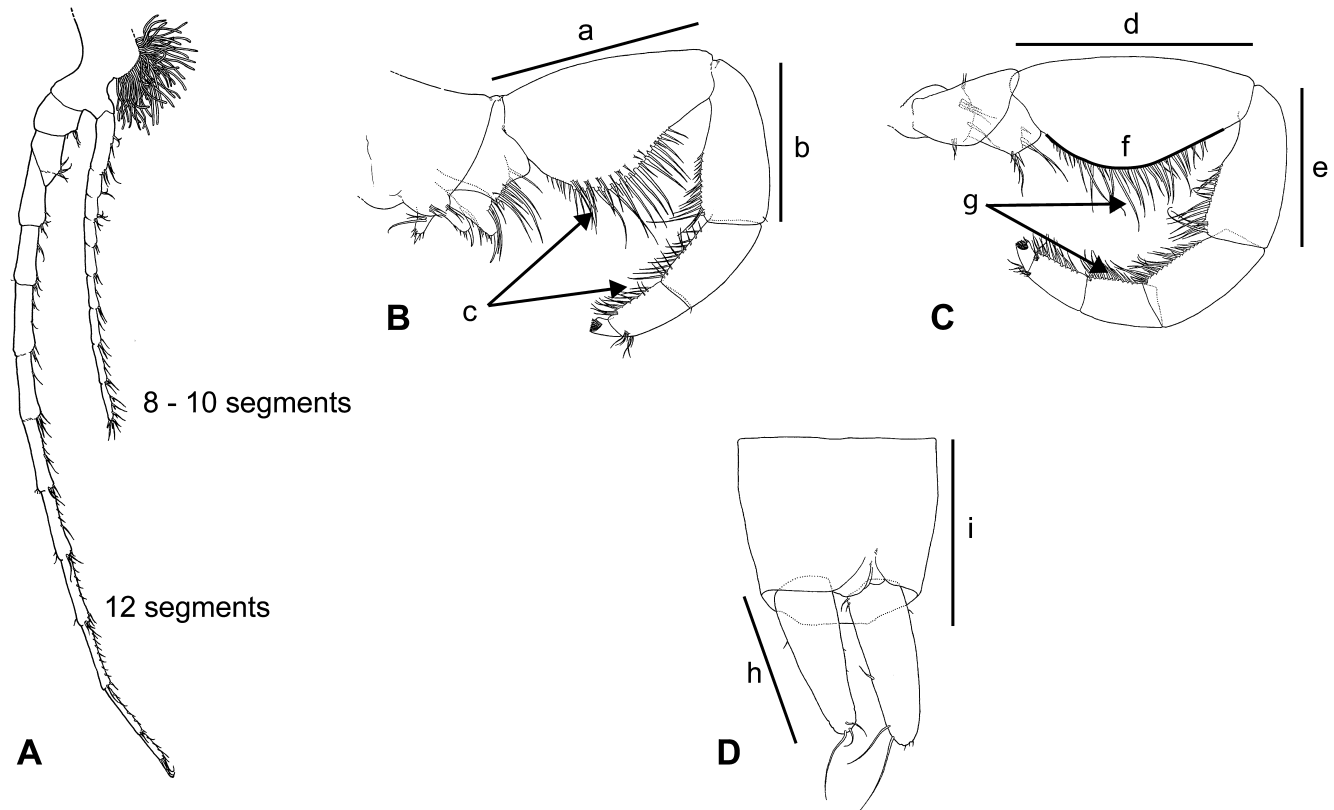
Fig. 6. Explanation of the diagnostic characters of clade C by taking the example of *S. kakuki* Daenekas et al., 2009. A = antennule, B = first maxillule, C = second maxilla, D = maxilliped, E = anal segment and caudal rami (modified from Daenekas et al., 2009). a = length of lacertus, b = length of fourth segment, c = number, shape and distribution of setae, d = length of lacertus, e = length of fifth segment, f = shape of endite, g = number, shape and distribution of setae, h = length of caudal rami, i = length of abdominal segment.

1984) at which time a separate genus was recognized, *Morlockia*, in its own family, Morlockiidae. Based on our molecular data and distinct morphological features, a return to this status is warranted.

Morphologically, clades D and E are quite separated from clade C, wherein lies the type species of *Speleonectes*. It is clear that also a new genus is required for the species in clade E (*S. tulumensis* and *S. fuchscockburni*), for which we propose the name *Xibalbanus* n. gen. (see below).

Clade F

In all of our analyses, the species of *Cryptocorynetes* form a clade with *S. benjamini* and *S. parabenjamini* that is distinctly separated from the clade C of "core speleonectids." All representatives of this clade have several morphological features in common. These features support a separate familial group consisting of *Cryptocorynetes*, *S. parabenjamini* and *S. benjamini*, which in turn requires a new genus to accommodate *S. parabenjamini* and *S. benjamini*.

Taxa and Species of Uncertain Systematic Position

We have already noted above gaps in our current knowledge of molecular sequences for several species. The affiliation of these taxa can only be undertaken based on their morphological characters; we present some hypotheses for these affiliations here.

Kaloketos pilosus Koenemann et al., 2004

Kaloketos pilosus shares the pattern of sternal bars bearing posterolateral projections with *Cryptocorynetes*, *S. parabenjamini* and *S. benjamini*. Furthermore, the ventral rami of the antennules are very long and are composed of 18 segments. Therefore, we assign *K. pilosus* to clade F, i.e., as a separate genus in Cryptocorynetidae n. fam.

Speleonectes gironensis

The topologies we obtained reveal conflicting positions for *S. gironensis*. In Run 4 (see above), it is the sister taxon to the clade with [[*S. atlantida*, *S. ondinae*], [*S. emersoni*, *S. williamsi*]], while in Runs 1 and 5, it is sister to the clade [[*S. kakuki*, *S. lucayensis*], *L. entrichoma*].

On the one hand, the lacerti of maxillae and maxillipeds of *S. gironensis* are covered with setae almost entirely along the medial margin, and their lacerti are longer than the segments distal to the elbow. The endites of the lacerti of the maxillae and maxillipeds are elongated and expanded. These features suggest an assignment of *S. gironensis* to clade C. On the other hand, the ventral flagella of the antennules are composed of 10 segments, the sternal bars are isomorphic (Table 1), and the caudal rami are longer than the anal segment. The endites of segment 4 of the maxillules show characters of both clades, they are conical but also protracted. These characters would ally *S. gironensis* with members of clade D.
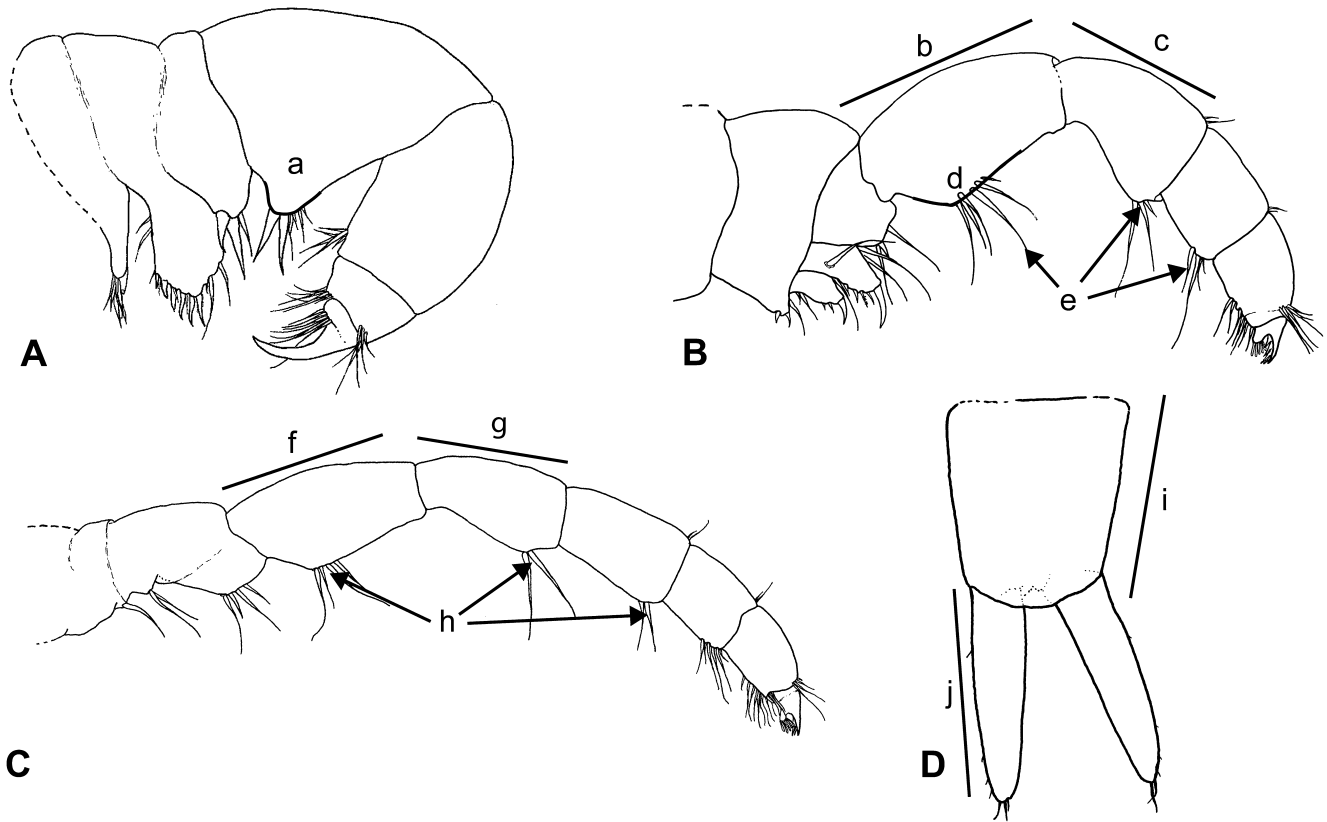
Fig. 7. Explanation of the diagnostic characters of clades D and E by taking the example of *S. emersoni* Lorentzen et al., 2007 (proposed new assignment: *Morlockia emersoni*). A = first maxillule, B = second maxilla, C = maxilliped, D = anal segment and caudal rami (modified from Lorentzen et al., 2007). a = shape of endite, b = length of lacertus, c = length of fourth segment, d = shape of endite, e = number, shape and distribution of setae, f = length of lacertus, g = length of fifth segment, h = number, shape and distribution of setae, i = length of abdominal segment, j = length of caudal rami.

Consequently, an unambiguous assignment of *S. gironensis* to a particular clade is not possible at this time, neither by molecular analyses nor morphologically, although in the combined analysis this species clearly fits in clade D.

Speleonectes minnsi Koenemann et al., 2003

An assignment of *S. minnsi* to [*L. entrichoma*, [*S. kakuki*, *S. lucayensis*]] is highly plausible, because it shares all described apomophies of this clade.

Speleonectes epilimnius and *Speleonectes tanumekes* Koenemann et al., 2003

Lorentzen et al. (2007) noted that *S. emersoni* is morphologically similar to the species *S. epilimnius* and *S. tanumekes*. Indeed, *S. epilimnius* and *S. tanumekes* could be assigned to clade D because they share the apomorphies of this group. However, *S. epilimnius* is equipped with setae of medium length on the maxillipeds, and has only a small number of trunk segments (21), which is more typical for the members of clade D, while *S. tanumekes*, on the other hand, has long setae on the segments of the maxillipeds and a high number of trunk segments (38-40), and therefore might fit better to clade E.

SYSTEMATICS
[M. Hoenemann, M. T. Neiber, F. R. Schram, and S. Koenemann]

Micropacteridae Koenemann, Iliffe, and van der Ham, 2007

Diagnosis.—Cephalon long and narrow. Body very slender, no lateral epimeral extensions of trunk tergites; trunk composed of 16 segments. Sternal bars almost completely reduced. Frontal filaments with bifid, subterminal, accessory branches. Dorsal rami of antennules with 10 segments, ventral flagella short with 3 segments. Third endites of maxillules greatly reduced, lacerti deep and proximally spinose, brachia deep, margins naked except terminally. Maxillae and maxillipeds subequal in length, subchelate, lightly setose along median edges, brachial claws opposed to lacertal bases, lacerti relatively deep, brachia fused to 2 equally long segments (plus claws); claws different on each limb pair, terminal claw complexes of maxillae composed of 1 dominant denticle and 4 shorter denticles. Prominent denticle is almost twice as long as adjacent denticles, with pore-like opening on mid-proximal stem. Claw complexes of maxillipeds developed as horseshoe-like arcs of 9-10 fused denticles, with pore-like openings on distal (fused) part of each arc (see Table 2). Anal somite fused with trunk somites 16 and 15; caudal rami tiny.

Type genus.—*Micropacter* Koenemann, Iliffe, and van der Ham, 2007.

Remarks.—*Micropacter* is the only, monotypic genus of the family.

Godzilliidae Schram, Yager, and Emerson, 1986

Diagnosis.—Head shield not subrectangular, lateral margins with bulges (*Godzillognomus*) or slightly concave (*Godzillius*). Dorsal rami of antennules with 10-11 segments, ventral flagella tiny, two-segmented. Third endites of maxillules reduced and virtually naked; fangs long and stiletto-like. Maxillae and maxillipeds markedly subchelate; lacerti blade-like, armed with finely packed short setae; brachia very narrow, fused, with 1 (*Godzilliognomus*) or 2 (*Godzillius*) faint sutures distally, brachia segments immobile to each other, armed with densely packed small scale-like setae; lacerti and brachia subequal on maxillae, brachia larger than lacerti on maxillipeds. Terminal claws of maxillae and maxillipeds pronged, grappling-hook-like. Caudal rami terminally setose.

Type Genus.—*Godzillius* Schram, Yager, and Emerson, 1986.

Included Genera.—*Godzillius*, *Godzilliognomus* Yager, 1989.

Included Species.—*Godzillius robustus* Schram, Yager, and Emerson, 1986; *Godzillius fuchsi* Gonzalez, Singpiel, and Schlagner, 2013; *Godzilliognomus frondosus*, Yager, 1989; *Godzilliognomus schrami* Iliffe, Otten, and Koenemann, 2010.

Pleomothridae n. fam.

Diagnosis.—Head shield trapezoidal, with posterolateral corners developed as projections. Ventral rami of antennules short. Maxillules with terminal chelae, segments 3 without endites. Maxillae and maxillipeds subequal; brachia with fused segments, exhibiting one faint suture distally; lacerti and brachia subequal in length; lacertal and brachial margins with scale-like setae. Caudal rami as long as or longer than anal somite. Terminal claw complexes of maxillae and maxillipeds each composed of one prominent spine flanked by shorter spines.

Type Genus.—*Pleomothra* Yager, 1989.

Included Species.—*P. apletocheles* Yager, 1989; *P. fragilis* Koenemann, Ziegler, and Iliffe, 2008.

Kumongidae n. fam.

Diagnosis.—Dorsal rami of antennules with 13 segments, those of ventral flagella with 10-12 segments. Endites of maxillulary segments 2 with dense clusters of long setae apically and subapically; endites of segments 3 bearing single seta with broad base and 5 spine-like setae of medium-length; expanded inner margins of segments 4 densely packed with long setae. Segments 3 of maxillae bulbous and expanded, endites strongly enlarged. Brachia of maxillae and maxillipeds longer than lacerti, equipped with dense rows of medium-sized to long plumose setae. Terminal claw complexes of maxillae and maxillipeds composed of one prominent spine flanked by shorter spines. Caudal rami longer than anal segment.

Type Genus.—*Kumonga* Hoenemann, Neiber, Schram, and Koenemann, n. gen. (type species: *Lasionectes exleyi* Yager and Humphreys, 1996).

Etymology.—Kumonga, a giant spider, is one of the legendary Japanese Kaiju monsters that battled with Godzilla.

Remarks.—At present, only one genus and species are recognized, for which the diagnoses remain the same as that of the family.

Included Species.—*K. exleyi* (Yager and Humphreys, 1996) n. comb.

Speleonectidae Yager, 1981

Diagnosis.—Head shield subrectangular to trapezoidal. Dorsal rami of antennules composed of 12 segments, ventral rami with 8-10 segments. Maxillulary, third endites well developed, with two spine-like setae, but shorter than endites 1 and 2; lacerti and brachia distinctly expanded. Maxillae and maxillipeds with rows of long setae on distomedial margins of lacerti and brachia; lacerti expanded; maxillae smaller than maxillipeds; brachia longer than segments distal of elbow. Terminal claw complexes of maxillae and maxillipeds composed of densely spaced denticles arranged as horseshoe-shaped crests. Terminal claws trifid, longest denticle central (arcuate spine in *Speleonectes*, long finger-type in *Lasionectes*); pores on posterior surfaces of claws. Anal somite and caudal rami subequal in length, rami with terminal setal tufts.

Type Genus.—*Speleonectes* Yager, 1981.

Included Genera.—*Speleonectes*, *Lasionectes* Yager and Schram, 1986.

Included Species.—*S. kakuki* Daenekas, Yager, Iliffe and Koenemann, 2009; *S. lucayensis* Yager, 1981; *L. entrichoma* Yager and Schram, 1986.

Morlockiidae García-Valdecasas, 1984

Diagnosis.—Head shield subrectangular; frontal filaments dilated, accessory branches located distally, longer than main filaments. Trunk with 19 to 25 somites. Third endites of maxillules with 2 stout setae, opposed by generally 2 (3) similar setae on lacerti; these stout setae flanked by small number of simple setae; fangs long and curved at 90° to brachia axes. Maxillary and maxillipedal segments moderately slender, lacerti wider ½way along length, relatively few scattered simple setae at the widest points and not densely arrayed; first brachial segments inflated distally, with clusters of scattered setae located mediodistally on brachial segments. Terminal claw complexes of maxillae and maxillipeds subequal, horseshoe type composed of free arcuate spines and each arc of 7-14 denticles with lateral ones somewhat more robust. Anal somites and caudal rami subequal in length, rami virtually naked, with only a few scattered simple setae.

Type Genus.—*Morlockia* García-Valdecasas, 1984.

Morlockia García-Valdecasas, 1984

Type Species.—*Morlockia ondinae* García-Valdecasas, 1984.

Included Species.—*Morlockia ondinae* García-Valdecasas, 1984; *M. atlantida* (Koenemann et al., 2009a) n. comb., *M. williamsi* (Hartke et al., 2011 n. comb., and *M. emersoni* (Lorentzen et al., 2007) n. comb.

Cryptocorynetidae n. fam.

Diagnosis.—Accessory branches of frontal filaments arising basomedially, thumb-like, shorter than main filaments. Antennules with very long (50% of body length or longer) dorsal rami, composed of a minimum of 14 segments. Sternal plates with posterolateral projections; heteromorphic sternal bars on trunk segments 1 to 13 concave, those of trunk segment 14 large and convex. Maxillae and maxillipeds slender, maxillipeds distinctly longer than maxillae. Terminal claw complexes of maxillae and maxillipeds of horseshoe-type.

Type Genus.—*Cryptocorynetes* Yager, 1987a

Included Genera.—*Cryptocorynetes* Yager, 1987a; *Kaloketos* Koenemann, Iliffe, and Yager, 2004; *Angirasu* n. gen.

Included Species.—*C. haptodiscus* Yager, 1987a; *C. longulus* Wollermann, Koenemann, and Iliffe, 2007; *C. elmorei* Hazerli, Koenemann, and Iliffe, 2009; *K. pilosus* Koenemann, Iliffe, and Yager, 2004; *A. benjamini* (Yager, 1987a) n. comb.; *A. parabenjamini* (Koenemann, Iliffe, and van der Ham, 2003) n. comb.

Angirasu n. gen.

Diagnosis.—Fangs of maxillules very long, only moderately curved; stiletto-like. Maxillary and maxillipedal lacerti with barely or only slightly expanded margins; only with simple setae on anterio- to midmedial margins; brachia with simple setae on distomedial margins, not equipped with feathered setae or discoid organs. Terminal claw complexes of terminal maxillae and maxillipeds subequal, horseshoe-type with 7-8 small denticles flanked by 2 stronger, separate spines. Anal segment slightly longer than wide; caudal rami with terminal clusters of setae and few medial and basomedial setae.

Etymology.—Angirasu is another of the legendary Japanese Kaiju monsters that battled with Godzilla.

Type Species.—*Speleonectes benjamini* Yager, 1987a.

Included Species.—*A. benjamini* (Yager, 1987a) n. comb.; *A. parabenjamini* (Koenemann et al., 2003) n. comb.

Incertae familiae
Xibalbanus n. gen.

Diagnosis.—Head shield subrectangular. Frontal filaments dilated, accessory branches located mediodistally, shorter than main filaments. Trunk segments up to 42, usually more than 30 in adults; sternal bars isomorphic. Third maxillulary endites and lacerti with 2 opposing serrate setae each, accompanied by few simple setae. Maxillipeds distinctly longer than maxillae; maxillary and maxillipedal lacerti slightly expanded with few simple setae; first brachial segments with distinctly expanded distomedial margins, bearing few simple setae, the following brachial segments subrectangular with few simple setae at distomedial margins.

Terminal claw complexes of maxillae and maxillipeds subequal, horseshoe-type each with arc of 10 small denticles each flanked by 1 stronger, separate denticle. Caudal rami very long, at least 2.5 times longer than anal segment, with few scattered setae.

Type Species.—*Speleonectes tulumensis* Yager, 1987b.

Etymology.—Composed from Xibalba, the underworld in ancient Mayan mythology, and the Latin suffix -anus, meaning "originating from."

Included Species.—*X. tulumensis* (Yager, 1987b) n. comb., *X. fuchscockburni* (Neiber et al., 2012) n. comb.

Remarks.—The position of this genus shifts on our trees depending on the molecules and taxa used: either on the clade with morlockiids, or on a clade with pleomothrids and some yet-to-be-described taxa. We suspect *Xibalbanus* belongs with the former (Fig. 8), but for the time being we leave its familial affiliations as uncertain.

CONCLUSIONS

The molecular data derived from 16S rDNA (16S), histone 3 (H3), and cytochrome c oxidase subunit I (COI) reveal several inconsistencies within the current taxonomic classification of Remipedia. Amongst the currently recognized families, Godzilliidae, as well as the genera *Speleonectes* and *Lasionectes* emerge as polyphyletic groups, while Speleonectidae appears to be paraphyletic. We discuss current taxonomic diagnoses based on morphologic characters, and suggest taxonomic changes that accord with the topologies of the phylogenetic analyses, which we summarize here for the extant remipedes:

Remipedia Yager, 1981
  Nectiopoda Schram, 1986
    Cryptocorynetidae n. fam.
      Cryptocorynetes Yager, 1987a
        C. haptodiscus, C. elmorei, C. longulus
      Angirasu n. gen.
        A. benjamini, A. parabenjamini
      Kaloketos Koenemann, Iliffe, and Yager, 2004
        K. pilosus
    Godzilliidae Schram, Yager, and Emerson, 1986
      Godzillius Schram, Yager, and Emerson, 1986
        G. robustus, G. fuchsi
      Godzillognomus Yager, 1989
        G. frondosus, G. schrami
    Kumongidae n. fam.
      Kumonga n. gen.
        K. exleyi
    Micropacteridae Koenemann, Iliffe, and van der Ham, 2007
      Micropacter Koenemann, Iliffe, and van der Ham, 2007
        M. yagerae
    Morlockiidae García-Valdecasas, 1984
      Morlockia García-Valdecasas, 1984
        M. ondinae, M. atlantida, M. emersoni, M. williamsi
        [? "*S.*"*gironensis* Yager, 1994]
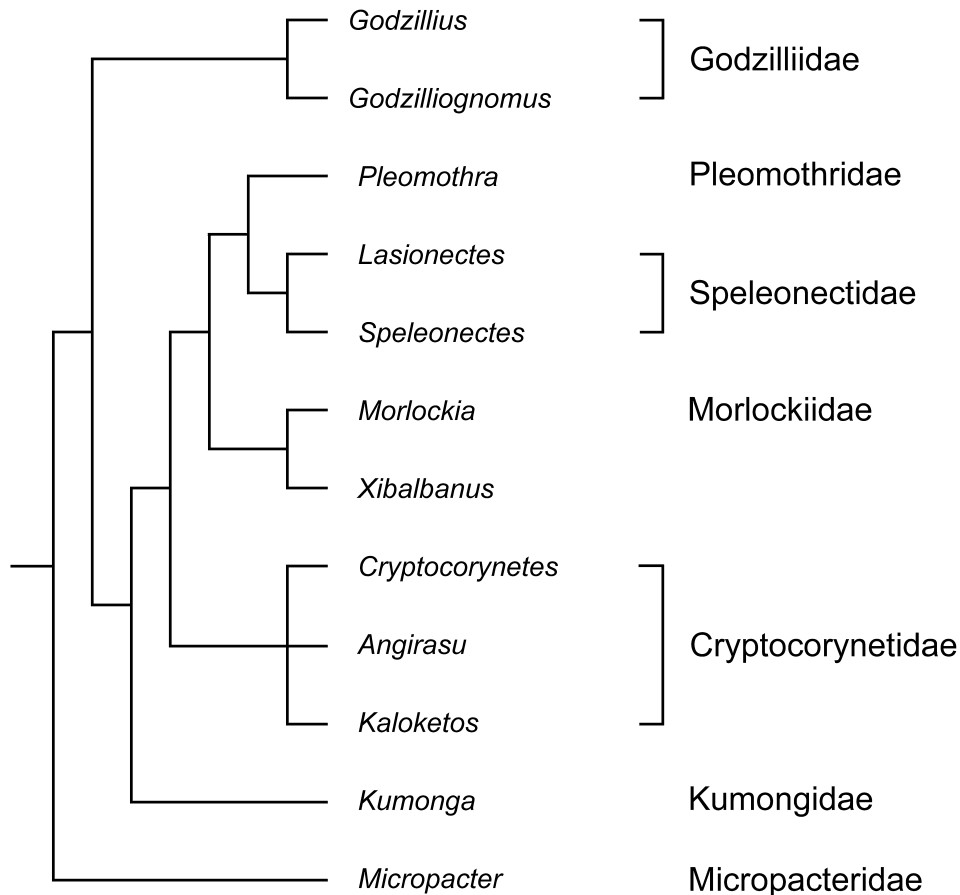
Fig. 8.   Summary rendition of Fig. 3, with new taxonomic nomenclature proposed herein.

Pleomothridae Yager, 1989
   Pleomothra Yager, 1989
      P. apletocheles, P. fragilis
Speleonectidae Yager, 1981
   Speleonectes Yager, 1981
      S. lucayensis, S. kakuki, S. minnsi
   Lasionectes Yager and Schram, 1986
      L. entrichoma
Incertae familiae
   Xibalbanus n. gen.
      X. tulumensis, X. fuchscockburni
Incertae familiae and incerti generis
   ? *"S." epilimnius*
   ? *"S." tanumekes*

The descriptions of several new "speleonectids" are in preparation. Once these occur, and perhaps some new molecular data are generated, we may be able to clarify the taxonomic issues not resolved in this study, e.g., the family affiliation of *Xibalbanus* and the taxonomic position of *"S." gironensis*, *"S." tanumekes* and *"S." epilimnius*.

It is significant to note that in our revision of Remipedia, while some formerly geographically widespread genera, e.g., *Speleonectes* and *Lasionectes*, are divided into separate, more geographically restricted taxa, the genus *Morlockia* is resurrected and, by now including three additional species, has an amphi-Atlantic distribution. Five of the seven revised remipede families (Micropacteridae, Pleomothridae, Godzil-

liidae, Cryptocorynetidae, and Speleonectidae) are represented only from the Bahamas archipelago, with the latter three families extending across this chain of islands from the Caicos Bank in the southeast, through the Great Bahama Bank, to the Little Bahama Bank in the northwest. Morlockiidae, currently with a single genus, includes species from the Canary Islands, Cuba, Dominican Republic and the Little Bahama Bank. Finally, Kumongidae is represented by a single species from Western Australia. Thus, speculation as to the timing and potential modes of open ocean dispersal of remipedes persists.

The shallow epicontinental waters comprising the Neo-Tethys were fragmented by the break-up of Pangaea. The developing rift through Pangaea resulted in the westward extension of the Tethys into the opening Atlantic in the Early Jurassic (200 Ma), at that time an epicontinental sea extending from the far eastern coastline of Pangaea continuously to the Yucatán Plate. By the Middle Jurassic (170 Ma), the widening rift between 'Africa' and the 'Americas' allowed for more than 6 km deep oceanic water (Thiede, 1979) to extend into the developing Atlantic (see http://jan.ucc. nau.edu/rcb7/nat.html, accessed 5 April 2013), while by the Early Cretaceous (120 Ma) extensive carbonate deposits extended from the Bahamas area westward through the Florida Plateau to the Yucatán Peninsula. These geological episodes and also the closure of the Tethys Seaway in the present day Mediterranean region (19-10 Ma: McQuarrie et al., 2003;

Harzhauser et al., 2007), provide a framework against which to test dispersal versus vicariant models of remipede evolution against future molecular clock data.

The crustacean composition of anchialine faunas is highly predictable, often even at the generic level, no matter how far apart in the world they occur (Wagner, 1994; Jaume et al., 2001). Remipedes are members of the core anchialine fauna suite along with other crustacean taxa such as *Danielopolina* Kornicker and Sohn, 1976 (thaumatocyridid Myodocopa), thermosbaenaceans of the genus *Halosbaena* Stock, 1976, and epacteriscid copepods (Boxshall and Iglikowska, 2012). The remipede distribution fits closely with the hypothesis that many widespread, disjunct, anchialine species have descended from marine species in the Tethys Ocean, whose disjuncture can be explained by sea floor spreading due to plate tectonic movement (Wägele, 1985; Humphreys, 1993; Wagner, 1994; Sanz and Platvoet, 1995; Jaume et al., 2001; Kano and Kase, 2004; Page et al., 2008). However, the origin and timing of remipede evolution remains enigmatic. A number of studies using morphological (Metacrangonyctidae: Jaume and Christenson, 2001) or molecular clock analyses (Atyidae: Page et al., 2008; Cirolanidae: Baratti et al., 2010; Metacrangonyctidae: Bauzà-Ribot et al., 2012; Gobiiformes: Chakrabarty et al., 2012) have recently presented results consistent with amphi-oceanic or inter-oceanic divergence. Conversely, oceanic dispersal within some of these higher anchialine taxa (*Danielopolina* and *Halosbaena*) is indicated by their presence on isolated seamounts (Humphreys and Danielopol, 2006; Humphreys et al., 2009; Shimomura, and Fujita, 2009).

Our remipede data proved unsuitable for molecular clock analysis. We were neither able to relate branching patterns in our phylogenetic trees to major vicariant events, nor to assumed evolutionary splits in our out-group taxa. This was also found by von Rintelen et al. (2012) in their molecular phylogeny of 32 of the 42 genera of Atyidae. These authors were unable to relate branching patterns in their phylogenetic trees to the opening of the Atlantic due to inconsistencies in the three calibration dates they used. Nevertheless, what we now have is a quantum leap in improvement in our understanding of the evolution of remipedes.

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SUPPLEMENTARY MATERIAL

Table S1. Newly generated Remipedia sequences. The numbers indicate the sequenced fragment in comparison to the reference sequences (COI and 16S = *S. tulumensis*; GenBank acc. no. NC_005938; H3 = *Homo sapiens*, GenBank acc. nr. NM_003493). The numbers in parentheses next to the gene name show the overall length (in base pairs) of the reference sequence; see Table 2 for full versions of abbreviated generic names.

Species	Voucher	Amplified region		
		COI (1539)	H3 (411)	16S (1333)
G. robustus	03-19	58-638	24-351	152-1216
G. fuchsi	AB-06-RS1	44-702	–	–
Gn. frondosus	06-048-4	63-656	–	232–1196
	06-047-8	–	24-351	–
	06-50	–	24-351	–
	AB06-SS-4.1	–	–	609-1196
Gn. schrami	07-048-2	85-702	–	662-1246
	07-49	–	24-351	–
	BH-1 Eleuthera	85-702	–	–
P. apletocheles	AB06-DC-5.1	20-1121	24-351	–
	AB06-RS-2	85-702	–	638-1250
	AB06-SS-2	90-661	–	697-1113
	AB-06-L2	88-681	–	–

Table S1.   (Continued.)

Species	Voucher	Amplified region		
		COI (1539)	H3 (411)	16S (1333)
P. fragilis	BH_EC	126-702	–	–
P. n. sp.	07-038	44-702	24-351	662-1158
C. elmorei	07-035B	44-702	24-351	231-1196
C. haptodiscus	AB06-SS-1.1	20-674	24-351	130-1230
C. longulus	C3-04-23	69-667	24-351	–
	04-20	–	24-351	–
L. entrichoma	03-16	223-684	24-351	648-1229
L. exleyi	BES-10169	44-1066	24-351	136-1241
S. atlantida	LZ 2.3	95-702	–	169-1173
	LZ 2.1	–	24-351	169-1132
	Dzul 9999-GBIF	–	–	334-1132
	LZ 1.1	–	–	294-1123
S. benjamini	06-047-2	88-702	24-351	133-1209
	06-046-1	44-702	24-351	–
	04-23	–	–	606-1209
	AB06-SS-3	46-702	–	620-1209
	AB06-TM-1	44-1313	–	619-1209
S. emersoni	05-020-01	85-702	–	–
	05-020-02	44-702	–	–
	05-022-01	66-702	24-351	153-1229
	05-022-02	44-702	–	–
	05-022-03	88-702	–	–
S. fuchscockburni	09-005	85-702	24-351	–
S. gironensis		–	24-351	668-1210
S. kakuki	04-021-1	44-702	–	604-1234
	04-021-2	44-637	–	–
	BH-330	–	24-351	136-1234
S. lucayensis	AB06-LR-1	43-702	24-351	657-1215
S. n. sp. 2	AB-06-047-6	85-702	–	659-1082
S. n. sp. 4	AB06-DC-1.1	217-943	–	649-1235
S. ondinae	LZ 1.2	36-707	24-351	165-1171
S. parabenjamini	04-023_SK	–	24-351	661-1068
S. tulumensis		–	24-351	–
S. cf. *tulumensis*	YUC-04-4C	63-1266	–	–
	28 VIII 03	63-1266	–	–
	CC-044B2	62-1266	–	–
	06-41H	–	24-351	661-1084
S. williamsi	08-033-4	44-702	24-351	713-1196
M. yagerae	03-18	–	24-351	–

Table S2.   List of taxa used for phylogenetic analysis, including GenBank accession numbers of COI, H3 and 16S sequences, and voucher numbers of specimens from the research collection of S. Koenemann; newly generated sequences are shown in boldface.

Species	Voucher	Sampling site	COI	H3	16S
Godzilliidae					
Godzillius robustus	03-19	North Caicos Island	JF332152	**KC989960**	**KC990000**
Godzillius fuchsi	AB-06-RS1	Great Abaco Island	JF332153	–	–

Table S2.   (Continued.)

Species	Voucher	Sampling site	COI	H3	16S
Godzilliognomus frondosus	06-048-4	Great Abaco Island	FJ527839	–	**KC989998**
	06-047-8	Great Abaco Island	–	**KC989961**	–
	06-50	Great Abaco Island	–	**KC989983**	–
	AB06-SS-4.1	Great Abaco Island	–	–	**KC989999**
Godzilliognomus schrami	07-048-2	Eleuthera	JF332154	–	**KC990013**
	07-49	Eleuthera	–	**KC989962**	–
	BH-1	Eleuthera	**KC989994**	–	–
Pleomothra apletocheles	AB06-DC-5.1	Great Abaco Island	FJ527840	**KC989963**	**KC990006**
	AB06-RS-2	Great Abaco Island	**KC989995**	–	**KC990004**
	AB06-SS-2	Great Abaco Island	GU067682	–	**KC990005**
	AB-06-L2	Great Abaco Island	FJ527838	–	–
Pleomothra fragilis	BH_EC	Exuma Cays	**KC989984**	–	–
Pleomothra n. sp. E	07-038	Eleuthera	JF332155	**KC989964**	**KC990014**
Speleonectidae					
Cryptocorynetes elmorei	07-035B	Eleuthera	JF332156	**KC989966**	**KC989996**
Cryptocorynetes haptodiscus	AB06-SS-1.1	Great Abaco Island	FJ527837	**KC989967**	**KC989997**
Cryptocorynetes longulus	C3-04-23	Cat Island	JF332157	**KC989968**	–
Lasionectes entrichoma	03-16	North Caicos Island	JF332158	**KC989969**	**KC990001**
Lasionectes exleyi	BES-10169	Cape Range Penninsula	JF332159	**KC989970**	**KC990002**
Speleonectes atlantida	LZ 2.3	Lanzarote	FJ905040	–	FJ905034
	LZ 2.1	Lanzarote	–	**KC989971**	FJ905033
	Dzul 9999-GBIF	Lanzarote	–	–	FJ905031
	LZ 1.1	Lanzarote	–	–	FJ905032
Speleonectes benjamini	06-047-2	Great Abaco Island	FJ527841	**KC989972**	**KC990007**
	06-046-1	Great Abaco Island	**KC989985**	–	–
	04-23	Cat Island	–	–	–
	AB06-SS-3	Great Abaco Island	**KC989986**	–	**KC990011**
	AB06-TM-1	Great Abaco Island	**KC989987**	–	**KC990012**
Speleonectes emersoni	05-020-01	Dominican Republic	JF332161	–	–
	05-020-02	Dominican Republic	**KC989988**	–	–
	05-022-01	Dominican Republic	**KC989989**	**KC989973**	**KC990008**
	05-022-02	Dominican Republic	**KC989990**	–	–
	05-022-03	Dominican Republic	**KC989991**	–	–
Speleonectes gironensis		Cuba	AF370851	**KC989974**	AF370874
Speleonectes kakuki	04-021-1	Cat Island	JF332163	–	–
	04-021-2	Cat Island	**KC989992**	–	–
	BH-330	North Andros	–	**KC989975**	**KC990009**
Speleonectes lucayensis	AB06-LR-1	Great Abaco Island	JF332160	**KC989976**	**KC990010**
Speleonectes n. sp. 2	AB-06-047-6	Great Abaco Island	JF332164	–	**KC990015**
Speleonectes n. sp. 4	AB06-DC-1.1	Great Abaco Island	**KC989993**	–	**KC990016**
Speleonectes ondinae	LZ 1.2	Lanzarote	J905037	**KC989977**	FJ905035
Speleonectes parabenjamini	04-023_SK	Cat Island	–	**KC989978**	**KC990017**
Speleonectes tulumensis		Yucatán Penninsula	AY456190	**KC989979**	AY456190
	YUC-04-4C	Yucatán Penninsula	JF297645	–	–
	28 VIII 03	Yucatán Penninsula	JF297646	–	–
	CC-044B2	Yucatán Penninsula	JF297647	–	–
	06-41H	Yucatán Penninsula	–	KC989982	**KC990019**
Speleonectes williamsi	08-033-4	Grand Bahama Island	JF332162	KC989980	**KC990018**
Speleonectes xibalba	09-005	Yucatán Penninsula	JF297644	KC989981	–
Micropacteridae					
Micropacter yagerae	41698	Providenciales Island	–	**KC989965**	**KC990003**
Outgroup taxa					
Branchinella occidentalis (COI, H3)/ *B.* sp. (16S)		–	EF189664	EF189600	AF110871
Hutchinsoniella macracantha		–	AY456189	AY456189	AF110867
Penaeus monodon (COI, 16S)/ *P. semisulcatus* (H3)		–	AF217843	AF217843	DQ079698
Campodea fragilis (H3)/ *C. tillyardi* (COI, 16S)		–	AF370844	DQ529236	AF110860

Table S3.   List of primers used in this study, including information on amplification direction, and annealing temperatures for PCRs.

Primer name	Direction	Sequence (5′ → 3′)	Annealing temperature (°C)
COI			
LCO1-1490	Forward	GGTCAACAAATCATAAAGATATTG	50
HCO1-2198	Reverse	TAAACTTCAGGGTGACCAAAAAATCA	50
COI s	Forward	T(AGT)AT(CT)GGAGGATT(CT)GG	50
COI as	Reverse	CGTCG(AT)GG(CT)AT(AT)CC	50
16S			
CRUST16SF	Forward	TAATTCAACATCGAGGTCGCAA	50
CRUST16SR	Reverse	TTTGTACCTTKTGTATTAGG	50
mt16S-ar	Forward	CGCCTGTTTATCAAAAACAT	57
mt16S-br	Reverse	CCGGTCTGAACTCAGATCACGT	57
H3			
H3 AF	Forward	ATGGCTCGTACCAAGCAGACVGC	50
H3 AR	Reverse	ATATCCTTRGGCATRATRGTGAC	50

Table S4. 16S alignment of Runs 2, 4, 6 and 7; dashes indicate gaps, and question marks marks missing nucleotide information.

Species code	Sequence
Campodea	TATTTTTTAA-TAATTAAGCAAAT--AAGCGCTCGCCTGTTTATCAAAAACATGGTTTTTGA------------------CTATAAAAAAATTTGG-CCTGCTC
Penaeus	GTATAATTAAGGAACTCGGCAAAT-ACTACTTTTGCCTGTTTATCAAAAAACATGTCTATATGA------------------TTGTTATATAAAGTCTAG-CCTGCCC
Branchinella	??AG--ATTTAAGGTCCAA-CCTGCCC
Hutchinsoniella	CTTAATTCAAGGAACTCAGCAAAATAACTTCCCGCCTGTTTAATAAAAACATGTCTTCCTGT------------ACATAATA-GGAA-GTCCAACTCTGCCCC
G_robustus	TCAATTCAGAAGGAACTTGTCAATT-ATAATTTCCGCCTGTTTATCAAAAACATGGCTTCTTGT------------ATAATTAAGGAGGTCGTA-CCTGCCC
Gn_frondosus	TTATTTTTAAGGAATTTGGCAAAA-CAAGTTTCCGCATGTTTATCAAAAACATGGCCTTTCGA------------ATAGAAAATGTAAGTTCTGA-CCTGCCC
Gn_schrami	??????????????????????????CAC-TATAGAATCGCCTGTTTATCAAAAAACATGGCCTTTTGT------------TTTAAATATGAAGTCTGA-CCTGCCC
P_apletocheles	??AAACATGGCCTTTTGT-----GTTTTGATATATAAGGTCTGA-CCTGCTC
P_fragilis	???AAACATGGCCTTTTGT------------CTTGGA-ATATAAGGTCTGA-CCTGCTC
P_nsp	???
M_yagerae	TCATCGTGAAGGAACTCGGCAAAT-GTGGTTTCTGCCTGTTTATCAACAAAAAACATGGCCTTTTGT------------GGATATATAAGGTCGGG-CCTGCCC
C_elmorei	TTGTTGTAAAGGAACTCGGCAAAT-ATGGTTTCTGCCTGTTTATCAAAAACATGGCCTTTTGT------------GAAAATATAAGGTCGGG-CCTGCCC
C_haptodiscus	??
C_longulus	??CGCCTGTTTATCAAAAAACATGGTTTTTTGT------------GGATATAGAAGATCGGG-CCTGCCC
L_entrichoma	ATGTTATGAAGGAACTCGGCAAAT-AACTTCTCTGCCTGTTTATCAAAAAACATGGCTTTTTGT------------TGGAGATAAGAGGTCTTTTCCTGCTC
L_exleyi	TTTCAGTAAAGGAACTAGGCAAAA-ATAGCATCTGCCTGTTTATTAAAAACATGGCCTTTTGT------------TATATATAATAAGTCTGG-CCTGCTC
S_atlantida	GTGTTATTAAGGAATTCGGCAAAT-ATGGTTTCTGCCTGTTTATCAAAAACATGGCCTTTTGT-----GTGGTTGATATATAAGGTCTGG-CCTGCCC
S_benjamini	TTAAGTTAAAGGAATTAGGCAAAA-ATGATATCTGCCTGTTTAATATCTGCCTGTTTATTAAAGATTTAAGGTCCGG-CCTGCCC
S_emersoni	GTTATATGAAGGAACTTGGCAAAT-TTAATGTCTGCCTGTTTAATACAAAAACATGGCTCTTTTGT------------TGATATAAAAGGTCTGA-CCTGCCC
S_gironensis	??GCCTGTTTATCAAAAAAACATGGCCTTATGT--TTAAAAAGTTGTATATATAAGGTCTTA-CCTGCTC
S_kakuki	TTTTAATAAAGGAATTAGGCAAAAAGATAAATGTCTGCCTGTTTAATAAAAAACATGGCTTTTTGT------------TTAATATAATTAAGTCTGG-CCTGCCC
S_lucayensis	TTTACATAAAGGAACTCGGCAAAT-AACACTTCCACCTGTTTATTAAAAAACATGGCCTCTTGT-----AAGGGTGAATATATGGAGGTCGGA-CCTGCCC
S_nsp2	??AAAAACATGGCCTCTTGT-----GCAGTTTGATATAGGAGGTCGGA-CCTGCCC
S_nsp4	??AAAAACATGGCCTCTTGT------------??????????????????
S_ondinae	???AAAAACATGGCCTCTTGT-----GCGGTTTGATATAGGAGGTCGGA-CCTGCTC
S_parabenjamini	??
S_tulumensis	??
S_williamsi	??
S_xibalba	??
S_cf_tulumensis	??

Species code	Sequence
Campodea	AATGA------AAT---TTAAATAGCTGCAGTAATT-TAACTGTACAAAGGTAGCATAATCATTAGTCTTTTAATTGTTGGCTGGAATGAATGGTTTT
Penaeus	ACTGA-ATTATTT------TTAAAGGGCCGCGGTATAC-TGACCGTGCGAAGGTAGCATAATCATTAGTCTTTTAATTGAAGGCTTGTATGAATGGTTGG
Branchinella	ACTGA-----GTA------TTGAAGGGCCGTGGTATAC--TGACCATGCGAAGGTAGCATAATCATTTGCCCCTTAATTAGGGGCTGGAATGAAGGGTTAG
Hutchinsoniella	ACTGA----AATAAT---TTAAAAGGCCGCGGTAATTTTGACCGTGCGAAGGTAGCATAAATAATTGTCTCCTAATTAGAACTAGAATGAAAAGTCAA
G_robustus	ACTGA----TAGTAG------TTGAAGGGCCGCGGTAATTCTGACCGTGCGAAGGTAGCATAATCATTTTCCAATTAATTGTTGTATGAATGGTTTG
Gn_frondosus	ACTGA---TTTATAA------TTGAAGGGCCGCGGTAAAT-TAACTGTGCTAAGGTAGCATAATCATTTTCCAATTAATTGTTGGATGAATGGTTTG
Gn_schrami	ACTGA-TTAAATAA------TTGAAGGGCCGCGGTAAAT-TAACTGTGCTAAGGTAGCATAATCATTTTCCAATTAATTGTTGGATGAATGGTTTG
P_apletocheles	ACTGA---GGTTACAC---TTAAAAGAGCTGCAGTATATCTGACGTGGTAAGGTAGCGTGATAATTTGTCTATTAATTGTAGACTTGGATGAATGGTTTG
P_fragilis	??
P_nsp	ACTGA---GGTAAAAC--TTAAAAGAGCTGCAGTATACCTGACGTGTAAGGTAGCAAAGGTAGCATAAATGGTTTGCCTATTAATTGTCTATTAATTGTAGACTTGTATGAATGGTTTG
M_yagerae	??
C_elmorei	GCTGT--TTGT------ATGAAGGGCTGCGGTATACTGACCGTACAAAGGTAGCGTAATTGTCTATTAATTGTCTATTAATTGTGACTTGTATGAATGGTTTG
C_haptodiscus	ACTGT--TTAG------ATGAAGGGCTGCGGTATACTGACCGTACAAAGGTAGCGTAATTGTCTATTAATTGTCTATTAATTGTGACTTGTATGAATGGTTTG
C_longulus	??
L_entrichoma	GCTGT---ATATATT----ATGAAGGGCTGCGGTATATTTAACTGTACGAAGGTAGCATGATAATTTGTCTATTAAATGTTGACTTGTATGAATGGTTTG

Table S4.   (Continued.)

Species code	Sequence
L_exleyi	GCTGC-TTTGTTAAA----GTAAAGGGCTGCAGTAGTACTTGACTGTACGAAGGTAGCATAATAAATTGCCTATTGATTGTTGGCTGGTATGAATGGAATG
S_atlantida	TCTTGA-TATCATTATA---TTGAAGAGCTGCAGTAGTACTTGACTGTACAAAGGTAGCATAGTAGTTTGCCTATTAATTATTGGCTTGTATGAATGGTTTG
S_benjamini	GCTGT-AGGA--------ATGAATGGCTGCGGTAGTACTTGACTGTACGAAGGTAGCATAATAATTTGCCTATTAAATGTTGGCTTGTATGAATGGTTTG
S_emersoni	TCTTGA-TATTTAGTAA---TTGAAGGGCTGCAGTAGTACTTGACTGTACAAAGGTAGCATAAAATATTTTGCCTTTAAATGTTGGCTTGTATGAATGGTTTG
S_gironensis	TCTTGATTCATAAATA----TTAAAGGGCTGCAGTAGTACTTTTGACTGTACAAAGGTAGCGTAATTGTCTATTAATTGTTGACTTGGATGAATGGCCCG
S_kakuki	ACTGA-AATGTTTGG----TTAAAGGGCTGCAGTAGTATTTTGACTGTACAAAGGTAGCGTAATTGTCTATTAAATTGTTGACTTGGACTGAATGGTTTG
S_lucayensis	GCTGA-ATGGATATGG----TTGAAGGGCTGCGGTAGTAT-TAACTGTACAAAGGTAGCGTGATAAATTGTCTATTAAATTGTTGGACTTGGATGAATGGTTTG
S_nsp2	GCTGA-TAAGTTTTA----TTAAAGGGCTGCAGTAGTATTTAACTGTACAAAGGTAGCGTAGTAATTTGTTTATTAAATTGTTGACTTGGATGAATGGTTTG
S_nsp4	GCTGA-TAAGTTTTA----TTAAAGGGCTGCAGTAGTATTTAACTGTACAAAGGTAGCGTAGTAATTTGTTTATTAAATTGTTGACTTGGATGAATGGTTTG
S_ondinae	TCTTGA-TATTTGATAA---TTGAAGGGCTGCAGTAGTACTTGACTGTACAAAGGTAGCGTAGTAGTTTGCCTATTAATTGTTGGCTTGTATGAATGGTTTG
S_parabenjamini	GCTGC-----TTCG-----GTGAAGGGCTGCGGTAGTACTTGACTGTACAAAGGTAGCATAGTAATTTGCCTATTAATTGTTGGCTAGTATGAATGGTTTG
S_tulumensis	TCTGAATTGGTTTTAGGGTTTAAAGGGGTTTAAAGGGCTGCAGTAGTACTTGACTGTACAAAGGTAGCATAGTAGTTTGGCTTGGCTGAATGAATGGTTTG
S_williamsi	?????TCTGATGGATA---TTGTAGGGCTGCGGTAATACTTGACTGTACAAMGGTMGCATAATAGWTTGTCTACTAWRTGTTGGCTTGTATGAMCGGTTTG
S_xibalba	??
S_cf_tulumensis	TCTGAATTGGTTTTAGGGTTTAAAGGGCTGCAGTAGTACTTGACTGTACAAAGGTAGCATAGTAGCTTGACTGTACAAAGGTAGCATAGTAGCCTATTAATTGTTGGCTGGTTTG
Campodea	ACGGAGTGTTTACTTTTTTTAAAAATAT----TAA-TTGAATTTTA-TAATT-TAG-TGAAAAAGCTAAGATATGGATAAGGACGATAAGGACGATAAGGACCCTATAGA
Penaeus	ACAAAAAGTAATCGTCTCAGTTATAA----TAG-TTGAACTTAACTT-TT-AAG-TGAAAAAGCTTAAAATACTTAAGGGACGATAAGGACGATAAAA
Branchinella	ACGAGAAAACTAGCTGTCTCTCTTCTTATTT-----AC-TTGAAGTTAA-TTATT-TGG-TGAAAAAGCTAAATTTCTCTTAGAGGACGATAAGGACCCTATAGA
Hutchinsoniella	ACGAGGTAGTATCTGTCTCCTAATAAA----TAT-TAAAAAATTTACCT-TT-AAG-TGAAAAAGCTTAAATAAATCATAAG-ACGACAAGGACCCCGTAGA
G_robustus	ACGARAAGTTGAAATGTCTCCGTTGTG---TTTA-TTGAATTTTA-TTTTT-TAG-TGAAGATGCTTGAATGTTGCTAGGGACGAGGACCCTGTAGA
Gn_frondosus	ACGAGAAATTGAAATGTCTTAATAGTAT---TTAA-GTGAATTTTACT--TTCTCG-TGAGGAGGCTAGAATTTTGTTGAGGGACGAGGACCCTGTAGA
Gn_schrami	ACGAGAAATTAACTGTCTTAGGATTAT---TTTT-ATGAATTTTACTT--TT-TAG-TGAAGAGGCTAGAATATTATTAAGGGACGAGAATATAGGACCCTGTAGA
P_apletocheles	ACAAGGTGAATACTGTCTCCTTCAAAA--AGGG-TTGAATTTCA-TTTTC-TAG-TGAAGAAGCTGGAATGAATCCAAGGGACGAGAAGAGAGGACCCTATAGA
P_fragilis	??
P_nsp	ACAAGGAGGAAAACTGTCTCTTTTGAAA---ATTG-TTGAATTTCA-TTTTT-TAG-TGAGGAAGCTAGAATGATTCCAAGGACGAGAAAAGACCCTATAGA
M_yagerae	??
C_elmorei	ACAAGAGATCGACTGTCTCTGTGGTGA---TATA-TTGAATTTTACTT-TC-TGG-TGAGGAGGCTAGAATTTTGCCAAGGGACGAGAAGGACCCTGTAGA
C_haptodiscus	ACAAGAGATYGACTGTCTCTATAATAA---TTGA-TTGAATTTTACTT--CC-AGG-TGAGGAGGCTTGGAYTTTGCCAAGGGACGAGGACCCTGTAGA
C_longulus	??
L_entrichoma	ACAAGATGTTAGCTGTCTCTGTAATAA---TAAGTTTTAATTTAA-TTTAC-TAG-TGAGTAGGCTGGTATGTTTCTAAGKGACGAAAAAGACCCTATAGA
L_exleyi	ACAAGGGATTAACTGTCTCTCCATAATAT---TTTGATTGAAGTTCACAT-TT-TGG-TGAAGAGGCCAAAATTTTGCCARGGGACGATAAGGACGATAAGGACCCTATAGA
S_atlantida	ACAAGATGTTGACTGTCTCTATTGTAA---GTATA-TTTAATTTTACCTCCTAAAG-TGAAGAGGCTAGGATGGTTCTGAGGGACGAGGGACCCTGTAGA
S_benjamini	ACAAGAGATCTACTGTCTCTATAATAA---TATA-TTGAATTTCACTT--CCTTAG-TGAAGAGGCTAGGATTTAGCCAAGGGACGAGGGACCCTGTAGA
S_emersoni	ACAAGATATTGACTGTCTCTGATTTAT---TGAC-TTTAAATTCACTTTCCTAAG-TGAGGAGGCTGGAATGTATTTGAGGGACGAGGGACCCTATAGA
S_gironensis	ACGAGATATAAACTGTCTCTACTACGA---TACAATTGAACCTCACCTCCCAAAG-TGAACAGGCTGGGATACAACCGGGGACGAGAAAAGACCCTATAGA
S_kakuki	ACGAGATGTTAGCTGTCTCTCATTTAAGTGAATATAGAATAATTTAAATTAA-TTTTT-TAG-TGAAGAAGCTAGGATGTGTTTAAGGGACGAAAAAGACCCTATAGA
S_lucayensis	ACGAGATATTAACTGTCTCCATTTAAT----TTTT-TTGAATTTTACTT--TT-TAG-TGAAGAAGCTAGGATGTGTTTAAGGGACGAAAAAGACCCTATAGA
S_nsp2	ACGTGATACTGACTGTCTCTGGCATAATTATTG-TTGAAATTTACTT-TT-TAG-TGAACGAGGCTAAAATGTTTCCAAGGGACGAAAAAGACCCTATAGA
S_nsp4	ACGTGATACTGACTGTCTCTGGCATAATTATTG--TAGA-TTTAATTTTTACCTCCTAAG-TGAATAGGCTAGGATGGTTCTGAGGGACGAAAAAGACCCTATAGA
S_ondinae	ACAAGATGTTAACTGTCTCTATTATAT---ATTG-TTTAATTTTACCTCCTTAAG--AG-TGAGGAGGCTGGGATTTTACCAAGGGACGAGGACCCTATAGA
S_parabenjamini	ACAAGAGACTTGCTGTCTCTCGTAGTAT---TAGA-TTGAAATTCACATTTC--AG-TGAGGAGGCTGGGATTTTACCAAGGGACGAGGACCCTATAGA
S_tulumensis	ATGAGAGATGTGATCTGTCTCTGTGTTAT--GATAG-TAGAATTTCACTT-TG-TGG-TGAATAGGCCATAATGTTTCCGAGGGACGAGAAAAGACCCTATAGA
S_williamsi	ACRAGATGTTWMCTGTCTCTCCWTTGTAA--ATGA-TTGAMATWCMCTT-CCTTAMKTGAAGAGGCTAGGATGTTTTGAGGGACGAGGACCCTATAGA
S_xibalba	??
S_cf_tulumensis	ATGAGAGATGTGATCTGTCTCTGTGTTAT--GATAG-TAGAATTTCACTT--TG-TGG-TGAATAGGCCATAATGTTTCCGAGGGACGAGAAAAGACCCTATAGA

Table S4. (Continued.)

Species code	Sequence
Campodea	GCTAATTAT------------------TTAATAGA------------TTTTTA-TTTTA--G-GTG-AATTAA--------TTATTTG-TTAAG----
Penaeus	ACTTAACAA-----------TAATTTGATTAAATT---------------ATAAAATTG-TTA--G--TATAACT---TGAT-----TTTAA-TTA--ATGT---
Branchinella	TCTTTTATAA-------AATTATATTAG------------TTTTTTA-G---A-TG-TTAT---C----------AAGTTAATA-GGTT
Hutchinsoniella	ACTTCATAC-------AAAAATTT---------------AATA---TTA--G-TT---CTTTATAAA------------AAATTT
G_robustus	GTTTTTAGTG--T---GTATTTT----------CAT---------------GTGTGGAGTGT--A--TG-GT-----------TATGTATATTATTT
Gn_frondosus	TTTTTTAGTA---A-TG--TTGT------------------AATT----TTTTTTGTGT-ATTTT-------------A-TAAA--TA---T
Gn_schrami	TTTTTAAATA--TA--G--TTTT------------------------TTTTTGTGTGACTT----------------ATTGAA------T
P_apletocheles	TTTTTAGTA-------AATTGATTTAT-GATAGG----TTAG----------TTAATGTTT-AAATTGTATC--GACGG-AGAAGT-TTAGGTCTGTT
P_fragilis	??
P_nsp	TTTTTAGTA-------ATTGGTTTTTCGTTA------TTAG----------TTA-TGTTTATAATT-TA----GTTGA---GTATTGAGTCTGTT
M_yagerae	??
C_elmorei	TTTTTAATTTCCT--GC-TTT-GTTGGGG--------TTAG------TA-TGTTT--GA-TCTTGA--GTTTA----AAGATTTGTTGG
C_haptodiscus	TTTTTTAAATTTCTTA-G--TTTTGTTGGG--------------ATT-GG----TATTGTTT--GG-TTTTGATGTGTTTA---GAA--TGGATTTG
C_longulus	??
L_entrichoma	TTTTTTAATT-----------TTTGATTTTTAGTTGT-------------TGATGATTA-TGTTGTAT---------TG-G---A-TTG-AGG-T-TTAG-T
L_exleyi	TTTTTTATTT----TTTATAATTGCTTGG--------------TTTTATTATGTGTTATGCTTATGA--------TTTG-TTT-T-TAAT-T
S_atlantida	TTTTTACTT---ATTG-ATTT-ACTT----ATG-TTTATTAGGAG-CGAA--TTTA-TGTTATT-AGTT---------GTA-TAATAGATA
S_benjamini	TTTTTTAGTT--CT---G-------TTTGGAATG--------AG--AATTGTTA-TGTT---A--------GTTTT--GTTC--TTGAGTA-GTA
S_emersoni	TTTTTTATTA---ATTG-TTT--GTTTAATA------------TAAA-TTTA-TGTTTTT---AATTTT--------ATTTTTA--TAATTA
S_gironensis	TTTTTATAC---CAAAAGAATTATTA-----------TA--AG-AAATTAA--TTAACCGTCTAACT-------GTA--A-TAA-TCC--A-ATAGGT
S_kakuki	TTTTTGAGTA--------TTATCAATTTGTTTA---TATTAG------GTTTA--G--ATAG-----------A-TTT--TTT--G-GTAA-T
S_lucayensis	TTTTTGAAATT----ATTTTGTTTTGTTTG-----------TGATATGTTTA--G---ATAA-----------G-TTT--AGT-A-ATGT-A
S_nsp2	TTTTTTAGTT--------GTATTTTA-ATGTTAATG----------AA--TTTA-TGTTT---A----------GTTTTT-GTTGTTATTTTTATACTT
S_nsp4	TTTTTTAGTT--------GTATTTTA-ATGTTAATG----------AA--TTTA-TGTTT---A----------GTTTTT-GTTGTTATTTTTATACTT
S_ondinae	TTTTTTACTT---AATG-ATTT-ATAT----ATA--TTATT-GG---CGAAA--TTA-TGT-ATTAA-TC-------GCTT----GTA--TAATGTATT
S_parabenjamini	TTTTTGAGTT--------TATGCGAAAG-----T-GGAG-TTAA---TTA-TGTTTGTGAT-------------GTTTT--GCTTTGTGTATGTA
S_tulumensis	TTTTTTAGCT----TGTATT--ATATGT-ATTA---T-----C--A-TGTTAATGTTT--AAGT--------GTAA----TCATATTTAAGC
S_williamsi	TTTTTTATTAATTA-TG-T------ATTTGATT--TTATTAG-------TTA-TGTTT--GGAAATATTT-------AGGTATAGTAATTG
S_xibalba	??
S_cf_tulumensis	TTTTTTAGCT-----TGTATT--ATATGT-GTTA--------T---------C--A-TGTTAATGTTT--AAGT-----GTAA----TCATATTTAAGC
Campodea	TAAGATTAC--TGGGGCGG---------------------------TATAGTTTTTT--------CAAATTATT--TGATA-GTTATTGATCATATTA--
Penaeus	TTG--TTGCGTTGGGGCGACGGGAATATAATAATTAGTAACTGTTCTTAAAATATTTTATTAA-----CAAGTATAA--TTGAAGAATAATTGATCCTTTAT-T
Branchinella	TTTTTAATTTCGTTGGGGCGACGTTGAGGGTTGAGATATCTCCAAAAATGTTTTTA----------CATTAATAA--ATG---ATTTTTGATCCTTTAG---
Hutchinsoniella	TTGTTATTTCGTTGGGGTGACCAAT-TTTAAAAATAAACAAAAACTTATTTTTA---------CATATATAA-ATGAAACTTTTATTGACCCAGATATT
G_robustus	AT---TTTTGGTTGGGGCGATTAAT-TAAGATACGTATCTTAATTTTGTTTAAT-----CAGTGTTGG--CTG-AATTTTATAGATCCATTAT-T
Gn_frondosus	AC---TTTTGGTTGGGGCGATTTTA-AAAGAAAAATATCTTTTGTTTAATGATTTAT-------CAATTATTTT--TTG---TTTTATTGATCCAGAAT-T
Gn_schrami	AT---TTTTGGGGCGGGCGATTTAA-AAAGAAGATTATCTTTTAATTATTATTTTT------CAGATGTTTT--TTG---TTTTATTGATCCAGAAT-T
P_apletocheles	AT---TTTTGCTGGGGCGCAGTT-GAAGAAAAGTATCTTCAGTTATAAGTAAAT-----------CATTTGTGG--ATG-----AGATGATCCCATAT-T
P_fragilis	??
P_nsp	AT---TTTTGCTGGGGTGGCAGTT-GAAGATAAGAAGAATCTTCAGTTATTTAAAGT--------CATTTATGG--GTG----AATTGATCCTTTAT-T
M_yagerae	??
C_elmorei	GATGTTTTAGCTGGGGCGGCGCTGTG-AGAGAGACTGATCTCCTGTTTGTATTGTGG------CAATTATGG--TTG-----TTGTGATCCTTTAT-T
C_haptodiscus	GATGTTTTAGCTGGGGCGGCGCTGTG-GGAGGATGAATATCTCCTGTTTGTATTGTGG--------CAATTATGG--TTG-----TATTGATCCTTTAT-T
C_longulus	??
L_entrichoma	AT---TTTTGCTGGGGCGGCAGTT-GAGGAAGAGAGAATCTTCAGTTTTTTTTGAT-------CATTGGTGG--GTG-----ATTTGAYCCTTTATAT

Table S4. (Continued.)

Species code	Sequence
L_exleyi	AA---TTTAGCTGGGCGGCTATT-GAAGATGAGGATCTTCAGT-TGATTTTTGG-------CAGATTTGT--TTG-----TAGTGATCCTTTAT-T
S_atlantida	A--G-TTTTACTGGGGCGGTAGTT-AAAGATGATGAATCTTAGTTTGATAGTAATG-------CACTGATGG--GTG-----TAATGATCCTTTAT-T
S_benjamini	AT---TTTTGCTGGGTGGCTGTT-GAAGATGAGAATCTTCAGTTTTATTTGGTTGG-------CATTGTTGA--GTG-----TAATGATCCTTTAT-T
S_emersoni	A----TTTTACTGGGGCGTATTT-GAAGATCCGGATCTTCAAAITTT-ASTGATATTT-------CATTGTTGG--GTG-----TATTGATCCTTTAT-T
S_gironensis	G---ATTTACTGGGGCGGTGCTCTGAAGAAAAAAATCTTCAAGTATTTAATATT-------CACCAATCA--GTG-----ATCTGATCCCTTAT-T
S_kakuki	AT---TTTTGCTGGGGCGGCGATT-GAAGATGTGAAATCTTCAGTTGGTTAGAAG-------CATTGTTGG--GTG-----TGGTGATCTTGTGT-T
S_lucayensis	AT---TTTTGCTGGGGCGGCGGTT-GAATGTAATGATCTTCAGTTGTTATGTATTG-------CATTAGTGA--GTG-----TAATGATCCTTTAT-T
S_nsp2	-----TT--GCTGGGGCGGCTGTT-GAAGATAAGAATCTTCAGTTTTTGTTGTTG-------CGAATTAATTGTTG---TTTGTTGATCCTGTATTT
S_nsp4	-----TTTTGCTGGGGCGGCTGTT-GAAGATAAGAATCTTCAGTTTTTGTTGTTG-------CAATTAATT-GTTG---TTTGTTGATCCTGTATTT
S_ondinae	GA-G-TTTTACTGGGGCGTAGTT-AAAGATATAGATCTTTAGTTTATTTAATT---------CACTTATAA--GTG-----TGGTGATCCTTTAT-T
S_parabenjamini	AT---TTTTACTGGGGCGTTGTT-GAAGATGAGGATCTTCAGTTTTTTAATTT-------CACCGGTGG--GTG-----TTTTG??????????
S_tulumensis	AG-GTTTTTACTGGGGCGTATTT-GAAGAAGTAGATCTTCAGATTTTTAATGAGATTTACACTCACTTGTGG--GTA--TTGTTTTGATCCTATATAT
S_williamsi	G----TTTTGCTGGGGCGGCAATT-GAGGATTTTATCTTCAGTATAITTAAAT---------CATCTATGG-ATGT------AATGATCCTTTAT-T
S_xibalba	???????????????????????TTTTGCTGGGGCGTATCT-GAAGAAGTAGATCTTCAGATTTTTAATGAGGTTTACACTCACTTGTGG---GTA---TTGTTTTGATCCTATATAT
S_cf_tulumensis	AG-GTTTTTACTGGGGCGTATCT-GAAGAAGTAGATCTTCAGATTTTTAATGAGGTTTACACTCACTTGTGG---GTA---TTGTTTTGATCCTATATAT
Campodea	---ATAAAAATTAGTGAAAGTTACCTTAGGGATAACAGTATAATTATTTTTGAGAGTACAAAATTGACAAAATAG--TTTATAACCTCGATGTTGAATTAAA
Penaeus	AAAGATTAAAAGATT-AAGTTACTTTAGGGATAACAGCGTAATCTTCTTTGAGAGTCCTCATCGACAAGAAGG--TTTTGCGACCTCGATGTTGAATTAAG
Branchinella	--TGA--ATTAGGATAAAGTTACCTTAGGGATAACAGCGTAATTTTTCTTGAGAGTCCTTATCGACAGAAAAG--TTTTGCGACCTCGATGTTGGTTCAGG
Hutchinsoniella	TCTGATT-AAAAGAACAAGTTACCTCGGGGATAACAGCGTAATTCTTTTCAAAAGCACACATTAACACAAAGAG--ATTTGCGACCTCGATGTTGGACTAAG
G_robustus	ATTGGTTAAAAGATC-AAATTACCTCAGGGATAACAGCGTTATTGTATTTTAGAGTTCTTATCGATAATATAG--TTTTGCGACCTCGATGTTGAATTAGG
Gn_frondosus	TTTGATTATAAGATT-AAAATACCTCAGGGATAACAGCGTAATTTTTTTTAAGAGTTCTTATTTGAATAAAAG--TTTTGCGACCTCGATGTTGAATTAAG
Gn_schrami	TTTGATTATAAGATT-AAAATACCTCAGGGATAACAGCGTAATTTTTTTTGAGAGTTCTTATTTGAATAAGAG--TTTTGCGACCTCGATGTTGAATTAAA
P_apletocheles	ATGGATAGAAAGATAAAAAAATACCTTAGGGATAACAGCGTAATCTTTTTTTGAGAGTTCATATCGACAAGAGAG--ATTGCGACCTCGATGTTGAATTAGG
P_fragilis	??
P_nsp	ATGGATTATAGAGATG-AAAATACCTTAGGGATAACAGCGTTATTCTTTTTTGAGAGTTCATATCGACGAAAGAG--ATTGCGACCTC????????????????
M_yagerae	???
C_elmorei	ATGGAT-ATAAGAA--AAAATACCTCAGGGATAACAGCGTAATTTCTTTGAGAGTTCTTTGAGAGTCGTATCGATAGAGAAG--TTTTGCGACCTCGATGTTGAATTAAA
C_haptodiscus	ATGGATATTAAGAAA-AAAATACCTCAGGGATAACAGCGTAATTTTTCTTGAGAGTACTTATCGATAGGAAAG--TTTTGCGACCTCGATGTTGAATTAAA
C_longulus	??
L_entrichoma	ATGGATAATAAGGAG-TAAATACCTTAGGGATAACAGCGTAATATTTCTGAGAGTTC-TATCGACAGATTA---TTTTGCGACCTCGATGTTGAATTAGG
L_exleyi	ATGGATAATAAGATT-AAAATACCTTAGGGATAACAGCGTATTTCTCTTGAGAGTTCTTATCGATAGGGAAG--TTTTGCGACCTCGATGTTGAATTAGG
S_atlantida	ATGGATAATAAGATT-TAAATACCTTAGGGATAACAGCGTAATCTTTTTTCTGAGAGTTCTTATCGACGAATAATGATTTGCGACCTCGATGTTGAATTAGG
S_benjamini	ATGGATAATAAGATT-AAAATACCTTAGGGATAACAGCGTTATTGGCTTGAGAGTTCTTATTGATAGTGAAG--TTTTGCGACCTCGATGTTGAATTAGG
S_emersoni	ATGGATAAGAAGAGA---AAAATACCTTAGGGATAACAGCGTTATTTATTTTATTTCTTCCAAGAGCCGTATCGAAGAGAATGA-TTTTGCGACCTCGATGTTGAATTTAG
S_gironensis	AGGGATAACAACAAGAAA-CAAATACCTTAGGGATAACAGCGTTATTTATCGTTATAGATCTTAAAATATCCTGAAATAATGATTTG--TTTTGCGACCTCGATGTTGAATTTAG
S_kakuki	ATAAAATAAGAAGAAA-AAAAATACCTTAGGGATAACAGCGTTAAAATATCCTGAAATATCCTGAGAGATCTTGAGAGTTCTTATCGACACAGATTTG--TTTTGCGACCTCGATGTTGAATTAGG
S_lucayensis	ATGGAAAAATAAGAGG-AAAAATACCTTAGGGATAACAGCGTTAAAATATCCTGAGAGTTCTTATCGACGGATTATG--TTTTGCGACCTCGATGTTGAATTAGG
S_nsp2	ATGG??
S_nsp4	ATGGATAATAAGATA-AAAATACCTTAGGGATAACAGCGTTATTTTCTTTGAGAGTTCTTATCGACACAGGAAAG--TTTTGCGACCTCGATGTTGAATTAGA

Table S4. (Continued.)

Species code	Sequence
S_ondinae	ATGGATAGTAAGATT-TAAATACCTTAGGGATAACAGCGTTATTCTTTCTGAGAGTTCTTATCGACGAATGTGA-TTTGCGACCTCGATGTTGAATTAGG
S_parabenjamini	? ?
S_tulumensis	ATGGATAAGAGGAAA-TAAATACCTTAGGGATAACAGCGTTATCTTCCCTGAGAGTTCTTATCGACGGGGGGG--TTTGCGACCTCGATGTTGAATTAGA
S_williamsi	ATGGAAAAGAAAGAA--TAAATACCTTAGGGATAACAGCGTTATTTTTCCGGAGAGTTCTTATCGATGGAAATGA-TTTGCGACCTCGATGTTGAATTAGG
S_xibalba	? ?
S_cf_tulumensis	ATGGAT? ?
Campodea	ATTT-AT-T-ATTAGTGAAGAAGCTAGTAAAAT------AGGTCTGTTCGACCAATAAA------ATTTTACATGATTTGAGTTCAGACCGG
Penaeus	GTAT-CC-T-T---ATAATGCAGCAGTTACAAA--GGA--AGGTCTGTTCGACCTTTAAA------TCCTTACATGATTTGAGTTCAGACCGG
Branchinella	GTTC-CT-T-TA-GGCGCAGCAGTTTAGTAA----GGTAGTCTGTTCGACCTACTAAA------TCCCTACG? ? ? ? ? ? ? ? ? ? ? ? ? ?
Hutchinsoniella	AAAC-CT-A-T--AA-AATGCAGCAGTTTTATA----AGAAGGTCTGTTCGACCTTTAAT------ATCTTACATGATCTGAGTTTAAACCGG
G_robustus	TTAC-GT-G-G-ATG-GGTGTAGAAGTTCTC-Y--TGGG-TARTCTGGTCGACTATTGGA------TACCTACGTGTCGG? ? ? ? ? ? ? ? ? ? ?
Gn_frondosus	GGTT-ATTG-A--TA--GGTGTAGTAGTTTAT-C--GT-TTTAAATCTGTTCGACTA? ?
Gn_schrami	GATT-TA-C-A-ATA--GGTGTAGCAGCTTAT-T--TA-ATTAGTCTGTTCGACTAATAGT------TCTTTACGTGATCTC? ? ? ? ? ? ? ? ? ? ?
P_apletocheles	AGTG-AGTAGT--TA-GGTGTAGGAGCTTAAAT-TCT---GGGTCTGTTCGACCTTTAAA------TTTCTACGTGATCTGAGTTCAGACCGG
P_fragilis	? ?
P_nsp	? ?
M_yagerae	GGTG-GAAA-T--TT-GGTGTAGGGGCTAAA-T-GTT-GTGGGTCTGTTCGACCC? ?
C_elmorei	GGTG-GA-G-T--TT-GGTGTAGGGGCTGAA-T--GTAGTGGGTCTGTTCGACCCTTAAA-----GTTTTACGTGATCTGAGTTCAGACCGG
C_haptodiscus	? ?
C_longulus	AGTA-GA-A-A--TG-GATGGAAGGATTCAA-T--TGGCTAGGTCTGTTCGACCTTTAAA------TTTCTACGTGATCTGAGTT-AGACCGG
L_entrichoma	GTAA-GTAGAT-TTT-GGTGTAGTAGTTA? ?
L_exleyi	AAAT-TA-C-C--TT-GGTGTAGAGGCTTTG-G--TTGGAAGGTCTGTTCGACCTTTAAT------ATTTTAC? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
S_atlantida	ATTT-GG-A-ATTTT-GGTGTAGTAGCTGGT-TTTCT---TGGTCTGTTCGACCATTAATA-----ATTCTACGTGATCTGAGTTCAGACCGG
S_benjamini	GAAA-AA-G-A--AA-GGCGCAGAAGCCTAC-T--CAGA-TGGTCTGTTCGACCAACACGTT-----TCCT-TCA? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
S_emersoni	AGTG-GT-A-G--TA-GGTGGAAGGACTTAT-T-TTAC-C-AGGTCTGTTCGACCTTTTAA------ATTCTACGTGATCTGAGTTCAGACCGG
S_gironensis	ATTAAGT-G-A--TG-GGTGGAAGGACTTAT-T-TACT--AGGTCTGTTCGACCTTTTAA------ATTCTACGTGATC? ? ? ? ? ? ? ? ? ? ? ? ?
S_kakuki	? ?
S_lucayensis	ATAA-GG-G-T--TATGATGTAGGAGTCTAA-T--TTTG-TGGTCTGTTCGACCGTTTAAAAGTAATATTCTACGTGATCTGAGTTCAGACCGG
S_nsp2	GTAA-GAAGAT-TTT-GGTGTAGTAGT? ?
S_nsp4	ATTA-AT-C-C--TA-TAAGTAGTCATATGG-G--TTATTTGGTCTGTTCGACCATTAAAT------ATTCTTCATGATTTGAGTTTAAACCGG
S_ondinae	GTTT-GA-A-TTTTG-TGTGAAGTAG? ?
S_parabenjamini	? ?
S_tulumensis	? ?
S_williamsi	? ?
S_xibalba	? ?
S_cf_tulumensis	? ?