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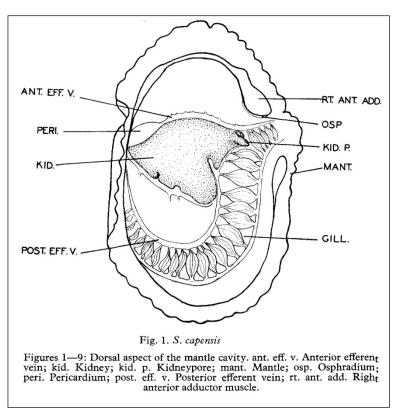
by

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INTRODUCTION

The first species of *Siphonaria* (*laciniosa* and *pectinata*) were described by Linné in the mid-18th century. Due to the limpet-like appearance of these siphonarians, Linné placed the two species into the genus *Patella*, which is currently comprised of true limpets. The difference between true limpets and false limpets (limpet-like pulmonates in the genera *Siphonaria*, *Trimusculus*, and *Williamia*) is the morphology of the vascular cavity. In true limpets, the vascular cavity consists of a space between the mantle and the visceral mass of the gastropod that opens to the external environment at both the anterior and posterior ends of the animal. The vascular cavity of false limpets is entirely enclosed and is connected to the environment via a small contractile opening on the right side of the organism (see Figure 1, taken from Allanson 1958). In 1823, Sowerby created the generic name *Siphonaria* which was inspired by the characteristic siphon (or tube) located on the right side of the organism that connects the vascular cavity to the

Fig. 1. *S. capensis*

Figures 1—9: Dorsal aspect of the mantle cavity. ant. eff. v. Anterior efferent vein; kid. Kidney; kid. p. Kidneypore; mant. Mantle; osp. Osphradium; peri. Pericardium; post. eff. v. Posterior efferent vein; rt. ant. add. Right anterior adductor muscle.

environment. The protrusion of the siphon interrupts the continuity of the muscle scar on the internal side of the shell and produces a horseshoe-like impression; true limpets have muscle scars that are in an unbroken ring. Due to the presence of an enclosed vascular cavity, false limpets have been considered pulmonates. However, some scientists hypothesize that siphonarians are more closely related to opisthobranchs (sea slugs) due to the structure of the gill in the vascular cavity.

Of the three false limpet genera, siphonarians are the most speciose and abundant which has led to a great deal of literature that consists of species descriptions, taxonomic discussions, and regional species checklists. Few species of *Siphonaria*

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have received extensive morphological study; those that have are typically large, widely distributed, or numerous in a specific region (e.g. *gigas*, *pectinata*, *lessonii*). *Siphonaria compressa* is also another well-studied species due to the decrease in habitat and threat of extinction. Information regarding reproduction, behavior, physiology, ecology, polypropionate metabolites, etc. is also usually limited to these same species of *Siphonaria*. Siphonarians from only one location, South Africa, have received comprehensive research, including molecular studies. Some species from Australia and New Zealand have received taxonomic revisions, but no molecular studies. The acquisition of molecular sequence data from a broad sampling of *Siphonaria* species for phylogenetic investigations was lacking until I completed my dissertation research. As for a comprehensive taxonomic revision of *Siphonaria*, Hubendick published his monograph in 1946; the previous year he produced an extensive publication on the distribution and phylogeny of siphonarians. To date, Hubendick's publications are the most inclusive, but revisions need to be made to the monograph (i.e. incomplete citations, addition of new species described since 1946, spelling errors, synonymies).

The first subject I addressed in my dissertation was the evolutionary relationship of siphonarians to other pulmonates and opisthobranchs. Morphological features are limited in siphonarians, as well as other gastropods, and the characters available indicate a close relationship of siphonarians to both pulmonates and opisthobranchs. Which character is more phylogenetically informative – the vascular cavity (pulmonates) or the structure of the gill (opisthobranchs)? Taking a step back and widening the inquiry with respect to the evolutionary relationships of the higher pulmonates and opisthobranchs, the high variability of each morphological character across taxa, as well as the homoplasic nature of some of these characters, greatly complicates the resolution of gastropod phylogenies. Molecular sequence data is an additional data set that can avoid the problems presented by morphological data.

The use of consistent molecular characters across gastropod taxa has been limited. Portions of 16S, 12S, 28S, 5.8S rRNA and COI sequences; complete 18S rRNA and ITS-2 sequences; and entire mitochondrial genomes have been used to infer evolutionary relationships among gastropods (Yamazaki et al. 1997, Kurabayashi and Ueshima 2000, Medina and Walsh 2000, Dayrat et al. 2001, Dayrat and Tillier 2003,

Klussmann-Kolb et al. 2008, Grande et al. 2008, Dayrat et al. in press). I employed the latter technique and while sequencing entire mitochondrial genomes increases the molecular dataset, the downfall is the decrease in taxon sampling due to the sheer volume of work needed to sequence, assemble, annotate, and analyze the approximately 14,000 base pairs. However, Cunha et al. concluded that individual mitochondrial genes provided less topological resolution of the caenogastropod evolutionary tree than data from an entire genome.

One siphonarian mitochondrial genome had been previously sequenced (Grande et al. 2008), *Siphonaria pectinata*, and I sequenced an additional siphonarian to include in the analyses: *Siphonaria gigas*. With the hopes of understanding the higher relationships among pulmonates, our lab also sequenced the mitochondrial genomes from representatives of non-stylommatophoran taxa traditionally regarded as basal (Amphibolidae, Ellobiidae, Onchidiidae, Trimusculidae, and Veronicellidae) to be included in analyses along with some of the gastropod genomes utilized by Grande et al. (2008). In addition to the pulmonate genomes, six opisthobranch genomes were incorporated in the analyses to elucidate siphonarian relationships within the Euthyneura.

The second task of my dissertation was a taxonomic review, mostly due to the fact that I would be obtaining molecular sequence data from numerous siphonarians to create a phylogenetic tree; I needed a good understanding of the taxonomy and distribution of siphonarians so I could identify the species indicated by the clusters of individuals in the phylogeny. This chapter is not a taxonomic revision of *Siphonaria*, which would require studying the type specimens (if they can be located) of each species and then trying to straighten out the ensuing nomenclatural clutter. My review is to provide a comprehensive list of all the names associated with *Siphonaria*, whether they are subspecific, specific, supra-specific, or supra-generic, and what the authors in the secondary literature think about the validity of these names. A total of 269 species-group names were discussed, of which 204 are available. The hope is that individuals describing new species of siphonarians in the future will first consult this review and use one of the available names instead of compounding the nomenclatural problems. The probability that new species will be described in the future is great since the results of

the molecular sequence data are revealing what are likely cryptic and previously undescribed species (see Chapter 3).

Hubendick's (1946) monograph of the *Siphonaria* provided a good starting point for the second chapter, but more often than not, I would spend hours trying to decipher one of his cryptic citations or the identity of authors mentioned in a list of synonyms. He also did not include information regarding the supra-generic nomenclature pertaining to *Siphonaria*. My review of the nomenclature is thorough, especially the references section which contains 355 complete citations, and will be critical to all future taxonomic work related to siphonarians.

As alluded to above, the third and final chapter of my research is the analysis of molecular sequence data from a large sampling of *Siphonaria* species; this endeavor has only been completed for the siphonarians from South Africa. My research incorporated 159 individuals from several collections of museum specimens that were collected from localities all over the world, with a high number of specimens from the Indo-West Pacific. This area is species-rich in siphonarians and the likelihood that there are species from this area yet to be described is high. Hubendick (1946, 1955) acknowledged the Indo-West Pacific as problematic due to the high variation of shell morphology and transitional forms connecting species. Siphonarians are primarily identified based on shell morphology, but given that the shield-shaped shells of siphonarians lack very many distinguishing morphological characters and can be heavily impacted by the environment, molecular sequence data will provide a useful tool in distinguishing species.

Another topic I hoped the molecular data would address is the ancestral mode of development. The amount of data collected about the reproduction and development of siphonarians is again limited to a small number of species, but the mode of development is typically either planktotrophic or direct development. Knowing the developmental mode of the basal siphonarians could also shed light on which subclass of gastropods were their close relatives, the Pulmonata or the Opisthobranchia (see Chapter 1).

CHAPTER 1: Siphonarians: Pulmonate or Opisthobranch?

Mitochondrial phylogenomics of pulmonate gastropods

Abstract

Background: Reconstructing the higher relationships of pulmonate gastropods has been difficult. Morphology is problematic due to high homoplasy. Molecular studies have suffered from low taxon sampling. Forty-one complete mitochondrial genomes are available for gastropods, seven of which are pulmonates. Ten new complete mitochondrial genomes of pulmonates are presented here: *Salinator rhamphidia* (Amphiboloidea); *Auriculinella bidentata*, *Myosotella myosotis*, *Ovatella vulcani*, and *Pedipes pedipes* (Ellobiidae); *Peronia peronii* (Onchidiidae); *Siphonaria gigas* (Siphonariidae); *Succinea putris* (Stylommatophora); *Trimusculus reticulatus* (Trimusculidae); and *Rhopalocaulis grandidieri* (Veronicellidae). Also, 94 new pulmonate-specific primers across the entire mitochondrial genome are provided, which were designed for amplifying genomes through simultaneous, short reactions.

Results: The structural features of the 10 new mitochondrial genomes are summarized. All genomes share similar gene orders. Phylogenetic analyses were performed including the 10 new genomes and 16 genomes from Genbank (outgroup, opisthobranch, and other pulmonate species). Bayesian Inference and Maximum Likelihood analyses produced the same topology, based on the concatenated amino acid sequences of the 13 protein-coding genes. The pulmonates are paraphyletic and basal to the opisthobranchs that are monophyletic at the tip of the tree. *Siphonaria*, traditionally regarded as a basal pulmonate, is nested within opisthobranchs. *Pyramidella*, traditionally regarded as a basal (non-euthyneuran) heterobranch, is nested within pulmonates. Several hypotheses are rejected, such as the Systellommatophora, Geophila, and Eupulmonata. The Ellobiidae is polyphyletic, but the false limpet *Trimusculus reticulatus* is closely related to some ellobiids.

Conclusions: Despite recent efforts for increasing the taxon sampling in euthyneuran gastropods (opisthobranchs and pulmonates) phylogenies, most deep nodes are still uncertain, mainly due to low support values as well as some incongruence between analyses based on complete mitochondrial genomes and those based on individual genes (18S, 28S, 16S, CO1). Additional genomes are still needed, especially for veronicellids, ellobiids, freshwater pulmonates, taxa for which no genome is currently

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available (*Williamia*, *Otina*, and, *Smeagol*), as well as basal heterobranchs, closely related to euthyneurans. Step by step, however, new relationships are being unveiled, such as the close relationships between the false limpet *Trimusculus reticulatus* and ellobiids, the fact that a pyramidelloid is nested within pulmonates, and that *Siphonaria* is closely related to sacoglossan opisthobranchs.

Background

Elucidating the higher phylogenetic relationships of pulmonate gastropods has remained difficult. A morphology-based phylogenetic analysis revealed a high level of homoplasy and resulted in a poorly-resolved tree [Dayrat & Tillier 2002]. Molecular studies have been based on few individual genes, essentially 18S, 28S, 16S, and COI data [Klussmann-Kolb et al. 2008; Dinapoli and Klussmann-Kolb 2010; Jorger et al. 2010; Dayrat et al. 2011], or few complete mitochondrial genomes [Grande et al. 2008; Castro and Colgan 2010; Medina et al. 2011].

Analyses based on individual gene sequences all provide similar relationships (Figure 1) [Klussmann-Kolb et al. 2008; Dinapoli and Klussmann-Kolb 2010; Jörger et al. 2010; Dayrat et al. 2011]: pulmonates are monophyletic, but they include a few taxa not traditionally classified as pulmonates (Acochlidia, traditionally regarded as opisthobranchs, and Glacidorbidae and Pyramidelloidea, traditionally regarded as basal heterobranchs); also, opisthobranchs are paraphyletic, basal to pulmonates; finally, the false limpet *Siphonaria*, traditionally regarded as a pulmonate, is in some cases found to be more closely related to opisthobranchs than pulmonates. In recent years, taxon sampling has significantly increased in analyses utilizing individual genes: the largest data set (18S) established so far includes 79 species representing all major taxa of pulmonates [Dayrat et al. 2011].

Analyses based on complete mitochondrial genomes provide different phylogenetic relationships, at least for the deep nodes (Figure 1) [Grande et al. 2008; Castro and Colgan 2010; Medina et al. 2011]: pulmonates are paraphyletic, basal to the monophyletic opisthobranchs; *Siphonaria* is nested within the opisthobranchs. Taxon sampling is still limited in analyses based on complete mitochondrial genomes, mainly

because gastropod mitochondrial genomes are still difficult to obtain. Since the first complete gastropod mitochondrial genome was published in 1995 [Hatzoglou et al. 1995], 41 complete genomes have been made available (Figure 2). The use of shotgun sequencing and the decrease in sequencing costs caused a noticeable increase in the production of gastropod mitochondrial genomes a few years ago (Figure 2). Ten genomes became available in nine different publications between 1995 and 2006; since 2008, 31 genomes became available, 26 of which appeared in only three publications, although a few papers with only one genome were published.

At present, Opisthobranchia and Neogastropoda are the taxa for which the largest number of complete mitochondrial genomes is available, with 17 and 12 genomes, respectively (Figure 2). Seven genomes are available for pulmonates, but only some of the pulmonate higher clades are represented. The taxon sampling for the other gastropods is either insufficient (Patellogastropoda, Vetigastropoda, Neritimorpha, basal caenogastropods, and basal heterobranchs) or missing (Cocculiniformia).

In the present contribution, we report 10 new, complete, mitochondrial genomes of pulmonates, with a special focus on clades that were poorly or not sampled (Figure 2, Table 1): *Salinator rhamphidia* (Amphiboloidea); *Auriculinella bidentata*, *Myosotella myosotis*, *Ovatella vulcani*, and *Pedipes pedipes* (Ellobiidae); *Peronia peronii* (Onchidiidae); *Siphonaria gigas* (Siphonariidae); *Succinea putris* (Stylommatophora); *Trimusculus reticulatus* (Trimusculidae); and *Rhopalocaulis grandidieri* (Veronicellidae). Here we also provide a set of 94 new, pulmonate-specific primers spanning the entire mitochondrial genome and specifically designed for the present study. These new primers were combined in multiple pairs, or with previously published mitochondrial primers, to amplify genomes through simultaneous, short reactions. This direct approach was of great help for amplifying mitochondrial genomes in the present study. Pulmonate relationships are evaluated through phylogenetic analyses based on these new genomes as well as 16 genomes that were published previously. The impact of this new data on our understanding of the relationships and evolution of pulmonates is discussed.

Results

Genome Structural Features

The structural features of each of the 10 mitochondrial genomes sequenced in this study are summarized in Table 2. Each genome consists of 13 protein-coding genes, two rRNA genes, and 22 tRNA genes. The genomes vary in size from 13,968 bp (*Peronia peronii*) to 16,708 bp (*Pedipes pedipes*) with most in the range of 14,000 bp. In all 10 genomes, 13 of the 37 genes are coded on the minus strand: *trnQ*, *trnL2*, *atp8*, *trnN*, *atp6*, *trnR*, *trnE*, *rrnS*, *trnM*, *nad3*, *trnS2*, *trnT*, and *cox3*. In *Succinea putris*, *trnY* and *trnW* are also coded on the minus strand, as well as *trnH* in *Siphonaria gigas*. In the majority of the protein-coding genes (59 of 130), the start codon is TTG. Alternatively, the start codon is either ATG (43), GTG (17), ATT (6), ATA (3), CTG (1), or TTA (1). The stop codon is either TAA (52), TAG (41), T (36), or TA (1), none of which being used solely for a particular protein-coding gene.

All 10 mitochondrial genomes have adjacent overlapping genes, typically 11 to 12 genes; the highest number (15) of overlapping genes is found in *Peronia peronii* and the fewest number (7) is found in *Pedipes pedipes*, which is likely correlated with genome size. The amount of overlap between genes is typically between 1 and 30 bp. Only one pair of overlapping genes is common to all 10 mitochondrial genomes: *trnK*/*cox1* (5 to 8 bp). With the exception of *Pedipes pedipes*, the other nine mitochondrial genomes all have *nad6*/*nad5* (2 to 18 bp) overlapping and *nad5*/*nad1* (14 to 26 bp) overlapping. The largest overlaps in adjacent genes are 39 bp between *nad2*/*trnK* in *Succinea putris* and 45 bp between *nad4L*/*cob* in *Auriculinella bidentata*. The number of intergenic spacers range from four in *Peronia peronii* to 20 in *Pedipes pedipes*. The typical size of the intergenic spacers varies from 1 to 80 bp. A large intergenic spacer (651 bp) is found in *Rhopalocaulis grandidieri* between *trnS1*/*trnS2*, and another one (270 bp) in *Ovatella vulcani* between *trnM*/*nad3*. Of the 20 intergenic spacers found in *Pedipes pedipes*, five of them are sizeable and AT-rich: 288 bp between *nad6*/*nad5*, 447 bp between *trnS2*/*trnT*, 397 bp between *cox3*/*trnQ*, 700 bp between *trnR*/*trnS1*, and 317 between *nad4*/*trnI*. An AT-rich intergenic spacer between *cox3*/*trnI* is found in all 10 mitochondrial genomes, and this was determined to be the potential origin of replication (POR) which concurs with previous findings [Grande et al. 2008]. Due to gene rearrangements, the POR for *Pedipes pedipes* may be located between *cox3*/*trnQ* (397

bp) or between *nad4*/*trnI* (317 bp). The POR of *Pedipes pedipes* is likely adjacent to the start of *cox3* for two reasons. First, the percentage of A+T in the 50 bp adjacent to *cox3* is higher than the 50 bp adjacent to *trnI* (62.0% and 58.8%, respectively). Second, a POR adjacent to *cox3* was previously found in other gastropod mitochondrial genomes [Cunha et al. 2009].

The 22 tRNAs for each of the 10 mitochondrial genomes were easily located, with the exception of *trnS1* in *Rhopalocaulis grandidieri*. Unlike the *trnS1* of the other nine mitochondrial genomes, the anticodon loop sequence is CTGCTAG instead of the typical CTGCTAA and there are two base mispairings in the anticodon loop, which is also uncommon. All of the *trnS1* and *trnS2* genes lack the DHU stem.

Molecular Phylogeny

The trees produced from the amino acid data set ML analysis (-LnL = 99725.17) and the BI analysis (-LnL = 99741.69) had identical topologies (Figure 3). Pulmonates form a paraphyletic group at the base of the Euthyneura; *Pyramidella dolabrata*, traditionally regarded as a basal heterobranch external to Euthyneura, is nested within pulmonates. *Siphonaria*, traditionally regarded as a basal pulmonate, is nested within Opisthobranchia which form a derived, monophyletic group at the tip of the euthyneuran tree. The veronicellid slug *Rhopalocaulis grandidieri* is the most basal species of the euthyneurans, with high node support. The two stylommatophorans *Succinea putris* and *Albinaria coerulea* and the freshwater *Biomphalaria glabrata* form a clade emerging just after *Rhopalocaulis grandidieri*. The ellobiids (*Pedipes pedipes*, *Myosotella myosotis*, *Ovatella vulcani*, and *Auriculinella bidentata*) do not form a monophyletic clade and are spread throughout the basal portion of the tree. However, the false limpet *Trimusculus reticulatus* (Trimusculidae) is recovered as closely related to two ellobiids (*Ovatella vulcani* and *Auriculinella bidentata*), which is strongly supported. The three species of onchidiids (*Peronia peronii*, *Onchidella borealis*, and *Onchidella celtica*) form a highly-supported monophyletic group. *Salinator rhamphidia* (Amphiboloidea), traditionally regarded as a basal pulmonate (mainly because of the presence of an operculum), is sister taxon to a clade formed by two ellobiids, *Trimusculus reticulatus*, and the Onchidiidae, but is not basal with respect to all pulmonates. Within the clade Opisthobranchia, *Ascobulla fragilis* was found to be the most basal.

Genome Rearrangements

The arrangement of the protein-coding, rRNA, and tRNA genes in the mitochondrial genome is known to be potentially informative for phylogenetics [Boore and Brown 1998]. However, the genomes of pulmonate gastropods display limited variation (Figure 4).

Biomphalaria glabrata, *Salinator rhamphidia*, *Trimusculus reticulatus*, *Ovatella vulcani*, *Auriculinella bidentata*, *Peronia peronii*, *Onchidella borealis*, *Onchidella celtica* share an identical mitochondrial genome organization. *Albinaria coerulea* shares the same genome organization except that the position of *trnS1* and *trnS2* are switched and *trnS1* is inverted. The genome of *Rhopalocaulis grandidieri* differs in the location of seven tRNAs (*C*, *F*, *G*, *W*, *H*, *L2*, and *E*). The genome of *Succinea putris* differs in the location of three tRNAs (*F*, *Y*, and *W*), with the latter two genes being coded on the minus strand instead of the plus strand. In *Pedipes pedipes*, *trnT* + *cox3* swapped with *trnS1* + *nad4*, and *trnQ* and *trnR* moved between these two swapped sets of genes. *Myosotella myosotis* only differs from the most standard mitochondrial genome organization by the rearrangement of *nad4L* between *cox2* and *trnY*. The location of *trnY* before *cox1* is a unique and unusual feature of the mitochondrial genome of *Pyramidella dolabrata*. Other attributes, such as the location of *atp6* prior to *atp8* and the encoding of *trnG* by the minus strand, are exclusive to *Pyramidella dolabrata*.

The opisthobranch genomes only differ from the common mitochondrial genome arrangement in the position of *trnY*, *trnW*, and *trnC*. The *trnC* is located between *trnH* and *trnQ* in *Ascobulla fragilis*, *Chromodoris magnifica*, and *Berthellina ilisima*, and between *trnN* and *atp6* in *Aplysia californica*, *Pupa strigosa*, and *Hydatina physis*. The organization of the genome of *Siphonaria gigas* is more similar to the genome of opisthobranchs than pulmonates, which is also true for *Siphonaria pectinata* despite some moderate rearrangements (*trnY* and *trnW* are adjacent to *nad4L*).

Discussion

Species diversity of the pulmonate gastropods is largely dominated by the land snails and slugs, or Stylommatophora, which include at least 25,000 species. However, most of the pulmonate phylogenetic diversity is found in the ten other higher taxa, which together account for less than five percent of the pulmonate species diversity: Amphiboloidea, Ellobiidae, Hygrophila, Onchidiidae, Otinidae, Siphonariidae, Smeagolidae, Trimusculidae, Veronicellidae, and Williamiidae. The present contribution constitutes a significant increase in taxon sampling for complete mitochondrial genomes of pulmonates, especially regarding the non-stylommatophoran taxa (Figure 2, Table 1): complete mitochondrial genomes of amphiboloids, trimusculids, veronicellids, and two ellobiid "subfamilies" (Pedipedinae and Ellobiinae) are presented here for the first time. As of today, complete mitochondrial genomes are not available for only three of the pulmonate higher taxa: Otinidae (only one species known), Williamiidae (less than 10 species), and Smeagolidae (less than 10 species).

The topology of the consensus tree produced by our phylogenetic analyses (Figure 3) is very similar to the trees obtained previously based on complete mitochondrial genomes [Grande et al. 2008; Castro and Colgan 2010]: pulmonates are paraphyletic, at the base of euthyneurans (opisthobranchs and pulmonates); opisthobranchs (including *Siphonaria*) are monophyletic, at the tip of the tree. *Pyramidella dolabrata*, traditionally regarded as a basal heterobranch (outside euthyneurans), is closely related to pulmonates. *Biomphalaria glabrata* is found here to be sister-taxon to Stylommatophora at the base of pulmonates [Castro and Colgan 2010] instead of at a more derived position in the tree [Grande et al. 2008].

The trees based on complete mitochondrial genomes show some congruence with the trees based on individual genes (18S, 28S, 16S, COI). In particular, both data sets agree on some nodes that were unsuspected before, such as the close relationship of *Trimusculus reticulatus* and ellobiids (Figure 1). However, both data sets also show some noticeable differences. This might be explained by the fact that some of the deep nodes are poorly supported. Also, the taxon sampling differs greatly: nearly 80 species of pulmonates are included in a recent analysis using 18S sequences [Dayrat et al. 2011] while only 17 complete mitochondrial genomes of pulmonates are available,

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including this study. Below we discuss the impacts of our phylogenetic results on our understanding of the evolution of pulmonate gastropods. In particular, we focus on the new insights and new questions raised by the addition of the 10 new mitochondrial genomes.

In the present results, the most basal lineage of all euthyneurans are the terrestrial, veronicellid slugs, represented here by one species, *Rhopalocaulis grandidieri* (Figure 3). Traditionally, Veronicellidae has been classified in Systellommatophora, along with Onchidiidae and Rathouisiidae [Solem 1978], although no synapomorphies could be found for systellomatophorans in cladistic analyses [Dayrat and Tillier 2002]. The representation of veronicellids in molecular analyses is recent, but trees based on individual gene sequences support the monophyly of Systellomatophora (Figure 1) [Jörger et al. 2010; Dayrat et al. 2011]. A basal position of veronicellids with respect to other pulmonates was proposed based on morphology [Salvini-Plawen 1991; Salvini-Plawen and Steiner 1996]. However, this result was based on problematic interpretations of the anatomy of systellommatophorans, such as the fact that they supposedly lack a pneumostome and a lung. If confirmed, a basal position of veronicellids could lead us to re-interpret their extremely reduced pallial cavity. However, additional mitochondrial genomes of veronicellids will be necessary for testing this new result, because a single genome might introduce a bias (e.g. long-branch attraction) in the analyses.

That freshwater snails (here represented by *Biomphalaria glabrata*) are found to be closely related to land snails and slugs, or Stylommatophora (here represented by *Succinea putris* and *Albinaria coerulea*), is not new. Our findings confirm a previous result based on complete mitochondrial genomes and individual genes (Figure 1) [Castro and Colgan 2010; Dayrat et al. 2011]. However, the position of Hygrophila is still quite unstable and does vary from one tree to another [Klussmann-Kolb et al. 2008; Jörger et al. 2010; Dayrat et al. 2011]. Unfortunately, all our attempts to get new complete genomes of freshwater pulmonates failed (we started with fresh material from 13 species of freshwater pulmonates).

The basal position of Stylommatophora with respect to other pulmonates was obtained in previous analyses based on mitochondrial genomes and individual genes (Figure 1) [Grande et al. 2008; Castro and Colgan 2010; Dayrat et al. 2011]. Many derived features characterize land snails and slugs, especially in the excretory and pulmonary systems, which are physiologically so critical for life on land [Solem 1978; Dayrat and Tillier 2002]. As a result, land snails and slugs have often been regarded as the most derived – and thus most recent – lineage of pulmonates. However, several of those derived features are autapomorphic (e.g. ureter anatomy) or potentially homoplasic (e.g. eyes at the tip of the eye tentacles) [Dayrat and Tillier 2002]. A basal position of land snails and slugs supports Solem's theory according to which stylommatophoran land snails were the first pulmonates that emerged 350 Mya [Solem 1978; Dayrat et al. 2011].

The Ellobiidae is a diverse taxon with about 800 species names available in the literature, although only 250 of them are likely to be valid [citation]. More importantly, Ellobiidae is phylogenetically diverse because the 24 ellobiid genera are characterized by different combinations of plesiomorphic and derived characters [Morton 1955; Martins 2007]. As a result, no exclusive morphological synapomorphy can be found for ellobiids within the broader context of all pulmonates [Dayrat and Tillier 2002]. For many years, molecular analyses could not adequately test the phylogenetic status of ellobiids because of low taxon sampling [Grande et al. 2008; Klussmann-Kolb et al. 2008]. However, ellobiids were found to be monophyletic in a recent molecular analysis based on a new, comprehensive data set including 25 ellobiid species (Figure 1) [Dayrat et al. 2011], suggesting that additional sequenced mitochondrial genomes are needed to properly address the phylogenetic status of the Ellobiidae, especially considering that two subfamilies (Carychiinae and Melampodinae) are still not represented.

The phylogenetic status of Ellobiidae remains problematic, in particular, analyses based on complete mitochondrial genomes and those based on individual genes all agree that the false limpet *Trimusculus reticulatus* is closely related to ellobiids (Figure 1) [Klussmann-Kolb et al. 2008; Dinapoli and Klussman-Kolb 2010; Jörger et al. 2010; Dayrat et al. 2011]. This is a new result that had not been suggested using morphology. In fact, there is not any obvious anatomical feature that appears to be shared by

Trimusculus and ellobiids [Dayrat et al. 2011]. Another interesting result obtained here, as well as in recent analyses based on individual genes, is the close relationship between Onchidiidae and some ellobiids (Figure 1). Interestingly, Onchidiidae and Ellobiidae were suggested to be classified together in the Ellobioidea (Tillier 1984), partly based on characters from the nervous system.

Our present data reject the Geophila hypothesis (Systellommatophora and Stylommatophora) which is also not supported by Dayrat et al. [2011] (Figure 1). Morphological data supported the monophyly of Geophila mainly based on two synapomorphies, i.e. the loss of heterostrophy and the presence of eyes at the tip of the ocular tentacles [Dayrat and Tillier 2002]. Both of these features might have evolved independently in Stylommatophora, Onchidiidae, and Veronicellidae. The Eupulmonata hypothesis *sensu* Morton (Geophila and Ellobiidae) also is rejected here [Morton 1955].

The present analyses confirm two important results from recent molecular studies (Figure 1) [Grande et al. 2008; Klussmann-Kolb et al. 2008; Dinapoli and Klussmann-Kolb 2010; Dayrat et al. 2011]. First, Amphiboloidea, traditionally regarded as one of the most basal lineages of pulmonates, is not basal, suggesting that their operculum (amphiboloids are the only pulmonates with an operculum) was acquired secondarily. Second, the pyramidelloids, traditionally regarded as basal (i.e. non-euthyneuran) heterobranchs, are now consistently found to be nested within pulmonates. However, the pyramidelloids have always been difficult to classify. Some past authors have even regarded them as opisthobranchs [Hyman 1967, Thompson 1976, Salvini-Plawen 1980; Haszprunar 1988; Wise 1996]. The fact that pyramidellids differ so much from other pulmonates may be related to the fact that they live submerged in the seawater (*Williamia* species are the only other pulmonates that live submerged as adults).

Finally, the present data confirm that *Siphonaria* is more closely related to opisthobranchs than to pulmonates, although this relationship is much clearer with complete mitochondrial genomes than with individual genes (18S, 28S, 16S, and CO1) [Grande et al. 2008; Klussmann-Kolb et al. 2008; Dinapoli and Klussmann-Kolb 2010; Medina et al. 2011; Dayrat et al. 2011]. More specifically, *Siphonaria* appears to be more closely related to sacoglossans (here represented as *Ascobulla fragilis*). For most

of the 20th century, authors have classified *Siphonaria* within Pulmonata, mainly because they tend to live in the upper intertidal zone, exposed to the air for most of the day, unlike opisthobranchs, which all live submerged even when found in the intertidal zone. As a result, the pallial cavity of *Siphonaria* has been interpreted as a pulmonary cavity and their gills as secondary gills. However, early anatomists had recognized the similarity of the pallial gill of *Siphonaria* with that of cephalaspideans [Haller 1893, Köhler 1894], suggesting that they could be homologous [Dayrat and Tillier 2002, 2003]. Marcus and Marcus (1960) even referred to the pallial gill of *Siphonaria* as a cephalaspidean gill. *Siphonaria* and opisthobranchs share another important feature, i.e. the production of a milky white substance (polypropionate metabolites) when irritated [Paul et al. 1997], although defensive metabolites are also found in other pulmonates, such as *Onchidium* (Onchidiidae) and *Trimusculus* [Cimino and Ghiselin 2009]. Even the gene order of the mitochondrial genome of *Siphonaria gigas* (see the position of *trnY*, *trnW*, *nad4L*, and *cob*; Figure 4) supports an affinity with opisthobranchs.

Conclusion

The present data constitute a significant increase in taxon sampling for complete mitochondrial genomes of pulmonates (Figure 2). However, despite these efforts, we are still far from understanding higher relationships of pulmonates. Most of the deep nodes are still uncertain, mainly due to low support values as well as some incongruence between analyses based on different data sets (complete mitochondrial genomes *versus* individual genes –18S, 28S, 16S, CO1), these two issues being obviously related (Figures 1, 3). As discussed above, additional pulmonate genomes are needed, especially for veronicellids, ellobiids, freshwater pulmonates, and the taxa for which no genome is currently available (*Williamia*, *Otina*, and *Smeagol*). Euthyneuran relationships would also greatly benefit from the addition of new genomes of basal heterobranchs (Architectonicoidea, Valvatoidea, Omalogyroidea, Rissoelloidea, Orbitestellidae). Being the most closely related taxa to euthyneurans, basal heterobranchs could help stabilize the topology within euthyneurans.

Euthyneuran phylogenetics and, more broadly, molluscan phylogenetics are still based on limited data, at least compared with vertebrate or arthropod phylogenetic studies which may include more than 40kb of sequence data. Addressing some of the incongruence between trees based on individual genes (18S, 28S, 16S, CO1) and those based on complete mitochondrial genomes in euthyneuran phylogenetics is a long-term goal that is beyond the scope of the present study. Progress will obviously require increased taxon sampling (especially for complete mitochondrial genomes) and new, additional, individual genes [Dayrat et al. 2011]. In the future, when the number and diversity of molecular sequences and taxon samples are increased, merging all data into a single data set may provide greater resolution.

Meanwhile, we have to accept that our progress regarding euthyneuran phylogenetics will be slow. Step by step, important discoveries are being made though (Figure 1). Some of the results obtained from recent molecular studies constitute new, major findings [Dinapoli and Klussmann-Kolb 2010; Jörger et al. 2010; Dayrat et al., 2011]. In particular, all data sets support close relationships between the false limpet *Trimusculus reticulatus* and ellobiids. Also, pyramidelloids, regarded for many decades as basal (non-euthyneuran) heterobranchs, are nested within pulmonates. Finally, the false limpets *Siphonaria*, traditionally regarded as pulmonates, are closely related to the sacoglossan opisthobranchs; mitochondrial genomes strongly suggest that *Siphonaria* is nested within the monophyletic Opisthobranchia, while individual genes suggest that *Siphonaria* and sacoglossans could be at the base of the monophyletic Pulmonata (Figure 1). All those results reinforce the idea that opisthobranch and pulmonate phylogenetics and evolution should be studied together, as euthyneurans [Dayrat and Tillier 2002, 2003].

Methods

Taxon Sampling

In addition to the ten mitochondrial genomes successfully sequenced for the present study, our analyses also include 16 complete mitochondrial genomes of gastropods obtained from GenBank (Table 1).

Species Identification, Vouchers, and DNA Extraction

Species for which genomes were obtained in the present study were identified by taxonomic experts (and authors of the present article): Rosemary Golding identified the *Salinator*, Suzete R. Gomes *Rhopalocaulis*, Antonio M. de Frias Martins the ellobiids, Tracy R. White the *Siphonaria*, and Benoît Dayrat the *Peronia*, *Succinea*, and *Trimusculus*. Voucher specimens are deposited in museum collections (Table 1). For each species, the complete mitochondrial genome was obtained from a single individual (with the exception of the tiny *Pedipes pedipes* for which three individuals had to be used). In most cases, that individual is part of the lot deposited as voucher. However, the small specimen used for DNA extraction of *Salinator*, *Auriculinella*, and *Ovatella* had to be destroyed. In these cases, the voucher lot contains other individuals from the same population. DNA was extracted using the phenol-chloroform extraction protocol with cetyltrimethyl-ammonium bromide (CTAB) [Sokolov 2000].

PCR Amplification and Sequencing

Three approaches were combined to successfully obtain complete mitochondrial genomes (Table 3): 1) long PCR products (from ~3 to ~10 kb) were amplified and sequenced using shotgun sequencing; 2) short PCR products (less than ~1.5kb) were amplified using pulmonate-specific primers spanning the entire genome and specifically designed for the present study (pulmonate-specific primers were designed through the alignment of all the sequences of pulmonate mitochondrial genomes available when the present study started); 3) short PCR products were amplified by 'primer-walking,' i.e. using individual-specific primers designed in previously sequenced regions (by individual-specific primer, we mean that distinct primers were designed for each genome being sequenced). Sequence depth ranged from 2X (sequences from pulmonate- and individual-specific primers) to greater than 20X (sequences from shotgun sequencing of long PCRs). Only high-quality chromatograms were utilized in areas where sequence depth was 2X. Table 3 summarizes how these three approaches were combined to obtain each genome.

Long PCR Amplification

Five pairs of universal primers were utilized to generate short PCR products within five mitochondrial genes: *cox1*, *cox3*, *cob*, *rrnS*, and *rrnL* [Boore et al. 2005]. In order to

increase the success of long PCR amplification, individual-specific primers were designed within the short PCR fragments of *cox1*, *cox3*, *cob*, *rrnS*, and *rrnL* obtained with universal primers. Different combinations of individual-specific primers were then used to amplify large regions of the genome (approximately from ~3 to ~10 kb). In some cases, universal primers were combined with individual-specific primers (combinations of two universal primers very rarely yielded successful amplifications). The 25 μl short PCR reactions contained 10.9 μl of water, 2.5 μl of 10X PCR Buffer, 2 μl of 25 mM MgCl$_2$, 1 μl of each 10 μM primer, 2 μl of dNTP Mixture, 0.2 μl (1 unit) of TaKaRa Taq (Code No. R001A), 5 μl of 20 ng/μl template DNA, and 0.4 μl of 100X BSA. In some short PCR reactions, BSA was replaced with 5 μl of 5X Qiagen Q-Solution (water added to these reactions was 6.3 μl). The thermoprofile used for *cox3*, *cob*, and *rrnS* was five minutes at 94°C; 40 cycles of 40 seconds at 94°C, 1 minute at 46°C, and 1 minute at 72°C; and 10 minutes at 72°C. The thermoprofile used for *cox1* and *rrnL* was five minutes at 94°C; 30 cycles of 40 seconds at 94°C, 1 minute at 46°C, and 1 minute at 72°C; and 10 minutes at 72°C. The 25 μl long PCR reactions contained 3.8 μl of water, 2.5 μl of 10X LA PCR Buffer II, 0.5 μl of 25 mM MgCl$_2$, 5 μl of each 2 μM primer, 3 μl of dNTP Mixture, 0.2 μl (1 unit) of TaKaRa LA Taq (Code No. RR002M), and 5 μl of 20 ng/μl template DNA. The thermocycler profile for the long PCRs consisted of one minute at 98°C, followed by 30 cycles of 98°C for 10 seconds and 68°C for 15 minutes, with a final extension of 10 minutes at 72°C. All long and short PCR products were cleaned with Qiagen QIAquick PCR Purification Kit (Cat. No. 28106) prior to sequencing.

Shotgun Sequencing of Long PCR Products

The purified long PCR products were sheared using the HydroShear from GeneMachines. The sheared DNA was then blunt-end repaired and visualized on a 1% agarose gel stained with ethidium bromide. Gel fragments of the correct size (~250bp) were excised and purified from the gel. The repaired DNA fragments were then ligated into the pmcl vector plasmid and transformed into competent *Escherichia coli* cells by electroporation. The cells were then blue/white screened on agar plates and 96 white colonies were picked to form each clone library. A random selection of the library was then amplified by PCR to ensure the DNA insert was present. The libraries were sequenced at the Joint Genome Institute (JGI), Walnut Creek, California, in the context

of a Genomics course taught by Dr. Mónica Medina, in collaboration between the University of California at Merced and the JGI.

Short (Pulmonate-specific) PCR Amplification

Only one genome was sequenced in its entirety using only long PCR and shotgun sequencing (*Trimusculus reticulatus*; see Table 3). For six other genomes, long PCR and shotgun sequencing yielded partial genomes with gaps of various sizes that needed to be closed. A set of 94 pulmonate-specific primers were designed (Table 4) to close those gaps in the six partial mitochondrial genomes obtained through shotgun sequencing. Multiple combinations of pulmonate-specific primers were used to amplify gaps in partial genomes obtained from shotgun sequencing. Those combinations were also used to amplify genomes of species without going through shotgun sequencing (see, Table 3). In some cases, depending on the strand used for transcription, a combination of two forward primers (e.g. *Nad4*-879F and *Cox3*-164F) or two reverse primers (e.g. *Nad3*-128R and *Nad4*-642R) had to be used. For some individuals (e.g. *Salinator rhamphidia* and *Rhopalocaulis grandidieri*), the long PCR product was used as the template for amplification instead of the genomic DNA (for increasing chances of successful amplification). For those PCRs targeting gaps of ~900 bp or greater, the long PCR reaction and thermoprofile was used (see above). Short PCR reactions (see above) were used for gaps less than 900 bp with the following thermoprofile: two minutes at 94°C; 5 cycles of 40 seconds at 94°C, 45 seconds at 45°C, and 1 minute at 72°C; 30 cycles of 40 seconds at 94°C, 40 seconds at 55°C, and 1 minute at 72°C; and 3 minutes at 72°C. PCR products were cleaned with either the Qiagen QIAquick PCR Purification Kit or ExoSAP (2 μl of 1u/μl Shrimp Alkaline Phophatase, 0.1 μl of 20u/μl Exonuclease I, and 6 μl of water per 4 μl of PCR product) and sent for sequencing. Some PCR products proved difficult to sequence directly (typically longer PCR products) and were cloned using the Promega pGEM-T Easy Vector System II (Cat. No. A1380) then cleaned with the Promega Wizard Plus SV Minipreps DNA purification System (Cat. No. A1330) prior to sequencing.

Short (Individual-specific) PCR Amplification

For the gaps that remained in the mitochondrial genomes after using the pulmonate-specific primers and shotgun sequencing, individual-specific primers were designed and

the gaps were primer-walked until completion of the genome (Table 3). In some instances, a combination of a pulmonate-specific and an individual-specific primer was used in an attempt to close gaps. PCR conditions for the individual-specific primers were identical to those used for the pulmonate-specific primers.

Genome Assembly and Annotation

The shotgun sequence chromatograms produced by the JGI were read, bases were called, and a value was assigned to the quality of the called bases by the Phred program [Ewing et al. 1998]. The individual sequences were assembled into contigs using Phrap (www.phrap.org). The contigs created by Phrap were analyzed and assembled to form longer, more complete contigs using Consed [Gordon 2004]. Contig sequences from the shotgun sequencing were saved in MacVector with Assembler 9.5.2 (www.macvector.com). All other sequences (i.e. all sequences, except for those obtained through sequencing at the JGI; see Table 3) were assembled in Mac Vector.

Open reading frames (ORFs) of the assembled contigs were analyzed by MacVector and the tentative identity of each protein-coding gene was determined based on the map of the mitochondrial genome of *Aplysia dactylomela*. Each gene was added to its corresponding Se-Al v2.0a11 (evolve.zoo.ox.ac.uk) file containing the alignment of multiple homologous gastropods sequences and the gene was demarcated on the genome based on the results of the alignment. The limits of both the protein-coding and rRNA genes were adjusted manually based on location of adjacent genes. All tRNA genes were located by hand based on the anticodon and the fairly conserved anticodon stem and loop sequence.

Phylogenetic Analyses

The 13 protein-coding gene sequences were first translated into amino acid sequences and then individually aligned using the default parameters of ClustalW (1.6) in MEGA version 4.1 (Beta) [Tamura et al. 2007]. Each alignment was cropped to remove variation on either end and then sequences were concatenated. The concatenated protein-coding genes alignment (3,458 amino acids) was adjusted manually and a minimal number of sites were then removed (gaps created by insertions in the sequences of the caenogastropod outgroups). Three caenogastropod species were

used as outgroups: *Cymatium parthenopeum*, *Ilyanassa obsoleta*, and *Lophiotoma cerithiformis* (Table 1).

Because genes of animal mitochondrial genomes are fast evolving [Dawid 1972, Brown et al. 1979, Attardi 1985], phylogenetic analyses based on amino acid sequences are commonly preferred to analyses based on nucleotide sequences [Grande et al. 2008; Song et al., 2010; Medina et al. 2011]. Also, it has been shown that individual genes provide less topological resolution than concatenated genes [Cunha et al. 2010].

The amino acid substitution model was determined to be MTRev+I+G using the Akaike Information Criterion (AIC) in Topali version 2.5 [Milne et al. 2004]. The same model was obtained whether each gene was treated independently or all genes were concatenated. Maximum likelihood analysis of the amino acid was run using PhyML in Topali with bootstrap support values based on 1000 replicates. Bayesian Metropolis-coupled Markov chain Monte Carlo (MCMC) analysis was performed on the amino acid sequences, but ran locally using MrBayes in the Topali interface (two parallel analyses, 100 million generations, sampled every 100 generations, 25% burn-in).

Authors' Contributions

TW participated in the molecular work and genome annotation, performed phylogenetic reconstructions, and wrote a first draft of the manuscript. MC and SB participated in the molecular work and RT in the genome annotation. RG, SG, and AFM provided fresh samples and commented on the manuscript. RT and SB participated in the research while undergraduates at the University of California at Merced. BD designed and developed the entire project.

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course (BIO 142) taught by Dr. Mónica Medina in Spring 2007 and Spring 2008. Bioinformatics analyses (assembly and annotation) were initiated by undergraduate and graduate students in the context of that course. Jennifer Kuehl provided technical expertise with the libraries at the JGI.

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Table 1

List of the species included in the present study. Locality data and museum catalogue numbers of vouchers are indicated for the genomes newly sequenced here. Abbreviations for museum collections holding the vouchers are: California Academy of Sciences, San Francisco, United States of America (CASIZ); Natal Museum, Pietermaritzburg, South Africa (NM); Florida Museum of Natural History, University of Florida, Gainesville, Florida, United States of America (UF). An asterisk (*) next to a Genbank accession number indicates the 10 complete genome sequenced for the present study.

Classification	Species Name	Locality	Voucher	Genbank
Caenogastropoda	*Cymatium parthenopeum*	-	-	EU827200
Caenogastropoda	*Ilyanassa obsoleta*	-	-	DQ238598
Caenogastropoda	*Lophiotoma cerithiformis*	-	-	DQ284754
Basal Heterobranchia	*Pyramidella dolabrata*	-	-	AY345054
Pulmonata, Amphibolidae	*Salinator rhamphidia*	Australia, NSW	CASIZ 180470	*
Pulmonata, Ellobiidae	*Auriculinella bidentata*	Azores	To be deposited	*
Pulmonata, Ellobiidae	*Myosotella myosotis*	Azores	To be deposited	*
Pulmonata, Ellobiidae	*Myosotella myosotis*	-	-	AY345053
Pulmonata, Ellobiidae	*Ovatella vulcani*	Azores	CASIZ 180486	*
Pulmonata, Ellobiidae	*Pedipes pedipes*	Azores	CASIZ 180476	*
Pulmonata, Hygrophila	*Biomphalaria glabrata*	-	-	AY380531
Pulmonata, Onchidiidae	*Onchidella borealis*	-	-	DQ991936
Pulmonata, Onchidiidae	*Onchidella celtica*	-	-	AY345048
Pulmonata, Onchidiidae	*Peronia peronii*	Guam	CASIZ 180486	*
Pulmonata, Siphonariidae	*Siphonaria gigas*	Panama	UF 359645	*
Pulmonata, Siphonariidae	*Siphonaria pectinata*	-	-	AY345049
Pulmonata, Stylommatophora	*Albinaria coerulea*	-	-	X83390
Pulmonata, Stylommatophora	*Succinea putris*	France	CASIZ 180491	*
Pulmonata Trimusculidae	*Trimusculus reticulatus*	California	CASIZ 177988	*
Pulmonata, Veronicellidae	*Rhopalocaulis grandidieri*	Madagascar	NM L7086	*
Opisthobranchia, Anaspidea	*Aplysia californica*	-	-	AY569552
Opisthobranchia, Cephalaspidea	*Hydatina physis*	-	-	DQ991932
Opisthobranchia, Cephalaspidea	*Pupa strigosa*	-	-	AB028237
Opisthobranchia, Notaspidea	*Berthellina ilisima*	-	-	DQ991929
Opisthobranchia, Nudibranchia	*Chromodoris magnifica*	-	-	DQ991931
Opisthobranchia, Sacoglossa	*Ascobulla fragilis*	-	-	AY345022

Table 2

Structural features of the 10 new mitochondrial genomes. The size of each genome and the POR are in bp. Start and stop codons for protein-coding genes are indicated in parentheses.

	Auriculinella bidentata	*Myosotella myosotis*	*Ovatella vulcani*	*Pedipes pedipes*	*Peronia peronii*	*Salinator rhamphidia*	*Succinea putris*	*Rhopalocaulis grandidieri*	*Trimusculus reticulatus*	*Siphonaria gigas*
Total size	14,135	14,215	14,274	16,708	13,968	14,007	14,092	14,523	14,044	14,518
%A	25.8	25.2	25.0	28.6	27.1	26.7	33.8	29.3	26.4	24.3
%T	30.9	32.5	29.7	33.7	37.3	35.6	42.9	33.9	34.7	37.2
%C	20.4	20.3	21.6	18.4	15.4	16.9	10.8	19.7	18.2	15.1
%G	22.6	22.0	23.7	19.3	20.3	20.8	12.1	17.1	20.6	23.4
%A+T	56.7	57.7	54.7	62.3	64.4	62.3	76.7	63.2	61.1	61.5
POR	44	46	44	? (397)	54	44	47	42	47	72
rrnL	1,037	1,041	1,057	1,138	1,033	1,025	1,020	1,006	1,057	1,109
rrnS	704	714	711	786	714	714	755	716	719	755
cob	1,111 (TTG/T)	1,110 (TTG/TAG)	1,110 (TTG/TAA)	1,108 (TTG/T)	1,108 (TTG/T)	1,111 (TTG/T)	1,107 (TTG/TAG)	1,068 (TTG/TAG)	1,110 (TTG/TAA)	1,125 (TTG/TAA)
cox1	1,533 (TTG/TAA)	1,527 (ATG/TAA)	1,533 (TTG/TAA)	1,527 (TTG/TAA)	1,525 (TTG/T)	1,527 (TTG/TAA)	1,548 (TTG/TAG)	1,527 (TTG/TAA)	1,527 (TTG/TAG)	1,530 (GTG/TAG)
cox2	687 (TTG/TAG)	669 (GTG/TAA)	666 (TTG/TAG)	681 (GTG/TAA)	666 (TTG/TAA)	664 (GTG/T)	649 (ATG/T)	634 (TTG/T)	666 (TTG/TAA)	672 (GTG/TAA)
cox3	778 (ATG/T)	780 (ATG/TAG)	778 (ATG/T)	780 (GTG/TAG)	804 (ATG/T)	781 (ATG/T)	783 (ATG/TAG)	772 (ATG/T)	778 (ATG/T)	810 (ATG/TAA)
nad1	906 (GTG/TAA)	906 (TTG/TAG)	906 (TTG/TAA)	903 (ATG/TAG)	906 (TTG/TAA)	958 (TTG/T)	916 (TTG/T)	919 (TTG/T)	906 (TTG/TAA)	903 (TTG/TAA)
nad2	945 (ATG/TAG)	948 (ATG/TAG)	942 (CTG/T)	927 (ATG/TAA)	939 (GTG/TAG)	925 (TTG/T)	975 (TTG/TAA)	915 (GTG/TAA)	916 (TTG/T)	942 (ATG/TAA)
nad3	354 (TTG/TAA)	349 (TTG/TAA)	354 (TTG/TAA)	372 (ATG/TAA)	327 (ATT/TAA)	349 (TTG/T)	352 (ATG/T)	351 (GTG/TAA)	357 (ATG/TAG)	361 (ATG/T)
nad4	1,311 (TTG/TAG)	1,305 (TTG/TAA)	1,308 (TTG/TAG)	1,302 (ATG/TAG)	1,318 (TTG/T)	1,311 (TTG/TAG)	1,326 (ATG/TAA)	1,308 (ATG/TAA)	1,306 (TTG/T)	1,324 (TTG/T)
nad4L	327 (TTA/TAG)	291 (TTG/TAA)	286 (TTG/T)	288 (GTG/TAG)	283 (ATG/T)	279 (TTG/TAG)	275 (ATA/TA)	274 (TTG/T)	286 (ATG/T)	294 (GTG/TAA)
nad5	1,665 (ATA/TAG)	1,689 (ATA/TAG)	1,671 (TTG/TAG)	1,701 (ATG/TAG)	1,671 (TTG/TAG)	1,671 (TTG/TAG)	1,680 (ATG/TAA)	1,662 (ATT/TAA)	1,680 (TTG/TAG)	1,674 (GTG/TAA)
nad6	483 (ATT/TAA)	477 (TTG/TAA)	480 (ATT/TAG)	462 (TTG/TAA)	468 (ATT/TAA)	474 (TTG/TAA)	453 (ATG/TAA)	450 (ATG/TAG)	456 (TTG/TAG)	489 (ATT/TAG)
atp6	643 (GTG/T)	645 (ATG/TAG)	645 (GTG/TAG)	642 (ATG/TAG)	642 (TTG/TAA)	643 (ATG/T)	657 (ATG/TAA)	618 (ATG/TAA)	643 (ATG/T)	657 (ATG/TAA)
atp8	157 (GTG/T)	153 (ATG/TAG)	159 (ATG/TAG)	153 (ATG/TAA)	153 (ATG/TAA)	151 (ATG/T)	123 (TTG/TAA)	151 (GTG/T)	186 (ATG/TAG)	162 (ATG/TAA)

Table 3

Approaches used to obtain the 10 new mitochondrial genomes in the present study. The star (*) indicates individuals in which the long PCR product was used as the template for the majority of PCR reactions using pulmonate-specific and individual-specific primers.

Species	JGI Shotgun Sequencing	Pulmonate-Specific Primers	Individual-Specific Primers
Auriculinella bidentata	*cox3* to *nad1* (6,735bp), *cob* to *cox3* (6,012bp)		*nad1* to *cob* (1,803bp), *nad4* to *nad2* (1,274bp)
Myosotella myosotis	*trnM* to *trnN* (13,249bp)		*trnN* to *trnM* (1,996bp)
Ovatella vulcani	*nad3* to *cox1* (4,372bp), *cox1* to *trnY* (7,041bp)	*cox1* to *rrnL* (1,618bp)	*cox2* to *nad3* (2,691bp)
Pedipes pedipes	*cox1* to *cob* (7,474bp), *rrnS* to *nad2* (6,102bp)		*nad2* to *cox1* (1,343bp), *cob* to *rrnS* (~3,000bp)
Peronia peronii	*cox1* to *cox2* (6,705bp)	Combination of pulmonate-specific and individual- specific primers (~7,300bp) from *cox2* to *cox1*	
*Rhopalocaulis grandidieri**		*nad2* to *rrnL* (~2,850), 16S to *nad6* (~900bp), *nad1* to *nad4L* (~860bp), *cob* (~600bp), *cob* to *cox2* (~750bp), *cox2* to *atp6* (~600bp), *atp6* to *rrnS* (~500bp), 12S to *nad3* (~980bp), *nad4* to *nad2* (~2500bp)	Remaining gaps
*Salinator rhamphidia**		Combination of pulmonate-specific and individual-specific primers for the entire genome	
Siphonaria gigas		*cox1* to *nad6* (~2,700bp), middle of *cob* (~500bp), *atp6* to *nad4* (~2,300bp), *cox3* to *nad2* (~650bp), *nad2* to *trnK* (~650bp)	Remaining gaps
Succinea putris	*cox3* to *trnH* (4,585bp), *cob* to *cox2* (1,197bp)	Combination of pulmonate-specific and individual-specific primers to fill remaining gaps (~8,300bp)	
Trimusculus reticulatus	Complete sequence		

Table 4

Pulmonate-specific primers designed for the present study. Those pulmonate-specific primers were designed: 1) by building alignments for the sequences of each individual gene (except for tRNAs) from the seven complete, pulmonate, mitochondrial genomes available prior to the present study (Figure 2, Table 1), and 2) by locating conserved regions. All primers were specifically designed for the present study, with the exception of ten of them: in *cox1*, F14 and R698 [Folmer et al. 1994]; in *rrnL*, F437 and R972 [Palumbi et al. 1991]; in *cob*, F384 and R827 [Boore and Brown 2000]; in *rrnS*, F302 and R695 [Palumbi et al. 1991]; in *cox3*, F174 and R713 [Boore and Brown 2000]. Primer sequences are in the 5' to 3' direction. The naming system for primers is based on their position in the alignment of each particular gene (after short loose ends were cropped). For example, in *cox1*, the F14 primer refers to a *cox1* forward primer whose 5' end is at the 14th position in the aligned pulmonate sequences of *cox1*; in the same gene, the R3 primer refers to a reverse primer whose 3' end is at the 3rd position in the aligned pulmonate sequences of *cox1*. In most cases, the same conserved region was used to design both forward and reverse primers, but not always (to avoid issues such as self priming). Because truly conserved regions are scarce in the mitochondrial genome, most primers are degenerate. For amplification, appropriate combinations must be used, depending on the direction of the transcription of each gene. Each gene is always coded on the same strand across pulmonates, at least from the known mitochondrial genome of pulmonates, except for a few tRNA genes that may be coded on the plus or minus strand depending on the species. As for ribosomal and protein-encoding genes: *rrnL*, *cob*, *cox1*, *cox2*, *nad1*, *nad2*, *nad4*, *nad4L*, *nad5*, and *nad6* are on the plus strand; *rrnS*, *atp6*, *atp8*, *cox3*, and *nad3* are on the minus strand (underlined in the present table). As a result, for amplification, a forward primer and a reverse primer must be combined if the two primers are selected from only one gene (e.g. *cox1*-F253 and *cox1*-R839) or from two genes transcribed in the same direction (e.g. *nad4*-879F and *nad2*-324R); but two forward primers (e.g. *nad4*-879F and *cox3*-164F) or two reverse primers (e.g. *nad3*-128R and *nad4*-642R) must be combined if selected from genes transcribed in opposite directions. In order to estimate the potential length of the PCR products, one should refer to the (quite conserved) pulmonate mitochondrial gene order (Figure 4).

Gene	Primer	Sequence	Gene	Primer	Sequence
cox1	R3	CCAATRTCTTTRTGRTTHGTNGARWADTCAHCGC	*cox2*	F55	GARATRHTNTNHTNTTYCAYGAYCA
	F14	WYTCNACDAAYCAYAAAGAYATTGG		R55	TGRTCRTGRAANADNANADYATYTC
	R167	AYAAANGCRTGDGCWGTMAC		F301	AYHGGNCAYCARTGRTAYTG
	F253	GGNGCNCCWGAYATRAGHTTYCC		R307	TCRTANSWYCARTAYCAYTGRTG
	R253	GGRAADCTYATRTCWGGNGCNCC		F407	TNYTWGARGTDGAYAAYCG
	F466	TTRGGDGCNATTAATTTTATYAC		F514	AARRTRGAYKCDGTNCCNCG
	R466	GTRATAAAATTAATNGCHCCYAA		R514	CGNGGNACHGMRTCYATTTT
	F698	TGRTTYTTYGGDCAYCCNGARGTHTAYAT		F580	TAYGGNCARTGYTCNGARAT
	R698	ATRTADACYTCNGGRTGHCCRAARAAYCA		R580	ATYTCNGARCAYTGNCCRTA
	R839	GTAAAYATRTGHGCYCANACAATAAAWCC	*atp6*	F453	CGDCCNYTDACHTTRRCNGTDCG
	F844	GGWTTTATTGTNTGRGCDCAYATRTTTAC		R453	CGHACNGYYAADGTHARNGGHCG
	R1052	TCYAAHGAWGARTTWGAHARNACAATWCC		F483	GCHAAYATWAGNGCNCAYRTT
	F1055	GGWATTGTNYTDTCWAAYTCWTCDTTRGA		R483	AAYRTGNGCNCTWATRTTDGC
	F1281	TAGGDYTDKCWGGHATRCCNCGNCG	*rrnS*	F143	GGTGCCAGCADYCGCGGYCAWACC
	R1281	CGNCGNGGYATDCCWGMHARHCCTA		R143	TWTGRCCGCGRHTGCTGGCACC
rrnL	F437	CRNCTGTTTANCAAAAACATAGYY		F302	AAACTRGGATTAGAKACCCYAYTAT
	R437	RRCTATGTTTTTGNTAAACAG		R302	ATARTRGGGTMTCTAATCCYAGTTT
	F515	GGCCGCAGTACMYTGACTGTGCDAAGGTAGC		F695	GTGYACAAATCGCCCGTCAYYCY
	R515	CACAGTCARKGTACTGCGGCC		R695	RGRRTGACGGGCGATTTGTRCAC
	F972	CCTACATGATCTGAGTTCAGACCGGCGYAAGCCAGGTCAG		F735	AAGTCGTAACAHAGTARRRGTA
	R972	CCGGTCTGAACTCAGATCATGT		R735	TACYYYTACTDTGTTACGACTT
nad6	R197	AHADWACHARNADNCCHCCAA	*nad3*	F1281	TTYGARTGYGGNTTYGANCCBHT
	F208	TTGGDGGNHTNYTDGTWHTDTTTMTTTAT		R1281	ADVGGNTCRAANCCRCAYTCRAA
nad5	F371	TWGGNTGRGAYGGNYTHGG	*nad4*	F401	TGRGGNTAYCARCCNGARCG
	R371	CCDARNCCRTCYCANCCTA		R401	CGYTCNGGYTGRTANCCYCA
	R394	ANNCCDARNCCRTCYCA		F642	CCNAARGCNCAYGTNGARGC
	F639	TGRYDCCNGCNGCHATRGC		R642	GCYTCNACRTGNGCYTTNGG
	R663	ARDGCNCTNACNGGNGTNGG		F879	GCHTAYTCNRTDRSNCAYAT
	R940	ADNGYTTRAAHADNGCRTG		R879	ATRTGNSYHAYNGARTADGC
nad1	R55	TCNWWHARNGTDWARAADGCNAC		F1097	TNAAYATRGCWGCNCCNCC
	F76b	GARCGNAAGRTNYTAGG		R1097	GGNGGNGCWGCYATRTT
	R76	CYHARNAYYTTNCGYTC	*cox3*	F25	GTNGARTWYAGHCCHTGRCCNHTWYT
	F419	GCBCARACWATYTCDTAYGA		R25	ARWADNGGYCADGGDCTRWAYTC
	R419	TCRTAHGARATWGTYTGVGC		F164	TGRTGRYGDGAYRTHRTHCGWGA
cob	F288	GGHCGNGGNNTRTAYTAYCA		R164	TCWCGDAYDAYRTCHCRYCAYCA
	R288	TGRTARTAYANNCCNCGDCC		F596	ACNGGNTTYCAYGGNNYNCAYGT
	F384	GGNTAYGTNYTDCCDTGRGGNCARAT		R596	ACRTGNRNNCCRTGRAANCCNGT
	R399	GCNCCYCARWADGAYATYTGNCCCYCA		F713	TGRTAYTGRCAYTTYGTHGAYGT
	F809	CARCCNGARTGRTAYTTYYTNTTYGCNTAYGC		R713	ACRTCDACRAARTGYCARTAYCA
	R809	GCRTANGCRAANARRAARTAYCAYTCNGG	*nad2*	F324	TTYCCNKGBCAYTTYTGRGT
	R806	TANGCRAANARRAARTAYCAYTCNGGYTG		R324	ACYCARAARTGVCMNGGRAA
	R827	GGAATNGMHCGNARRAYDGCRTANGCRAA		F718	GGNHTNCCHCCHTTYHTHMTVTT
				R718	AABAKDADRAADGGDGG

Figure 1

Phylogenetic relationships of pulmonates. On the left, relationships obtained in the present study based on complete mitochondrial genomes, including 17 genomes of pulmonates. On the right, relationships obtained in a recent study based on individual genes (18S, 16S, COI), including 79 pulmonate species [Dayrat et al. 2011]; on the right, the asterisk (*) indicates that the clade Ellobiidae includes three taxa that have not been traditionally regarded as ellobiids (*Otina*, *Smeagol*, and *Trimusculus*). Node support values are cited using the following format: "1.00/77" means that BI posterior probability = 1.00, and that ML bootstrap value = 77%. Only BI posterior probabilities > 0.75 and ML bootstrap values > 50% are shown.
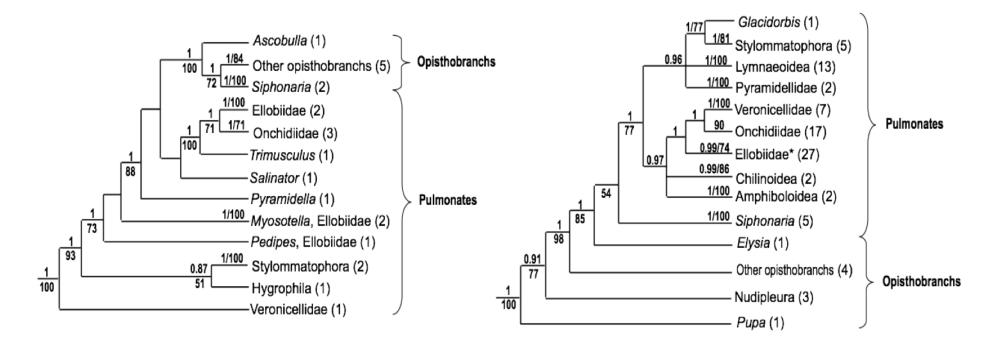
Figure 2

List of complete gastropod mitochondrial genomes available at present. The reference in which each genome was made available is indicated in brackets as well as the year of publication. The hypothesis of phylogenetic relationships is based on both morphological and molecular data [Atkipis et al. 2008].

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Figure 3

Phylogenetic relationships within euthyneurans (pulmonates and opisthobranchs). Topology obtained from the ML and BI analyses, based on the concatenated amino acid sequences of the 13 protein-coding genes. Opisthobranchs are indicated in green and pulmonates in blue. Node support values are cited using the following format: ''100/1'' means that ML bootstrap value = 100%, and that BI posterior probability = 1.00.
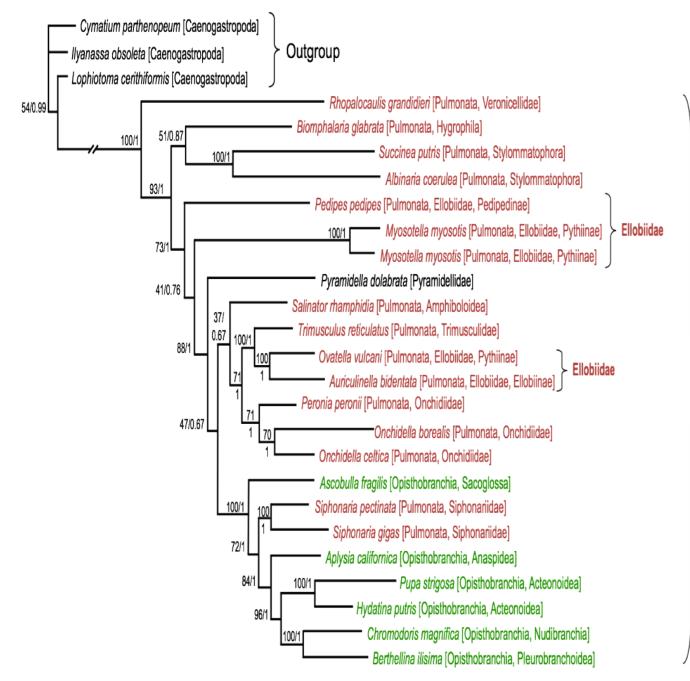
Figure 4

Hypothesized gene rearrangements of the genomes included in the present study. The phylogenetic topology is from the present study. Genes encoded by the minus strand are underlined.

CHAPTER 2: Taxonomic Review of *Siphonaria*

Diversity of the false limpets *Siphonaria* (Mollusca: Gastropoda: Pulmonata): Checklists of genus- and species-group names

Abstract

Not since Hubendick's 1946 monograph of the Patelliformia has a comprehensive taxonomic work been completed on the genus of false-limpets, *Siphonaria*, distributed worldwide, except from the northern Atlantic. The present contribution is the first step towards a revision of this group. A checklist of all published species-group names and details regarding each species description (i.e. type locality, complete reference citation, etc.) is provided. Additionally, a checklist of supra-specific names associated with *Siphonaria* is established. The nomenclatural status of taxon names is discussed (whether names are available, unavailable, permanently invalid, or potentially valid). The secondary literature is reviewed to assess the current taxonomic status of the names (whether they are valid, synonymous, or of doubtful application). Of the 269 species-group names included in the checklist, 204 are available and not permanently invalid. All other names are either not available (e.g. incorrect subsequent spellings) or available but permanently invalid (e.g. primary homonymy). Of those 204 names that are available and not permanently invalid: 44 specific and 10 subspecific names are considered valid by all authors; 17 specific and 1 subspecific names are regarded as synonyms by authors in the secondary literature; 96 specific and 5 subspecific names are regarded as valid or synonymous; and 9 specific names are considered valid, synonymous, or of doubtful application (*nomina dubia*). The status of the majority of the species-group names is uncertain, hence the important need for a revision. The geographic distribution of the type localities is also briefly presented; of the 204 species-group names that are available and not permanently invalid, 61 are from the tropical and subtropical Indo-West Pacific, which, as of today, is the biogeographic province with the highest richness of species of *Siphonaria*.

Key words: Alpha taxonomy, biodiversity, nomenclature, systematic revision

Introduction

Snails and slugs with a pulmonary cavity have traditionally been referred to as pulmonate gastropods. The species richness of Pulmonata is largely dominated by the land snails and slugs, or Stylommatophora, which include at least 25,000 species. However, Pulmonata also includes about ten other higher taxa which are much less speciose but constitute most of the phylogenetic, morphological, and ecological diversity of the pulmonates, such as the Otinidae (a single species of a tiny, marine limpet), the Veronicellidae (about 200 species of terrestrial, tropical slugs), the Hygrophila (about 1,000 species of freshwater snails), and, the focus of the present contribution, the Siphonariidae, more specifically the genus *Siphonaria*.

Siphonaria are marine limpets that live on rocky, intertidal shores. Where present, they are typically numerous (Vermeij 1973; Hubendick 1946, 1978; Hodgson 1999). They are often called false limpets, to distinguish them from the Patellogastropoda, or true limpets, one of the most basal branches of the gastropod tree. Shells of true and false limpets may seem difficult to separate but they actually differ in several ways. In particular, the pulmonary cavity of *Siphonaria* opens through a siphon located on the right side, often marked externally by a lateral siphonal expansion and marked internally by a gap in the right arm of the horse-shoe muscle scar. The dorsal lining of the pulmonary cavity is folded into a series of triangular, branchial leaflets (Yonge 1952; Hyman 1967; Dayrat and Tillier 2003). Because *Siphonaria* was regarded as a pulmonate, most authors assumed that its gill was a secondary structure acquired through convergence (e.g. Hubendick 1946, 1978). However, recent molecular data suggest that *Siphonaria* might actually be nested within opisthobranchs instead of pulmonates (Grande et al. 2008) or be the most basal lineage of pulmonates (Klussmann-Kolb et al. 2008), supporting the opposite idea that its gill could actually be homologous to the gill found in cephalaspideans (Pelseneer 1894; Plate 1894; Dayrat and Tillier 2003). In any case, the combination of a gill and a pulmonary cavity enables *Siphonaria* to respire both in and out of water (Hodgson 1999).

Siphonaria is distributed worldwide, although it is absent from the northern Atlantic, with the richest diversity in the tropical Indo-West Pacific. Some species have a broad distribution, such as *Siphonaria pectinata* that inhabits the Mediterranean and the

eastern and western Atlantic. Others have a more restricted distribution, such as *Siphonaria compressa*, an endangered South African species known from only two localities (Allanson and Herbert 2005). All species graze on algae. The development of most species is planktotrophic and occasionally direct. However, the developmental mode is known only for a few species (Chambers and McQuaid 1994b; Hodgson 1999).

Due to the abundance of easily-accessible specimens, some species of *Siphonaria* have been used as models in various kinds of studies: reproduction and development (e.g. Knox 1955; Creese 1980; Ocaña and Emson 1999), physiology and histology (e.g. Pal 2007; Pinchuck and Hodgson 2009; Wilson et al. 2009), intertidal ecology (e.g. Craig et al. 1969; Bastida et al. 1971; Bazterrica et al. 2007; Blockley and Chapman 2008; Russell and Phillips 2009), pharmacology (e.g. Paul et al. 1997; Beukes and Davies-Coleman 1999; Brecknell et al. 2000; Beye and Ward 2010), and environmental pollution (e.g. Tablado and Gappa 2001; Espinosa et al. 2007).

However, the species diversity of *Siphonaria* is still problematic. According to Hubendick's (1946) revision, there are approximately 70 valid species of *Siphonaria*. However, Hubendick's method for species delineation was mainly based on shell morphology, which is highly plastic because it may depend upon age, thermal stress, competition, diet, wave action intensity, predation, or even habitat (Vermeij 1973; Teske et al. 2007; Harley et al. 2009). A few genetic studies have been published, but targeting only a few, localized species (Black and Johnson 1981; Johnson and Black 1984; Chambers et al. 1996; Chambers et al. 1998; Teske et al. 2007; Wood and Gardner 2007). After Hubendick's (1946) monograph, only a small number of authors in South Africa (Allanson 1958; Chambers and McQuaid 1994a; Chambers et al. 1996; Chambers et al. 1998; Teske et al. 2007) and Australia (Jenkins 1981, 1983, 1984) have undertaken local taxonomic revisions. Without any doubt, a comprehensive taxonomic revision of *Siphonaria* is needed, integrating morphological and molecular approaches. The goal of the present paper is to provide a complete checklist of all genus- and species-group names available in *Siphonaria*, as a rigorous starting point towards a systematic revision of this taxon.

Supra-generic Classification and Names

There are three genera of marine limpet-like pulmonates: *Siphonaria*, *Williamia*, and *Trimusculus* (formerly *Gadinia*). According to Hubendick (1946), *Siphonaria* is by far the most speciose taxon with approximately 70 valid species, while *Williamia* and *Trimusculus* include less than 10 valid species. *Trimusculus* has a rounded shell, easily distinguishable from the oval shell of *Siphonaria*. Their ecology also differs: *Trimusculus* lives in small crevices, very low in the intertidal zone, and in small populations, whereas *Siphonaria* tends to be on exposed rocks, higher in the intertidal zone, and in large populations. While the shells of *Siphonaria* and *Williamia* may look more similar, *Williamia* is typically sublittoral. The three genera also differ anatomically (Hubendick 1946; Ruthensteiner 2006).

Currently, *Siphonaria* and *Williamia* are included in the family Siphonariidae and *Trimusculus* in the family Trimusculidae. The fact that *Siphonaria* and *Williamia* belong to the same taxon is not supported by phylogenetic data (whether morphological or molecular), but is not challenged here. The tempting idea that all limpet-like pulmonates should be classified together has found many supporters (Gray 1827; Gill 1871; Fischer 1883; Thiele 1921; Hubendick 1946; Van Mol 1967; Harbeck 1996). Many other possible affinities have been proposed, some of which are mentioned here: Tillier (1984) proposed that Siphonariidae and Trimusculidae be removed from the Basommatophora and placed with the Amphibolidae into the superfamily Amphiboloidea, leaving only the freshwater pulmonates in the Basommatophora; based on the organization of the central nervous system, Haszprunar and Huber (1990) placed Trimusculidae into the order Eupulmonata with the Ellobiidae and Stylommatophora, leaving the Basommatophora to contain the Siphonariidae, Amphibolidae, and freshwater pulmonates; Nordsieck (1992) also classified Trimusculidae within Eupulmonata, but lumped Siphonariidae and Amphibolidae into the Thalassophila. Recent molecular studies suggest that *Siphonaria* and *Trimusculus* represent two lineages that are not closely related: *Siphonaria* being the basal with respect to all other pulmonates and *Trimusculus* being nested within the crown clade of Eupulmonata (Klussmann-Kolb et al. 2008). Complete mitochondrial genomes even support the idea that *Siphonaria* is nested within opisthobranchs (Grande et al. 2008).

Listed below are the supra-generic names associated with *Siphonaria* (Bouchet and Rocroi 2005):

Archaeopulmonata Morton, 1955: 163. — Order of Basommatophora created to include the families Ellobiidae, Otinidae, Chilinidae, Latiidae, Amphibolidae, Gadiniidae, and Siphonariidae.

Divasibranchia Minichev and Starobogatov, 1975: 10. — Created as a subclass for the order Siphonariida being monotypic with only the family Siphonariidae. Later, Starobogatov (1976: 16) noted that the order Siphonariida contained two superfamilies, Rhytidophiloidea and Siphonarioidea, the latter of which included the families Anisomyonidae, Siphonacmaeidae, and Siphonariidae.

Fissuracea Reeve, 1842: 17. — Family in the order Cervicobranchiata created to contain *Lottia*, *Siphonaria*, *Parmophorus*, *Emarginula*, and *Fissurella*.

Inoperculata Fischer, 1883: 512. — A division of the basommatophoran suborder Thalassophila including the families Siphonariidae and Gadiniidae.

Liriolidae Golikov and Kusakin, 1978: 220. — Family created for the genus *Liriola* in the order Siphonariida.

Patelliformia Thiele, 1921: 147. — "Sippe Patelliformia" created by Thiele for the families Siphonariiden and Gadiniiden. Kuroda (1934: 324) considered Patelliformia a superfamily.

Petrophila Gill, 1871: 14. — Taxon at a level between suborder Basommatophora and family; created for the families Siphonariidae and Gadiniidae. Treated as a superfamily by Grant and Gale (1931: 462).

Pleurobranchia Deshayes, 1832: table between pp. 552–553. — "Les Pleurobranches" is the original spelling. Created as a suborder for the genera *Umbrella*, *Siphonaria*, *Pleurobranchus*, and *Pleurobranchaea*.

Siphonariacea Van Mol, 1967: 11. — Created as a suborder of Basommatophora for the families Trimusculidae and Siphonariidae. Minichev and Starobogatov (1975: 10) changed the spelling to Siphonariida and raised it to the rank of order. Golikov and Starobogatov (1989: 67) created the new subclass Siphonariiones that included the superorder Siphonariiformii and order Siphonariiformes. Nordsieck (1992: 48) changed the spelling to Siphonarioidei.

Siphonariidae Gray, 1827: plate Mollusca IV. — Siphonariadæ is Gray's original spelling. Family in the order Tectibranchia created to include the genera *Siphonaria* and

Gadinia. Wenz (1938: 67) referred to this family as Siphonariacea. Harbeck (1996: 19, 28) considered Siphonariidae to contain Trimusculinae (Gadiniinae) and Siphonariinae.

Steganobranchia von Ihering, 1876: 146. — Order in the class Ichnopoda containing the families Runcinidae, Siphonariidae, Pleurobranchidae, Aplysiidae, Philinidae, Bullidae, Cylichnidae, Aplustridae, and Actaeonidae.

Thalassophila Gray, 1850: 119. — Taxon name of undefined rank in the order Pneumobranchiata created to include the families Siphonariadæ and Amphibolidæ. Adams and Adams (1855: 102) treated Thalassophila as a suborder under the order Inoperculata.

Supra-specific Classification and Checklist of Genus-group Names

Since Hubendick's (1946) Monograph of Patellifornia, most authors have agreed that only one genus name should be used for all known species of *Siphonaria*. However, a total of 26 genus-group names exist in the literature for species that are now regarded as *Siphonaria* species. For instance, Iredale (1940) classified *Siphonaria* species into 11 distinct genera. Hubendick (1945b, 1946) recognized two subgenera (Table 1): *Liriola*, which includes species generally from the eastern Atlantic, the Americas, and around the southern polar region, and *Siphonaria*, with species mainly from the Indo-West Pacific. Hubendick (1946) also recognized five sectia in each subgenus (Table 1), some of which were originally created as generic names.

Listed below are the 26 genus-group names used for *Siphonaria* species:

***Benhamina* Finlay, 1927**: 442. — Type species by original designation, *Benhamina obliquata* Sowerby, 1825. Ranked as a genus by Powell (1939: 217; 1946: 91; 1955: 120; 1979: 293, pl. 54, figs. 12–13), Borland (1950: 385–393), Morton and Miller (1968: 302, 336, 338, 354, 378, figs. 121–122, pl. 19, fig. 10), and Morley (2004: 130), but treated as a sectio of the subgenus *Lioriola* by Hubendick (1945b: 60, 66; 1946: 9, 11, 18, 24–26, 64).

***Ductosiphonaria* Hubendick, 1945b**: 61. — Type species by original designation, *Siphonaria bifurcata* Reeve, 1856. Regarded as a sectio of the subgenus *Siphonaria* by Hubendick (1945b: 61, 70; 1946: 13, 31, 36–39), a valid generic

name by McAlpine (1952: 42), and a synonym of the sectio *Siphonaria* by Hubendick (1955: 129–132).

***Ellsiphon* Iredale, 1940**: 437, 438. — Type species by monotypy, *Ellsiphon marza* Iredale, 1940. Created originally as a generic name, regarded as a synonym of the genus *Siphonaria* by Hubendick (1946: 18), and as a valid generic name by McAlpine (1952: 40, 42).

***Hebesiphon* Iredale, 1940**: 437, 441. — Type species by monotypy, *Hebesiphon monticulus* Iredale, 1940. Created originally as a generic name, regarded as a synonym of the genus *Siphonaria* by Hubendick (1946: 18), and as a valid section name by Morrison (1972: 60–61).

***Heterosiphonaria* Hubendick, 1945b**: 61. — Type species by original designation, *Siphonaria gigas* Sowerby, 1825. Hubendick (1945b: 61, 70, 72; 1946: 13, 15, 39–41, 65, 66; 1955: 131) and Morrison (1963: 8) regarded *Heterosiphonaria* as a valid sectio of the subgenus *Siphonaria*.

***Hubendickula* McAlpine, 1952**: 42. — Type species by original designation, *Hubendickula diemenensis* Quoy and Gaimard, 1833. Created originally as a generic name, but ranked as a sectio of the subgenus *Siphonaria* by Hubendick (1955: 131–132).

***Hubendicula*.** — Incorrect subsequent spelling (Hubendick 1955: 131–132) of *Hubendickula*.

***Kerguelenella* Powell, 1946**: 91. — Type species by original designation, *Kerguelenella redimiculum* Quoy and Gaimard, 1833. Created as a new replacement name for *Kerguelenia*. Powell (1955: 120–122; 1979: 293–294), Dell (1964: 290–292), and Forcelli (2000: 132) regarded it as a valid generic name.

***Kerguelenia* Rochebrune and Mabille, 1889**: 27–28. — Type species by subsequent designation (Hubendick, 1945b: 60), *Siphonaria lateralis* Couthouy *in* Gould, 1848. Regarded as a valid generic name by Odhner (1924: 55), as a section of the subgenus *Liriola* by Hubendick (1945b: 60, 66–67, 70; 1946: 9, 11–12, 18, 19, 24, 26–30, 35), and as a subgenus of *Siphonaria* by Abbott (1974: 335).

***Legosiphon* Iredale, 1940**: 437, 440. — Type species by original designation, *Legosiphon optivus* Iredale, 1940. Created originally as a generic name, but regarded as a synonym of the genus *Siphonaria* by Hubendick (1946: 18).

***Liria* Gray, 1824**: 275. — No type species designated. Gray was going to create *Liria* for *Siphonaria* species, but Sowerby published the name *Siphonaria* before Gray published his findings.

***Liphonaria*.** — Incorrect subsequent spelling (Brazier, 1878: 135) of *Siphonaria* Sowerby, 1823.

***Liriola* Dall, 1870**: 32. — Type species by original designation, *Siphonaria thersites* Carpenter, 1864a. Dall created this name as one of two sections in the genus *Siphonaria*, the other section being *Siphonaria*. Several authors have treated *Liriola* as a subgenus of *Siphonaria* (e.g. Suter 1913: 601; Hubendick 1945b: 60; Hubendick 1946: 8–9, 18, 19; Morrison 1963: 7; Abbott 1974: 335). Hubendick (1945b: 60, 64; 1946: 8, 9, 19–20, 35) and Morrison (1963: 7) ranked *Liriola* as a sectio of the subgenus *Liriola*. Fischer and Crosse (1900: 108) regarded it as a valid generic name.

***Mallorisiphon* Iredale, 1940**: 437, 440. — Type species by monotypy, *Mallorisiphon oppositus* Iredale, 1940. Created originally as a generic name, but regarded as a synonym of the genus *Siphonaria* by Hubendick (1946: 18).

***Mestosiphon* Iredale, 1940**: 437, 439. — Type species by original designation, *Mestosiphon eumelas* Iredale, 1940. Created originally as a generic name, but regarded as a synonym of the genus *Siphonaria* by Hubendick (1946: 18), and as a sectio of the subgenus *Siphonaria* by Morrison (1972: 54, 56).

***Mouretus* Blainville, 1824b**: 161–162. — Type species by original designation, *Mouretus adansonii* Blainville, 1824b. Created originally as a generic name, regarded as a synonym of the genus *Siphonaria* by Hubendick (1946: 18) and as a valid subgeneric name by Iredale (1921: 207) and Morrison (1963: 8; 1972: 52–53).

***Pachysiphonaria* Hubendick, 1945b**: 60. — Type species by original designation, *Siphonaria lessonii* Blainville, 1827. Hubendick (1945b: 60, 64, 66; 1946: 9–11, 19, 20–24, 25–26, 30, 35, 65) considered *Pachysiphonaria* to be a sectio of the subgenus *Liriola*.

***Parellsiphon* Iredale, 1940**: 437, 438. — Type species by original designation, *Parellsiphon zanda* Iredale, 1940. Created originally as a generic name, but regarded as a synonym of the genus *Siphonaria* by Hubendick (1946: 18).

***Patellopsis* Nobre, 1886**: 32. — Type species by original designation, *Siphonaria algesirae* Quoy and Gaimard, 1833. Iredale (1921: 207) regarded it as a synonym of the

subgenus *Mouretus*, and Abbott (1974: 335) as a valid subgeneric name. Hubendick (1945b: 60, 70; 1946: 9, 12–13, 30–35) ranked it as a sectio of the subgenus *Liriola*.

Planesiphon Iredale, 1940: 437, 441. — Type species by subsequent designation (McAlpine, 1952: 42), *Planesiphon elegans* Iredale, 1940. Created originally as a generic name, but regarded as a synonym of *Siphonaria* by Hubendick (1946: 20) and later as a valid sectio by McAlpine (1952: 42) and Hubendick (1955: 131).

Pugillaria Iredale, 1924: 277. — Type species by original designation, *Pugillaria stowae* Verco, 1906. Created originally as a generic name, but regarded as a synonym of *Siphonaria* by Hubendick (1946: 20) and ranled as a section of the subgenus *Liriola* by Morrison (1963: 7–8).

Sacculosiphonaria Hubendick, 1945b: 61. — Type species by original designation, *Siphonaria japonica* (Donovan, 1834). Created by Hubendick (1945b: 61, 72; 1946: 13, 15, 41–44) as a sectio of the subgenus *Siphonaria*.

Simplisiphonaria Hubendick, 1945b: 61. — Type species by original designation, *Siphonaria cookiana* Suter, 1909a. Created by Hubendick (1945b: 61, 72; 1946: 13, 15, 41–44) as a sectio of the subgenus *Siphonaria*.

Siphonacmea Habe, 1958: 35. — Type species by original designation, *Acmaea oblongata* Yokoyama, 1926. Considered a valid generic name by Habe (1964: 144) and Toyohara et al. (2001: 27–35).

Siphonaria Sowerby, 1823: *Siphonaria* [unnumbered page]. — Type species by subsequent designation (Gray, 1847: 181), *Siphonaria sipho* Sowerby, 1823. Regarded as a valid name by all authors, although with different memberships depending on whether one genus (e.g. Hubendick 1946) or multiple (e.g. Iredale 1940) were accepted for *Siphonaria* species. All authors who recognized subgenera and sectia also accepted *Siphonaria* as a nominotypical subgeneric name and section name (e.g. Hubendick 1945b: 61; 1946: 8, 13, 35–60; Morrison 1963: 8; Jenkins, 1984: 113–123).

Talisiphon Iredale, 1940: 441–442. — Type species by original designation, *Talisiphon virgulata* Hedley, 1915. Created originally as a generic name. Hubendick (1946: 22) mentioned *Talisiphon tasmanicus* as a synonym of *Siphonaria tasmanica* but

did not mention *Talisiphon* as a synonym of the genus *Siphonaria*. Morrison (1963: 7) treated *Talisiphon* as a valid section of the subgenus *Liriola*.

***Torquisiphon* Iredale, 1940**: 437. — Type species by original designation, *Torquisiphon percea* Iredale, 1940. Created originally as a generic name, but regarded as a synonym of the genus *Siphonaria* by Hubendick (1946: 18) and as a synonym of the section name *Hebesiphon* by Morrison (1972: 60).

***Triellsiphon* Iredale, 1940**: 437, 439. — Type species by monotypy, *Triellsiphon acervus* Iredale, 1940. Created originally as a generic name, but regarded as a synonym of the genus *Siphonaria* by Hubendick (1946: 18).

Some species that do not belong to *Siphonaria* have been mistakenly originally described or temporarily placed in *Siphonaria*. Reciprocally, some species that belong to *Siphonaria* have been mistakenly described or temporarily placed in genera distinct from *Siphonaria*, such as *Trimusculus* (Pulmonata: Trimusculidae) and *Patella* (Patellogastropoda: Patellidae). However, the type species of these genera do not belong to *Siphonaria*, and the corresponding generic names are not synonyms of *Siphonaria*:

***Gadinia* Gray, 1824: 275**. — Generic name created for a western African species described by Adanson (1757) under a French name (Le Gadin) and then named by Gmelin (1791) as *Patella afra*. According to Hubendick (1946: 73), *Gadinia afra* (Gmelin, 1791), type species of *Gadinia* by monotypy, is a synonym of *Gadinia mammillaris* (Linné, 1758), the type species of *Trimusculus* Schmidt, 1818 (Pulmonata, Trimusculidae) by subsequent designation (Rehder, 1940: 68). Consequently, *Gadinia* is a synonym of *Trimusculus*. One species was originally described by mistake as a *Siphonaria*, but actually belongs to *Trimusculus*: *Siphonaria albida* Angas, 1878a. *Trimusculus mammillaris*, originally described as *Patella mammillaris* by Linné, was also temporarily placed by mistake in *Siphonaria* by Anton (1839) and Menke (1853). Finally, *Trimusculus peruvianus* (Sowerby, 1835) and *T. reticulatus* (Sowerby, 1835) were both placed in *Gadinia*, and, by mistake, in *Siphonaria* (see, below, the specific names *reticulata* and *peruviana*).

***Mouretia* Sowerby, 1835**: 6. — Created originally for three new species that, according to Hubendick (1946), belong to *Trimusculus*: *T. peruvianus* (Sowerby, 1835), *T. reticulatus* (Sowerby, 1835), and *T. stellatus* (Sowerby, 1835). *Mouretia* was

regarded as a synonym of *Gadinia* Gray, 1824 (which is a synonym of *Trimusculus*) by Gray (1840: 305). No type species was designated, originally or subsequently. *Siphonaria* was combined mistakenly with two specific names originally combined with *Mouretia* and that refer to taxa that do not belong to *Siphonaria*: *peruviana* Sowerby, 1835, and *reticulata* Sowerby, 1835.

Muretia. — Incorrect subsequent spelling (d'Orbigny 1846: 682) of *Mouretia* Sowerby, 1835.

***Nacella* Schumacher, 1817**: 56, 179. — Type species *Nacella mytiloides* Schumacher, 1817 (Patellogastropoda, Nacellidae). *Siphonaria* was combined mistakenly with three specific names originally combined with *Nacella* and that refer to taxa that belong to *Williamia* instead of *Siphonaria*: *peltoides* Carpenter, 1864c, *subspiralis* Carpenter, 1866, and *vernalis* Dall *in* Stearns, 1867b.

***Patella* Linné, 1758**: 780. — Type species *Patella vulgata* Linné, 1758 (Patellogastropoda, Patellidae). Fifteen *Siphonaria* species were originally described as *Patella* when all limpets, whether true or false, were all referred to as *Patella*: *alternata* Say, 1827; *deflexa* Helbling *in* Born, 1778; *grisea* Gmelin, 1791; *japonica* Donovan, 1824; *javanica* Lamarck, 1819; *laciniosa* Linné, 1758; *leucopleura* Gmelin, 1791; *lineata* Lamarck, 1819; *melanozonias* Gmelin, 1791; *melanoleuca* Gmelin, 1791; *pectinata* Linné, 1758; *serrata* Fischer, 1807; *stellata* Helbling, 1779; *striatula* Gmelin, 1791; and *tristensis* Leach *in* Sowerby, 1823. Another species, described as *Patella mammillaris* Linné, 1758, was mistakenly combined with *Siphonaria* because it actually belongs to *Trimusculus* (Pulmonata, Trimusculidae).

***Trimusculus* Schmidt, 1818**: 218. — Type species *Trimusculus mammillaris* (Linné, 1758), by subsequent designation (Rehder 1940: 68). *Trimusculus* (Pulmonata, Trimusculidae) is clearly distinct from *Siphonaria* (Pulmonata, Siphonariidae): *Siphonaria* was combined mistakenly with several specific names which refer to taxa that belong to *Trimusculus* (see above *Gadinia*).

***Williamia* Monterosato, 1884**: 150. — Type species *Williamia gussonii* (Costa, 1829). According to Hubendick (1946), *Williamia* belongs to Siphonariidae but differs from *Siphonaria*. This idea is not challenged here. Four specific names that refer to species that belong to *Williamia* were combined with *Siphonaria* by mistake: *gussonii* Costa, 1829; *peltoides* Carpenter, 1864c; *subspiralis* Carpenter, 1866; and, *vernalis* Dall *in* Stearns, 1867b.

Species-group Names

In his *Systematic Monograph of the Patellifornia*, Hubendick (1946) recorded 204 species-group names for *Siphonaria*. However, Hubendick (1946) did not provide any information (e.g. complete reference, type locality) for most of those names. The checklist of species-group names established here provides precise nomenclatural information for all of the *Siphonaria* species-group names that exist in the literature, including names that Hubendick missed or that were created after 1946. The present checklist contains 269 species-group names, of which 20 are subspecific names. Of all those names: 188 specific names and 16 subspecific names (*adjecans*, *albofasciata*, *comita*, *depressior*, *elatior*, *intermedia*, *kraussi*, *minor*, *nereis*, *nigra*, *opalescens*, *pallida*, *palmata*, *perplexa*, *tasmanica*, *turritus*) are available and not permanently invalid; 49 specific and 2 subspecific names are not available because they are incorrect subsequent spellings; 12 specific names are not available because they are *nomina nuda* (*anornata*, *crebidentata*, *crebricostata*, *gareensis*, *godeffroyi*, *laciniata*, *oblonga*, *rugosa*, *sedimaculina*, *stella*, *striatopunctata*, *subaquatilis*); 2 additional specific names are not available because some provisions for availability are not met (*aequilirata*, *mouret*); 10 primary homonyms are available but permanently invalid (*conica* Pallary, 1900; *costata* Hombron and Jacquinot, 1841; *depressa* Locard *in* Pallary, 1900; *intermedia* Davis, 1904; *lineolata* Krauss, 1848; *lineolata* d'Orbigny, 1841; *radiata* Adams and Reeve, 1848; *radiata* Sowerby, 1835; *sowerbyi* Adams and Adams, 1855; *stellata* de Roissy *in* Blainville, 1827); 4 names are unjustified emendations (*lecania*, *palpebra*, *redimicula*, *scutella*); finally, 8 specific names were combined with *Siphonaria* by mistake and are not currently classified in *Siphonaria* (*albida*, *gussonii*, *mammillaris*, *peltoides*, *peruviana*, *reticulata*, *subspiralis*, *vernalis*).

Checklist Format

The format used for each species-group name is as follows: specific (or subspecific) name, Author, year of publication: pagination, illustrations [species-group name as it appears in the original publication, if different from the current spelling], generic name combined with species-group name in the original description, type locality cited exactly as it appears in the original description [locality comments], name of the collector(s) of specimen(s) [collector comments].

Behind the horizontal bar (—) are remarks on the nomenclatural status (available, not available, permanently invalid) of the name. Whether a name is valid, synonymous, or of doubtful application (*nomen dubium*) is also discussed, based on all the secondary literature available for that given name. All original descriptions were checked by the authors. Because only one generic name is accepted here for *Siphonaria* species, species names are mentioned without a generic name, except in the rare cases in which it is necessary to avoid any confusion. Note that a comma separates author's name plus date when referring to the authority of a species-group name, but no comma is used for any other reference.

Checklist of *Siphonaria* Species-group Names

***acervus* Iredale, 1940**: 439, pl. xxxiv, figs. 22–23, *Triellsiphon*, Canala, New Caledonia, [leg. unknown]. — Regarded as valid as *Siphonaria acervus* by Hubendick (1945b: 29; 1946: 46, pl. 3, figs. 10–12) who recorded it from Mendanao near Billiton (Java Sea). Hubendick also thought that Reeve's (1856: Species 9, pl. II, figs. a–d) *sipho* (not Sowerby, 1823) from the Philippines, was a misidentification of *acervus* which then would be distributed from the Java Sea, Philippines, and New Caledonia.

acmaeodes. — Incorrect subsequent spelling (Galindo 1977: 416) of *acmaeoides*.

***acmaeoides* Pilsbry, 1894b**: 16 [as *acmæoides*], *Siphonaria*, Prov. Boshiu [Boso Peninsula], Japan, leg. Frederick Stearns. — Pilsbry (1895: 6, pl. VI, figs. 19–22) published again the original description with a few additional illustrations. Hirase (1934: 94, pl. 121, fig. 15), Hubendick (1945b: 19, 70, fig. 19; 1946: 30–31, pl. 6, figs. 12–15), Kira (1962: 201, pl. 69, fig. 9), and Galindo (1977: 416, as *acmaeodes*) regarded *acmaeoides* as valid.

***acuta* Quoy and Gaimard, 1833**: 334–335, pl. 25, figs. 35–37, *Siphonaria*, îles Célèbes et Vanikoro [Sulawesi, Indonesia, and Vanikoro, Solomon Islands], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Considered valid by Anton (1839: 26), Catlow and Reeve (1845: 99), Adams and Adams (1855: 271), Hanley (1858b: 151), Paetel (1889: 427), and Galindo (1977: 416). Reeve (1856: Species 9, pl. II, figs a–d), Schrenk (1867: 306),

Hutton (1880: 36), and Adam and Leloup (1939: 7) listed *acuta* as a synonym of *sipho* although Hubendick (1946: 46) thought that Reeve's *sipho* (not Sowerby, 1823) was a misidentification of *acervus* (see that specific name). Hubendick (1946: 47) regarded *acuta* as a synonym of *laciniosa*.

adansoni. — Incorrect subsequent spelling (Hanley 1858b: 151; Paetel 1889: 427; Hubendick 1946: 31) of *adansonii*.

adansonii **Blainville, 1824b**: 162, *Mouretus*, Gorée Island [Dakar, Senegal], [leg. unknown]. — Blainville created this name for a species originally described by Adanson (1757: 34–35, pl. 2, fig. 5) before January 1, 1758, and simply referred to as "Le Mouret" in the genus *Lepas* (see *mouret*). A few years later, Blainville (1827: 295) transferred *adansonii* into *Siphonaria*. In the same year, Blainville (1824a: 267) created another species name (*Siphonaria mouretus*) for the same species originally described by Adanson. Thus, *Siphonaria mouretus* Blainville, 1824 and *Mouretus adansonii* Blainville, 1824 are objective synonyms because they share the same type material (specimens originally illustrated by Adanson). There is, however, a third objective synonym: *Patella grisea*, created by Gmelin (1791: 3727) with a specific reference to Adanson's description of Le Mouret. Only *grisea* is potentially valid: *adansonii* and *mouretus* are objective synonyms of *grisea*. Paetel (1889: 427, as *adansoni*) regarded *adansonii* as valid. However, Hanley (1858b: 151, as *adansoni*), Hubendick (1946: 31, as *adansoni*), and Morrison (1972: 53, as "Adanson") all regarded it as a synonym of *pectinata*.

adjecans **Turton, 1932**: 9, pl. II, fig. 75, *Siphonaria*, [no type locality indicated, but in an article describing new species from the Port Alfred, South Africa], [leg. unknown]. — The name *adjecans* was created by Turton before 1961 for a variety of *concinna* and now should be regarded as a subspecific name (ICZN Article 45.6.4). Hubendick (1946: 59) considered *adjecans* to be valid at the specific level and a transitional form between *concinna* and *albofasciata*. Allanson (1958: 159, 163) examined the type material (a single, heavily eroded shell) and could not determine if the specimen was a variety of *concinna*. Also, because Allanson (1958: 159, 161) considered *concinna* to be synonymous of *deflexa*, he listed *adjecans* as a synonym of *deflexa*. Chambers and McQuaid (1994a: 265) concluded that *adjecans* was a synonym of *concinna* since they regarded *deflexa* as a *nomen dubium*.

aequilirata **Carpenter, 1857a**: 184 [as *æquilirata*], *Siphonaria*, Mazatlan, Gulf of California [Mexico], leg. Lieut. Shipley. — Carpenter (1857a: 184) described *aequilirata* as a new species but regarded it as a synonym of *aequilorata* in the same publication (Carpenter 1857a: 550). Therefore, ICZN Article 11.6 applies and *aequilirata* is not available (because treated in the original publication by its author as a synonym of a valid name). Carpenter also acknowledged that synonymy in a different publication published in the same year (Carpenter 1857b: 290). Therefore, *aequilirata* cannot be valid, despite the fact that it was regarded as valid by many authors (Binney 1867: 153, fig. 255; Dall 1870: 39; Paetel 1889: 427; Fischer and Crosse 1900: 107; Galindo 1977: 416), nor can it be a synonym of *aequilorata* (Morrison 1963: 8), *costata* (Hubendick 1946: 65), *leucanium* (Stearns 1895: 166–168), or *maura* (Keen 1958: 510). Also, *aeqilirata* cannot be a variety of *maura* (Burch 1945: 16). In addition, *aequilirata* was described based on a specimen from Mazatlan in the British Museum ("*L'pool Col.*") and the specimen from the Cuming Museum collection that was used by Reeve to describe *aequilorata*. Galindo (1977: 416) attributed the authorship of *aequilirata* to Gray by mistake (Gray is the author of *aequilorata*).

aequilorata **Gray *in* Reeve, 1856**: Species 15, pl. IV, figs. 15a–15b, *Siphonaria*, Mazatlan [Mexico], [leg. unknown]. — Regarded as valid by several authors (Hanley 1858b: 151; Paetel 1873: 117, 1883: 178; Dautzenberg 1896: LXV). Hubendick (1946: 65) regarded *aequilorata* as a synonym of *costata*, and regarded the latter as a probable synonym of *maura* (Hubendick 1946: 40). Keen (1958: 510) considered *aequilorata* a synonym of *maura*. Other authors gave a different status to *aequilorata* although they used by mistake the name *aequilirata* (see that name).

alba **Hubendick, 1945a**: 2–4, figs. 3, 7, 10, 11, and 13, *Siphonaria*, Nordwachter, Javasee [near Singapore, Java Sea], leg. C. Aurivillius. — Regarded as a valid species, endemic to the Java Sea (Hubendick 1945b: 29, 32, 72; 1946: 56, pl. 4, figs. 30–31). Morrison (1972: 57) listed *alba* as a synonym of *laciniosa*.

albicans. — Incorrect subsequent spelling (Reeve 1856: Species 9, pl. II, figs. 9a–d; Schrenk 1867: 306; Hutton 1880: 36; Catlow and Reeve 1845: 99; Adams and Adams 1855: 271; Hanley 1858b: 151; Paetel 1873: 117; 1883: 178; 1889: 427; Galindo 1977: 416) of *albicante*.

***albicante* Quoy and Gaimard, 1833**: 335–336, pl. 25, figs. 38–40, *Siphonaria*, île de Vanikoro [Solomon Islands] et celle de la Nouvelle-Irlande, au havre de Carteret [Carteret Harbor, New Ireland, Papua New Guinea], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — By mistake, all authors cited below refer to *albicante* as *albicans*, except Adam and Leloup (1939), Hubendick (1946) and Morrison (1972). Reeve (1856: Species 9, pl. II, figs. 9a–d), Schrenk (1867: 306), Hutton (1880: 36), and Adam and Leloup (1939: 7) listed *albicante* as a synonym of *sipho*. Catlow and Reeve (1845: 99), Adams and Adams (1855: 271), Hanley (1858b: 151), Paetel (1873: 117; 1883: 178; 1889: 427), and Galindo (1977: 416) regarded *albicante* as valid. Hubendick (1946: 47) and Morrison (1972: 56) regarded *albicante* as a synonym of *laciniosa*.

***albida* Angas, 1878a**: 314, pl. XVII, figs. 14–15, *Siphonaria*, St. Vincent's Gulf, South Australia, [leg. unknown]. — Angas (1878b: 869), Paetel (1889: 427), Adcock (1893: 11), Tate and May (1902: 419), and Verco (1907: 104–105) regarded *albida* as valid. Pritchard and Gatliff (1903: 221) regarded *albida* as a synonym of *baconi*. Verco (1907: 104) suggested that the specimens from Tasmania identified as *albida* by Tate and May (1902: 419) were misidentifications of *baconi* or *diemenensis*. Iredale (1910: 78–79; 1924: 277) regarded *albida* as a synonym of *Gadinia conica* Angas, 1867. Cotton and Godfrey (1932: 155) agreed that *albida* should be transferred to *Gadinia*, but as a valid species. Hubendick (1946: 37) suggested that the Tasmanian specimens of *albida* in Tate and May (1902: 419) were part of *baconi*, and that the specimens of *albida* in Iredale (1910: 78–79; 1924: 277) were a misidentification of *Gadinia conica* Angas, 1867. However, Hubendick (1946) did not discuss the status of *albida* as originally described by Angas in 1878. Finally, after examination of the type material, Jenkins (1983: 28) concluded that *albida* belongs to *Trimusculus* (with which *Gadinia* is synonymous) and is a synonym of *T. conicus* (Angas, 1867), and that the Tasmanian specimens of *albida* by Tate and May (1902: 419) are also part of *T. conicus*.

***albofaciata*.** — Incorrect subsequent spelling (Hubendick 1946: 12) of *albofasciata*.

***albofasciata* Krauss, 1848**: 60, pl. IV, fig. 4b, *Siphonaria*, Natalpoint [Natal, South Africa], [leg. unknown]. — The name *albofasciata* was created by Krauss before

1961 for a variety of *variabilis*, and now must be regarded as a subspecific name (ICZN Article 45.6.4). Both Sowerby (1892: 54) and Turton (1932: 10) regarded *albofasciata* as a valid variety of *variabilis*. For reasons unknown, Hubendick (1946: 60, pl. 5, figs. 19–22) treated *albofasciata* as a valid species and not a variety of *variabilis*. Allanson (1958: 159) considered the variety *albofasciata* to be a synonym of *deflexa*. Chambers and McQuaid (1994a: 265) regarded *deflexa* as a *nomen dubium*, and concluded that *albofasciata* was a synonym of *concinna*.

algeriae. — Incorrect subsequent spelling (Galindo 1977: 416) of *algesirae*.

algesira. — Incorrect subsequent spelling (MacAndrew 1857: 117, 146) of *algesirae*.

***algesirae* Quoy and Gaimard, 1833**: 338–339, pl. 25, figs. 23–25 [as *Algesiræ*], *Siphonaria*, détroit de Gibraltar [Strait of Gibraltar], vaste rade d'Algesiras [Algeciras Bay], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Regarded as valid by Anton (1839: 26), Jay (1839: 39), Catlow and Reeve (1845: 100), MacAndrew (1857: 117, 146, as *algesira*), Weinkauff (1866: 237), Petit de La Saussaye (1869: 92), Paetel (1873: 117; 1883: 178; 1889: 427), Nobre (1886: 32; 1936: 19–20), Kobelt (1888: 272), Dautzenberg (1889: 164; 1910b: 55; 1910c: 9; 1917: 65), Locard (1898: 98), Cooke (1911: 353–355), Dieuzeide (1935: 18–24, pl. I–XI), Burnay and Monteiro (1977: 19, fig. 3), and Galindo (1977: 416, as *algeriae*). Mörch (1852: 148) listed *algesirae* as a synonym of *striatula*. Hanley (1858b: 151), Hubendick (1946: 31), and Morrison (1972: 53) considered *algesirae* a synonym of *pectinata*. Petit de La Saussaye (1863: 142) discussed the possibility that *algesirae* may be a variety of a species called *Le Mouret* by Adanson (1757). Pallary (1900: 242–243, pl. VIII, fig. 8) listed *algesirae* as a synonym of the variety *conica* of a species referred to as *Siphonaria mouret* (Adanson, 1757), but the latter is not an available name. Iredale (1921: 207) regarded *algesirae* as a synonym of *grisea*. Dieuzeide (1935: 19) acknowledged that *algesirae* was a junior synonym of *pectinata*, but he did not retain the oldest name because Quoy and Gaimard were the first authors to give an anatomical description of this species. However, *pectinata* is the oldest name and has precedence over *algesirae*.

***alternata* Say, 1827**: 215–216, *Patella*, southern Coast of East Florida, [leg. unknown]. — The correct date of publication is 1827, although the authors who have mentioned a date

selected 1826. Say (1832: fig. xxxviii) placed *alternata* into *Siphonaria*. Regarded as valid by Hanley (1858b: 151), Binney (1867: 153, fig. 254), Dall (1870: 32–33; 1886: 287–288; 1902: 501–502, pl. XXVIII, figs. 12 and 14), Heilprin (1889: 176), Paetel (1889: 427), Baker (1891: 49), Peile (1927: 87), Hubendick (1945b: 29, 32, 72, figs. 45–46; 1946: 44–45, pl. 3, figs. 1–6), Morrison (1963: 8), Abbott (1974: 335, fig. 4112), Galindo (1977: 416), and Redfern (2001: 759, pl. 74, fig. 762). Pilsbry (1900: 505) listed Heilprin's (1889: 176) record of *alternata* (not Say, 1827) as a misidentification of *brunnea*. The description and figure in Binney (1867: 153, fig. 254) were copied from Say (1827: 215–216; 1832: pl. xxxviii), because he had not seen any specimen of *alternata*. In 1858, Binney also published *The Complete Writings of Thomas Say* which included Say's previous descriptions (Binney 1858: 124, 192–193) and figures (Binney 1858: pl. 38) of *alternata*.

alternicosta **Potiez and Michaud, 1838**: 55, plate X, figs. 18–20, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Menke (1843: 5) regarded *alternicosta* as a valid species, distributed on the west coast ("litore occidentali") of Australia, with *Patella dimya* as a synonym. However, *P. dimya* does not seem to appear anywhere else in the literature and *Dimya* is a genus of marine bivalves. Considered valid by Catlow and Reeve (1845: 100), Hanley (1858b: 151, as *alternicostata*), and Paetel (1889: 427, as *alternicostata*). Hubendick (1946: 34, 38) regarded *alternicosta* as a possible synonym of *belcheri* or *diemenensis*, although it is unclear which synonymy he favored.

alternicostata. — Incorrect subsequent spelling (Hanley 1858b: 151; Paetel 1889: 427) of *alternicosta*.

alterniplicata **Grabau and King, 1928**: 237, *Siphonaria*, [no type locality indicated, but in an article describing species from Peitaiho, i.e. Beidaihe, China], [leg. unknown]. — Considered valid by Ping and Yen (1932: 47), Hubendick (1946: 62–63), and Galindo (1977: 416).

amara **Nuttall** *in* **Reeve, 1856**: species 33, pl. VII, figs. 33a–b, *Siphonaria*, California [but very likely Hawaii], [leg. unknown]. — Jay (1839: 39) first cited *amara* in a list of shells held in his collection, with Nuttall as authorship and the Sandwich Isles, i.e. Hawaii, for distribution. However, *S. amara* Nuttall *in* Jay, 1839 is a *nomen nudum* because the name was not accompanied by any description, illustration,

or reference to a previous illustration. Catlow and Reeve (1845: 100) mentioned *amara* Nuttall *in* Jay, 1839 again, but still with no illustration or description. It only is with the publication of Reeve's *Monograph of the Genus Siphonaria in Conchologia Iconica* that *amara* became available. However, Reeve provided California as distribution. Regarded as valid by several authors, from California (Binney 1867: 154, fig. 256; Paetel 1883: 178; 1889: 427), Hawaii (Carpenter 1864b: 676; Paetel 1873: 117), with no distribution data mentioned (Hanley 1858b: 151; Pilsbry 1904: 36; Galindo 1977: 416), or even from New Guinea (Suter 1913: 599). Suter (1913: 599) cited "Hutt." as the author of *amara*, which likely was a spelling mistake for "Nutt.," although it is unclear where Suter got his distribution data. In any case, it seems that Hutton did not mention *amara* in any of his publications. Nor did he ever describe a new species of *Siphonaria*. Hubendick (1946: 66–67) included *amara* in a list of *nomina nuda*, because its type distribution (California *versus* Hawaii) and authorship (Nuttall *versus* Hutton) were confusing. However, *amara* Nuttall *in* Reeve, 1856 is available, although it probably should be regarded as a *nomen dubium*.

amphibia Oliver, 1915: 548, pl. XII, fig. 44, *Siphonaria*, Fleetwood Bluff, Sunday Island [Kermadec Islands, New Zealand], [leg. unknown]. — Hubendick (1946: 30–31, 63) regarded *amphibia* as a possible synonym of *acmaeoides*.

angulata Gray, 1825: 140, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Regarded as a possible synonym of *gigas* by Hubendick (1946: 39), although the lack of type locality and its brief original description of only 12 words jeopardizes any taxonomic status; it should probably regarded as a *nomen dubium*.

anneae Tomlin, 1944: 92–93, two unnumbered figures [as *anneæ*], *Siphonaria*, Umpangazi [Natal, South Africa], leg. Professor and Mrs. Stephenson. — Regarded as valid by Allanson (1958: 166–167, pls. Ib and IIb, figs. 3 and 13; 1963: 70), Chambers and McQuaid (1994a: 264–265, figs. 1H–1I), and Teske et al. (2007: 223, fig. 2). Hubendick (1946) did not mention *anneae*, even though it was described two years prior to his monograph.

anornata Menke. — Paetel (1889: 428) listed *anornata* as a valid species of *Siphonaria*, with Menke's name for authorship. However, as Hubendick (1946: 67) pointed

out, this citation is the only occurrence of *anornata* in the literature. As a result, *anornata* does not seem to be an available name (*nomen nudum*).

***antarctica* Couthouy *in* Gould, 1852**: 362–363, figs. 464–464b, *Siphonaria*, Cape Horn, [leg. unknown]. — No type locality is indicated within the body of the species description. However, at the end of the description of *lessoni*, which precedes that of *antarctica*, Gould (1852: 362) distinctly mention that Couthouy recognized two other species (*antarctica* and *lateralis*) in addition to *lessoni* from the Cape Horn. Paetel (1889: 428) and Rochebrune and Mabille (1889: 29) were justified to mention *antarctica* from the Cape Horn. Strebel (1907: 173) mentioned it from the Strait of Magellan as well. Hanley (1858b: 151), Rochebrune and Mabille (1889: 29), Paetel (1889: 428), Strebel (1907: 173–174, pl. 3, figs. 30–30a), and Hubendick (1946: 66) considered *antarctica* valid. Forcelli (2000: 132, fig. 423) listed *antarctica* as a synonym of *lateralis*.

***ashgar* Biggs, 1958a**: 249, *Siphonaria*, Hormuz Island, Persian Gulf, [leg. unknown, although likely Biggs himself]. — Considered valid by Biggs (1958b: 274), Galindo (1977: 416), and Bosch et al. (1995: 184, fig. 858).

***aspera* Krauss, 1848**: 60–61, pl. IV, fig. 5, *Siphonaria*, in litore capensi et natalensi [on the shore, near the Cape and in Natal, South Africa], [leg. unknown]. — Regarded as valid by Adams and Adams (1855: 271), Hanley (1858b: 151), Frauenfeld (1869: 878), Paetel (1873: 117; 1883: 178; 1889: 428), Martens (1874: 127), Sowerby (1892: 53), Köhler (1894: 37–43, pl. 4, figs. 45–51, pl. 6, figs. 11–12), Bartsch (1915: 10), Turton (1932: 10), Hubendick (1945b: 29; 1946: 60, pl. 5, figs. 13–15), Allanson (1958: 169–171, pls. Ia–Ib, figs. 7 and 15; 1963: 70), Kilburn and Rippey (1982: 135, pl. 32, fig. 12), and Jenkins (1983: 29). After examination of the type specimen of *serrata* and its similarity to *aspera*, Chambers and McQuaid (1994a: 264, 265) concluded that *aspera* was a junior synonym of *serrata*. Mörch (1852: 148) also mentioned *aspera*, but it seems that he regarded it as a synonym of *melanzonias*.

***aspersa* Krauss, 1848**. — Incorrect subsequent spelling (Galindo 1977: 416) of *aspera*.

***atra* Quoy and Gaimard, 1833**: 337–338, pl. 25, figs. 41–42, *Siphonaria*, Vanikoro [Solomon Islands], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Considered valid by Reeve

(1842: 20, pl. CXXXVIII, fig. 1), Catlow and Reeve (1845: 100), Mörch (1852: 148), Hanley (1858b: 151), Angas (1867: 233), Lischke (1871: 13, 105–106), Paetel (1873: 117, 1883: 178, 1889: 428), Brazier (1878: 134), Boettger (1892: 168), Pilsbry (1895: 5), Hedley (1909: 369), Melvill (1909: 73, 121), Iredale (1910: 71), Dautzenberg (1923: 24), Hirase (1934: 94, pl. 121, fig.17), Adam and Leloup (1939: 9–10, fig.2, pl. 2, figs. 3a–3b), Hubendick (1945b: 29, 72; 1946: 52, pl. 4, figs. 5–7; 1955: 128, erroneous authorship to Pilsbry), Habe (1964: 145, pl. 44, fig. 17), Cernohorsky (1972: 210, pl. 60, fig. 1), Galindo (1977: 416), Jenkins (1983: 29, 30), Fukuda (1994: 50), Tan (2000: 117), Hylleberg and Kilburn (2003: 133), Tan and Kastoro (2004: 50), and Zhongyan (2004: 198, pl. 108, fig. D). Oliver (1915: 547) listed Iredale's (1910: 71) *atra* (not Quoy and Gaimard, 1833) as a misidentification, and created the new subspecific name *perplexa* in the species *macauleyensis* for it. According to Hedley (1917b: 96), Angas's (1867: 233) record of *atra* from New South Wales is erroneous. Hubendick regarded *atra* from Adam and Leloup (1939: 9) as a misidentification of *subatra*, and *atra* from Dautzenberg (1923: 24) as a possible synonym of *kurracheensis*. Finally, Morrison (1972: 56) and Hasegawa et al. (2001: 29) listed *atra* as a synonym of *laciniosa*.

australis **Quoy and Gaimard, 1833**: 329–330, pl. 25, figs. 32–34, *Siphonaria*, détroit de Cook, à la Nouvelle-Zélande [Cook Strait, New Zealand], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Anton (1839: 26), Catlow and Reeve (1845: 100), Adams and Adams (1855: 271), Hanley (1858b: 151), Hutton (1873: 55; 1878: 42, 1880: 36; 1882: 341–344, pl. XV, figs. 1–12; 1883: 142–143, pl. XVII, figs. E–G), Paetel (1873: 117; 1883: 178; 1889: 428), Moss (1908: 41, pl. IX, fig. 25), Suter (1913: 598–599, pl. 24 [1915], fig. 6), Iredale (1915: 478), Finlay (1927: 442), Powell (1939: 217; 1946: 91; 1979: 292, pl. 54, fig. 11), Hubendick (1945b: 29, 72, 73; 1946: 49, pl. 3, figs. 28–31; 1955: 132), Morton and Miller (1968: 302, 312, 378, fig. 109, pl. 19, fig. 7), Jenkins (1983: 1–2, 11–23, 28–30, fig. 4, pl. 3, figs. a–i, pl. 4, figs. a–g, pl. 6, figs. d–f), Galindo (1977: 416), and Morley (2004: 130) considered *australis* valid. According to Hubendick (1946: 36), *australis* from Hutton (1882, 1883) is a misidentification of *cookiana*.

***baconi* Reeve, 1856**: Species 30, pl. VI, figs. 30a–30b, *Siphonaria*, Swan River, New Holland [Western Australia], leg. Bacon. — Considered valid by Hanley (1858b: 151), Angas (1865: 189), Paetel (1883: 178; 1889: 428), Pritchard and Gatliff (1903: 221), Verco (1907: 104), Cotton and Godfrey (1932: 154), Hubendick (1945b: 70; 1955: 129), and Galindo (1977: 416). Adcock (1893: 11) listed *baconi* as a synonym of *luzonica*. Hubendick (1946: 37, pl. 6, figs. 10–11) regarded *baconi* as valid or as a possible synonym of *bifurcata*. According to Jenkins (1983: 5, 10–11, 28), *baconi* is a synonym of *zelandica*.

***basseinensis* Melvill, 1893**: 243, pl. 1, fig. 21, *Siphonaria*, Bombay [India], leg. Abercrombie. — Melvill and Standen (1901: 331, 457) noted the "peculiar" occurrence of this species in India (Bombay). Tillier and Bavay (1905: 176) recorded *basseinensis* from the Suez Canal. Hubendick (1946: 54, 62) determined that Tillier and Bavay (1905) likely confused *basseinensis* with *kurracheensis* due to the location of *basseinensis* from the Suez Canal, which is likely the case for Melvill and Standon (1901), as well. However, Hubendick (1946: 62) could not regard *basseinensis* as a synonym of *kurracheensis* because he was unable to perform anatomical studies on specimens of *basseinensis*. Moazzo (1939: 131) also considered the possibility that *basseinensis* from Tillier and Bavay (1905) was a misidentification of *kurracheensis*.

***becki* Turton, 1932**: 10, pl. II, fig. 81, *Siphonaria*, Port Alfred [South Africa], [leg. unknown, but likely W. H. Turton]. — Regarded as valid by Hubendick (1946: 58), and as a synonym of *oculus* by Allanson (1958: 163, 166) after examination of the type material.

***belcheri* Hanley, 1858b**: 153, *Siphonaria*, [no type locality indicated, but "probably taken in the Indian seas"], leg. E. Belcher. — Considered valid by Paetel (1883: 178; 1889: 428), Hubendick (1945b: 19, 20, 70; 1946: 34, pl. 2, figs. 5–8), Bosch et al. (1995: 185, fig. 859), Albayrak and Çeviker (2001: 297), and Albayrak and Çağlar (2006: 292–294, fig. 2). Hubendick (1946: 54) noted that Moazzo's (1939: pl. XXXVIII, fig. 2) illustration of *kurracheensis* probably is a misidentification of *belcheri*.

***bifasciata*. —** Likely an incorrect subsequent spelling (Galindo, 1977: 416) of *bifurcata*.

***bifurcata* Reeve, 1856**: Species 22 [but actually Species 21 (see below)], pl. V, fig. 22, *Siphonaria*, Port Jackson, Australia [but actually Philippine Islands (see below)],

[leg. unknown]. — According to Jenkins (1983: 28), who examined the type material, the descriptions of *zebra* and *bifurcata* have been mixed up in Reeve's *Monograph* so that *bifurcata* is actually the Species 21 with figure 22 (instead of Species 22 with figure 22), and *zebra* is actually the Species 22 with figure 21. As a result, the type locality of *bifurcata* is the Philippines Islands, instead of Port Jackson. Iredale (1924: 276) had also noted this possible confusion. Although *bifurcata* was regarded as valid by several authors (Hanley 1858b: 151; Angas 1867: 232; Paetel 1873: 117; 1883: 178; 1889: 428; Hedley 1917b: 95; Hubendick 1945b: 22, 70; 1946: 37, pl. 2, figs. 9–13; McAlpine 1952: 42; Galindo 1977: 416, as *bifasciata*), Jenkins (1983: 5) considered *bifurcata* to be a synonym of *zelandica*. Finally, it seems that some specimens of *bifurcata* were misidentified by Hubendick (1946), which is detailed by Jenkins (1983: 28).

***blainvillei* Hanley, 1858b**: 153, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Listed as a valid species of *Siphonaria* by Paetel (1889: 428). Regarded as a synonym of *funiculata* by Hubendick (1946: 23) and Jenkins (1981: 2, 13, pl. 1, fig. a).

***bramnani*.** — Incorrect subsequent spelling (Galindo, 1977: 416) of *brannani*.

***brannani* Stearns, 1873a**: 249, *Siphonaria*, Santa Barbara Island [California, United States], leg. S. A. L. Brannan. — Regarded as valid by Dall (1921: 67, pl. 15, figs. 13–14), Oldroyd (1927: 57, pl. 2, fig. 18), Pilsbry and Lowe (1932: 108), Burch (1945: 15), Hubendick (1945b: 64, 73; 1946: 65), Keen (1958: 508–509, fig. 1029), Morrison (1963: 7), Abbott (1974: 335, fig. 4115), and Galindo (1977: 416, as *bramnani*).

***brasiliana* Reeve, 1856**: Species 17, pl. IV, figs. 17a–b, *Siphonaria*, Rio Janeiro [Brazil], [leg. unknown, from the collection of the Mus. Cuming]. — Considered valid by Hanley (1858b: 151) and Paetel (1883: 178; 1889: 428). Dall (1886: 288) listed *brasiliana* as a synonym of *lineolata* after examination of specimens labeled "*Braziliana* Reeve" in the Cuming Collection of the National Museum of Natural History (Smithsonian, Washington, DC). Due to Reeve's vague description, Hubendick (1946: 31, 64–65) regarded *brasiliana* as a synonym of either *pectinata* or *lepida*.

***braziliana*.** — Incorrect subsequent spelling (Hubendick, 1946: 31, 79) of *brasiliana*.

***brunnea* Hanley, 1858a**: 24, *Siphonaria*, insula Bermuda, [leg. unknown]. — Regarded as valid by Hanley (1858b: 151), Paetel (1883: 178; 1889: 428), Pilsbry (1900: 505), and

Peile (1927: 87). Dall (1886: 287–288; 1902: 501–502), and Davis (1904: 127) considered *brunnea* a darker geographical variety of *alternata*. Hubendick (1946: 44) and Morrison (1963: 8) listed *brunnea* as a synonym of *alternata*.

cancer **Reeve, 1856**: Species 7, pl. II, figs. 7a–b, *Siphonaria*, New Zealand, [leg. unknown]. — Considered valid by Hanley (1858b: 151), Hutton (1873: 55; 1880: 36), Paetel (1873: 117; 1883: 178; 1889: 428), Watson (1886: 674), and Galindo (1977: 416, as incorrect subsequent spellings *canicer* and possibly *canessi*). Hutton (1878: 41) regarded *cancer* as a possible variety of *zelandica*, and Suter (1913: 600) as a synonym of *zelandica*. Hubendick (1946: 49) and Jenkins (1983: 12, 18–19, 28–29) considered *cancer* a synonym of *australis*. Morrison (1972: 56) listed *cancer* as a synonym of *laciniosa*.

canessi. — Likely an incorrect subsequent spelling (Galindo, 1977: 416) of *cancer*.

canicer. — Incorrect subsequent spelling (Galindo, 1977: 416) of *cancer*.

capensis **Quoy and Gaimard, 1833**: 331–332, pl. 25, figs. 28–29, *Siphonaria*, cap de Bonne-Espérance, baie de la Table [Table Bay, Cape of Good Hope, South Africa], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Regarded as valid by Anton (1839: 26), Jay (1839: 39), Catlow and Reeve (1845: 100), Dunker (1853: 3), Adams and Adams (1855: 271), Hanley (1858b: 151), Frauenfeld (1869: 878), Paetel (1873: 117; 1883: 178; 1889: 428), Sowerby (1892: 53–54), Locard (1898: 98), Bartsch (1915: 10), Turton (1932: 10), Hubendick (1945b: 19, 70, fig. 20; 1946: 33–34, pl. 1, figs. 40–42, pl. 2, figs. 1–4), Allanson (1958: 157–159, pl. Ia, pl. IIa, fig. 1, fig. 10, 1963: 70), Galindo (1977: 416, with New Zealand as erroneous distribution), Kilburn and Rippey (1982: 134–135, pl. 32, fig. 13), and Chambers and McQuaid (1994a: 264–265, fig. 1E).

carbo **Hanley, 1858a**: 24, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Considered valid by Hanley (1858b: 151), Paetel (1889: 428), Hubendick (1946: 35, pl. 6, figs. 16–17), and Bosch et al. (1995: 185). Recorded from Oman (Bosch et al. 1995: 185) and South Africa (Hubendick, 1946: 35) although, according to Chambers and McQuaid (1994a: 264), it was originally described from the Caribbean.

***characteristica* Reeve, 1842**: 20, plate CXXXVIII, fig. 3, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Considered valid by numerous authors (e.g. Catlow and Reeve 1845: 100; Mörch 1852: 148; Reeve 1856: Species 8, pl. II, figs. 8a–b; Adams and Adams 1855: 271; Hanley 1858b: 151; Mörch 1861: 116; Paetel, 1883: 178; Paetel 1889: 428; Pilsbry and Lowe 1932: 108; Galindo 1977: 416). Dall (1870: 39) and Boone (1938: 300) thought *characteristica* could be a variety of *gigas*, and Hubendick (1946: 39) regarded *characteristica* as a synonym of *gigas*.

***cheesemani* Oliver, 1915**: 546–547, pl. XII, figs. 41–41a, *Siphonaria*, Sunday Island [Kermadec Islands, New Zealand], [leg. unknown]. — Regarded as a synonym of *cookiana* by Hubendick (1946: 36), but Jenkins (1983: 29) stated this synonymy was incorrect.

***cochleariformis* Reeve, 1856**: Species 28, pl. VI, figs. 28a–b, *Siphonaria*, Isle of Hainan, coast of China, [leg. unknown]. — Dunker (1861: 18), Angas (1867: 232), Frauenfeld (1869: 878), Lischke (1871: 13, 106–107), Paetel (1883: 178; 1889: 428), Pilsbry (1895: 6), and Hubendick (1945b: 25, 27, 72, figs. 35, 40, 43; 1946: 43–44, pl. 2, figs. 33–35) considered *cochleariformis* valid. Hedley (1917b: 96) argued that Angas erroneously recorded *cochleariformis* from New South Wales. Hubendick (1946: 43) argued that *cochleariformis* from Angas (1867: 232), Frauenfeld (1869: 878), and possibly Dunker (1861: 18) were misidentifications. Cooke (1886a: 133) regarded *cochleariformis* as a synonym of *kurracheensis*.

***comita* Iredale, 1924**: 277, *Pugillaria*, Twofold Bay, N.S.W. [New South Wales, Australia], leg. Dr. Torr. — The name *comita* was created by Iredale for a variety of *stowae*, and should now be ranked as a subspecies (ICZN Article 45.6.4). Hubendick (1946: 29) mentioned the existence of *comita* but did not provide any comment on its status.

***commixtus* Iredale, 1940**: 437, *Parellsiphon*, Noumea [New Caledonia], leg. Chas. Hedley. — Regarded as a synonym of *laciniosa* by Morrison (1972: 57).

***compressa* Allanson, 1958**: 173–174, text figs. 9 and 18, pls. III–IV [unnumbered figures], *Siphonaria*, Langebaan Lagoon, Saldanha Bay [South Africa], leg. J. H. Day. — Chambers and McQuaid (1994a: 264–265, fig. 1A), Kilburn and Rippey (1982: 134), and Allanson and Herbert (2005: 95–97, fig. 1) regarded *compressa* as valid. Bosch et

al. (1995: 185, fig. 861) mentioned *compressa* from southern Oman, although they acknowledged that the specimens could be part of an undescribed species.

concinna **Sowerby, 1823**: pl. 143, fig. 2, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Regarded as valid by Sowerby (1825: 32), Anton (1839: 26), Catlow and Reeve (1845: 100), Hupé (1854: 250), Reeve (1856: Species 13, pl. III, figs. 13a–13b), Hanley (1858b: 151), Paetel (1873: 117; 1883: 178; 1889: 428), Plate (1894: 222–224), Bartsch (1915: 10), Turton (1932: 9), Hubendick (1945b: 72; 1946: 58, pl. 5, figs. 9–12), Chambers and McQuaid (1994a: 264, 265, figs. 1F, 1K), and Galindo (1977: 416). According to Hubendick (1946: 21), the specimens from Chile referred to as *concinna* by Hupé (1854: 250) and Plate (1894: 222–224) were misidentifications of *lessonii*, because *concinna* is found in Gambia, eastern South Africa, Madagascar, and Mauritius. Mörch (1852: 148) mentioned *concinna*, but it is unclear whether he regarded it as valid or as a synonym of *variabilis*. Sowerby (1892: 54) indicated that *concinna* was a variety of *variabilis*. Allanson (1958: 159, 161) considered *concinna* a synonym of *deflexa*.

conica **Blainville, 1827**: 294–295, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Blainville (1827: 295) acknowledged that *conica* could be a variety of *radiata*, which he described in the same publication. Regarded by Hubendick (1946: 51) as a possible synonym of *subatra* and as a synonym of *javanica* by Morrison (1972: 52). Galindo (1977: 416) appears to have regarded *conica* as a valid species, but erroneously attributed the name to Angas. Also unclear is why Galindo cited Australia as the distribution of *conica* when no type locality was given in the original description and there appears to be no other mention of this species in the literature except by Paetel (1889: 428), with no distribution.

conica **Pallary, 1900**: 243, pl. VIII, fig. 8, *Siphonaria*, Oran [Algeria], [leg. unknown]. — The name *conica* was created by Pallary for a variety of a species he referred to as *Siphonaria mouret* Adanson, 1757, which he thought was a synonym of *S. algesirae*. Besides the fact that *mouret* is not available (see that specific name), *conica* is permanently invalid because it was already occupied by *S. conica* Blainville, 1827. Indeed, *conica* is to be regarded as a subspecific name (Article 45.6.4), and, because of the application of the principle of coordination to the species-group names (Article 46.1), Pallary is deemed to have simultaneously

establish *conica* at the species rank. Dieuzeide (1935: 30) and Hubendick (1946: 32) regarded *conica* simply as a variant of *pectinata*.

cookeana. — Incorrect subsequent spelling (Galindo 1977: 416) of *cookiana*.

***cookiana* Suter, 1909a**: 258, pl. XI, fig. 18, *Siphonaria*, Lyall Bay, Cook Strait [New Zealand], leg. Miss Mestayer. — Regarded as valid by Suter (1913: 599, pl. 24 [1915], figs. 7–7b), Iredale (1915: 478), Odhner (1924: 55), Powell (1933: 186, 1939: 217, 1946: 91, 1979: 292–293, pl. 54, figs. 8–9), Hubendick (1945b: 20, 22, 70, figs. 21, 24, 26; 1946: 36, pl. 6, figs. 20–22), and Morton and Miller (1968: 302, pl. 19, fig. 9). Both Knox (1955: 86, 88) and Powell (1979: 292) regarded Hubendick's (1945, 1946) *cookiana* as a misidentification of *zelandica*. However, Jenkins (1983: 1, 2, 13, 22–23, 29) discovered that the lectotype designated by Boreham (1959: 71) for *cookiana* actually was a young specimen of *australis*. Because *australis* has precedence over *cookiana*, the latter name became a junior synonym of *australis*. Jenkins (1983) created *propria* as a new name for the specimens remaining in the lot formerly referred to as *cookiana* by Suter.

***coreensis* Adams and Reeve, 1848**: 69, pl. XIII, figs. 1a–b, *Siphonaria*, Corean Archipelago [Korea], [leg. unknown]. — Reeve (1856: Species 14, pl. III, figs. 14a–14b), Pilsbry (1895: 5), Adam and Leloup (1939: 9), and Hubendick (1946: 52) listed *coreensis* as a synonym of *atra*. Lischke (1871: 105, 106) and Paetel (1889: 428) regarded it as a variety of *atra*. Hubendick (1946: 51) also listed *coreensis* as a possible synonym of *subatra*. Adams and Adams (1855: 271), Hanley (1858b: 151), Dunker (1861: 33, as *koreensis*), Paetel (1873: 117, 1883: 178), and Galindo (1977: 416) regarded it as valid. More recently, Hylleberg and Kilburn (2003: 133–134) regarded *coreensis* as a synonym of *laciniosa*.

***cornuta* Gould, 1848**: 153, *Siphonaria*, Mangsi Islands [Mangsee Islands, Philippines], [leg. unknown]. — Regarded as valid by Gould (1852: 355–356, figs. 461–461b), Adams and Adams (1855: 271), Hanley (1858b: 151), and Paetel (1889: 428). Pilsbry (1895: 5) listed *cornuta* as a synonym of *atra*, Hubendick (1946: 52, 51) as a possible synonym of *subatra*, and Morrison (1972: 56) as a synonym of *laciniosa*.

***corrugata* Reeve, 1856**: Species 31, pl. VI, figs. 31a–31b, *Siphonaria*, Puteao, Island of Luzon, Philippines, leg. Cuming. — Hanley (1858b: 151), Paetel (1883: 178, 1889: 428), and Brazier (1888: 1001) regarded *corrugata* as valid. Hubendick (1946: 54–55) and

Hylleberg and Kilburn (2003: 133) regarded *corrugata* as a synonym of *kurracheensis* and Hubendick more specifically listed *corrugata* as a synonym of the variety *luzonica* of *kurracheensis*. Morrison (1972: 56) regarded it as a synonym of *laciniosa*.

costata **Hombron and Jacquinot, 1841**: 295, *Siphonaria*, Otago (Tavaï-Pounamon, Nouvelle-Zélande) [Otago, New Zealand], [leg. expedition of *l'Astrolabe* and *la Zélée*]. — Both Hanley (1858b: 151) and Paetel (1889: 428) regarded *costata* as valid. Hubendick (1946: 48) thought it likely was a synonym of *australis*, but should be regarded as a *nomen nudum* and be rejected. Jenkins (1983: 12) regarded it as a *nomen nudum*, but listed it as one of the synonyms of *australis*. However, *costata* cannot be a *nomen nudum* because the name was accompanied by a description, which, although it is brief, exists nonetheless. Actually, the specific name *costata* was already occupied as *Siphonaria costata* Sowerby, 1835. Thus, *costata* Hombron and Jacquinot, 1841 is a junior, primary homonym of *costata* Sowerby, 1835, and is thus available but permanently invalid.

costata **Sowerby, 1835**: 6, *Siphonaria*, Americæ Centralis (Guacomayo) [Guacamayo, Central America], [leg. unknown]. — Regarded as valid by Catlow and Reeve (1845: 100), Reeve (1856: Species 19, pl. IV, figs. 19a–b), Adams and Adams (1855: 271), Frauenfeld (1869: 878), Dall (1870: 39; 1909: 205), Paetel (1873: 117, 1883: 178), Stearns (1892: 314), Burch (1945: 16), and Galindo (1977: 416). According to Hanley (1858b: 151), *costata* is a synonym of *lineolata*. Hubendick (1945b: 72) suggested that *costata* refer to the same species as *maura*, also created by Sowerby (1835). Keen (1958: 509, fig. 1030) agreed with Hubendick (1946: 40–41, 65) that *costata* is valid or a possible variety of *maura*. Finally, Morrison (1963: 8) listed *costata* as a synonym for *aequilorata*.

crebicostata. — Incorrect subsequent spelling (Galindo 1977: 416) of *crebricostata*.

crebidentata **Smith**. — Galindo (1977: 416) mentioned *crebidentata* as a valid species of *Siphonaria*. However, no original description and no other citation could be found in the literature. Thus, *crebridentata* is a *nomen nudum* and is not available.

crebricostata **Nuttall *in* Jay, 1839**: 39, *Siphonaria*, Sandwich Isles [Hawaii], [leg. unknown]. — Jay (1839: 39) first mentioned *crebricostata* with Nuttall as authorship and Hawaii for distribution. However, *crebricostata* Nuttall *in* Jay, 1839 is a *nomen nudum* because the name was not accompanied by any description,

illustration, or reference to a previous illustration. Later, several authors mentioned *crebricostata*, but only in species checklists and without any description (Catlow and Reeve 1845: 100; Paetel 1873: 117; 1883: 178; 1889: 428; Galindo 1977: 416, as *crebicostata*). Reeve (1856: Species 9, pl. II, figs. 9a–d), Schrenk (1867: 306), and Hutton (1880: 36) listed *crebricostata* as a synonym of *sipho*, and Hubendick (1946: 47) regarded it as a synonym of *laciniosa*. So, *crebricostata* has remained a *nomen nudum* and is thus not available.

***crenata* Blainville, 1827**: 295, [no type locality indicated, but likely the Red Sea], [leg. unknown]. — Blainville created *crenata* for a species of *Siphonaria* illustrated by Savigny (1817: pl. 3, figs. 3.1–3.5). Audouin (1827: 144–145) commented on the same species illustrated by Savigny, rightly pointed out that it was a *Siphonaria*, but did not create any specific name to refer to it. Hanley (1858b: 151), Paetel (1889: 428), Morrison (1972: 51, 60, 61), and Albayrak and Çağlar (2006: 292) regarded it as valid. Hubendick (1946: 54) listed *crenata* as a possible synonym of *kurracheensis*.

***currumbinensis* Hubendick, 1955**: 133, figs. 4–8, pl. 1, figs. 1–6, *Siphonaria*, Currumbin, Queensland [Australia], [leg. unknown]. — Noosa, Queensland, is provided by Hubendick as an additional (non-type) locality. No further mention of this species could be found in the literature.

***cyaneomaculata* Sowerby, 1906**: 37, unnumbered figure, *Siphonaria*, The Kowie [Kowie River, South Africa], leg. H. Becker. — Regarded as valid by Turton (1932: 9, as *cyaneo-maculata*) and Hubendick (1946: 58–59, pl. 5, figs. 16–17). Allanson (1958: 159, 161, 163) considered *cyaneomaculata* a synonym of *deflexa*. Kilburn and Rippey (1982: 135) and Chambers and McQuaid (1994a: 265 listed *cyaneomaculata* as a synonym of *concinna*.

***dayi* Allanson, 1958**: 169, text figs. 5, 16, pls. Ib, IIb, *Siphonaria*, Inhaca Island, Delagoa Bay [Mozambique], leg. M. Kalk. — Regarded as valid by Chambers and McQuaid (1994a: 264–265, 267, fig. 1L) and Teske et al. (2007: 223, fig. 2).

deflecta. — Incorrect subsequent spelling (Galindo, 1977: 416) of *deflexa*.

***deflexa* Helbling *in* Born, 1778**: 439, *Patella*, [no type locality indicated], [leg. unknown]. — Helbling (1779: 108–109, pl. I, figs. 9–10) published a description of *deflexa* in

Abhandlungen einer Privatgesellschaft in Böhmen zur Aufnahme der Mathematik, der vaterländischen Geschichte und der Naturgeschichte of which Born was the editor. However, Born (1778: 439) published *Patella deflexa* with a brief description and a reference to Helbling's (1779) work (cited as "Helbl. Abh. e. Priv. Ges. in Boehm, IV. I. t. 9. 10. f."), making it available in 1778 instead of 1779. Mörch (1852: 148) regarded *deflexa* as a possible synonym of *variabilis*, the latter being a synonym of *concinna* according to Hubendick (1946: 58). Martens (1869: 235) and Hubendick (1946: 58) regarded it as a possible synonym of *concinna*. Kilburn and Rippey (1982: 135) regarded it as a synonym of *concinna*. Allanson (1958: 159–163, text figs. 2, 12, pls. Ia, IIa; 1963: 70) considered *deflexa* valid and used the name for specimens from western Africa (mouth of Congo River). The locality of False Bay, Australia, mentioned by Galindo (1977: 416, as *deflecta*) is unclear as there is no reason to think that the type locality of *deflexa* is in Australia. Finally, Chambers and McQuaid (1994a: 264–265) regarded *deflexa* as a *nomen dubium* because they could not locate the type specimen.

***densatus* Iredale, 1940**: 441, pl. xxxiv, figs. 18–19, *Legosiphon*, Port Douglas, North Queensland [Australia], [leg. unknown]. — Regarded as a synonym of *laciniosa* by Hubendick (1946: 47).

denticula. — Incorrect subsequent spelling (Anton, 1839: 26) of *denticulata*.

***denticulata* Quoy and Gaimard, 1833**: 340–341, pl. 25, figs. 19–20, *Siphonaria*, partie sud de la Nouvelle-Hollande, au port Western, et probablement au port du Roi-Georges [Western Port and probably King George Sound, Australia], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Anton (1839: 26, as *denticula*), Reeve (1842: 20, pl. CXXXVIII, fig. 2; 1856: Species 4, pl. I, figs. 4a–4b), Catlow and Reeve (1845: 100), Menke (1852: 38), Adams and Adams (1855: 271), Hanley (1858b: 151), Angas (1867: 232), Hutton (1873: 55), Paetel (1873: 117; 1883: 178; 1889: 428); Adcock (1893: 11), Hedley (1909: 369), Galindo (1977: 416, authorship erroneously attributed to Sowerby), and Jenkins (1984: 113, 117) all regarded *denticulata* as valid. Menke's (1852) *denticulata* was regarded by Carpenter (1857a: 183) as a probable misidentification of the variety *palmata* of *lecanium*, and by Hubendick (1946: 40) as a synonym of *maura*. Hutton (1878: 42),

Pritchard and Gatliff (1903: 220), Suter (1907: 265), Verco (1907: 103), and May (1921: 88) regarded *denticulata* as a synonym of *diemenensis*. Tate and May (1902: 418) and Hubendick (1946: 38, pl. 2, fig. 17) regarded it as a variety of *diemenensis*. According to Hedley (1917b: 96), Angas (1867) geographical record from New South Wales *denticulata* was erroneous. McAlpine (1952: 40, 42, fig. 1) created the new combination *Ellsiphon denticulatus*.

depressa **Locard** *in* **Pallary, 1900**: 243, pl. VIII, fig. 11 Oran, Beni Saf [Algerian Mediterranean coasts], [leg. unknown]. — The name *depressa* was created by Pallary for a variety of a species he referred to as *Siphonaria mouret* Adanson, 1757, which he thought was a synonym of *S. algesirae*. Besides the fact that *mouret* is not available (see that specific name), *depressa* is permanently invalid because it was already occupied by *depressa* Pease, 1862. Indeed, *depressa* is to be regarded as a subspecific name (Article 45.6.4), and, because of the application of the principle of coordination to the species-group names (Article 46.1), Pallary is deemed to have simultaneously establish *depressa* at the species rank. According to Dieuzeide (1935: 29, 30) and Hubendick (1946: 32), *depressa* refers to individual variants of *pectinata*. In any case, *depressa* Locard *in* Pallary, 1900 is available but permanently invalid, and cannot be regarded as a synonym of *pectinata*.

depressa **Pease, 1862**: 279–280, *Siphonaria*, [no type locality indicated, but in an article describing new species from the Pacific Islands], [leg. unknown]. — Pease (1868: 98–99, pl. 11, fig. 23) provided an illustration of *depressa* based on material collected from "Insl. Apaian," i.e. Kiribati, central tropical Pacific Ocean. Pease's (1862) original description was reproduced without modification by Pease (1868), but the following remark was added: "A peculiar species, almost flat. The muscular impression occupies nearly the whole of the interior." However, it is unclear whether the specimen illustrated by Pease in 1868 was the specimen used in the original description, and Kiribati is not regarded here as the type locality. According to Hubendick (1946: 54), *depressa* is a synonym of the variety *luzonica* of *kurracheensis*. However, for the authorship of *depressa*, Hubendick gave "Pease, 1868: pl. 2, fig. 23." The plate number is 11 instead of 2; more importantly, it is unclear whether Hubendick wanted to refer to Pease's (1868) record of *depressa* from Kiribati, knowing that the species had been described

earlier by Pease (1862), or if he made a mistake with the authorship (which clearly is Pease, 1862). Paetel (1883: 178; 1889: 428) listed *depressa* as a valid name. Morrison (1972: 56) considered *depressa* a synonym of *laciniosa*.

***depressior* Schrenck, 1867**: 307–308, *Siphonaria*, Nordjapanischen Meere [north Sea of Japan], [leg. unknown]. — The name *depressior* was created by Schrenk for a forma of *sipho*, and should now be ranked as a subspecies (ICZN Article 45.6.4). Hubendick (1946: 48) mentioned the existence of *depressior* but did not provide any comment on its status.

***diemanensis*.** — Incorrect subsequent misspelling (Tenison-Woods, 1878: 99–100) of *diemenensis*.

***diemenensis* Quoy and Gaimard, 1833**: 327–329, pl. 25, figs. 1–12, *Siphonaria*, canal de d'Entrecasteaux, île de van Diémen [d'Entrecasteaux Channel, Tasmania], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Regarded as valid by Anton (1839: 26, as *diemensis*), Catlow and Reeve (1845: 100), Adams and Adams (1855: 271), Hanley (1858b: 151), Angas (1865: 189), Hutton (1873: 55), Tenison-Woods (1877: 56–58, 1878: 99–100, as *diemanensis*), Paetel (1873: 117, as *diemensis*; 1883: 178, as *diemensis*; 1889: 428, as *diemensis*), Adcock (1893: 11), Tate and May (1902: 418), Pritchard and Gatliff (1903: 220), Suter (1907: 265), Verco (1907: 103); Iredale (1910: 71, 78), May (1921: 88), Cotton and Godfrey (1932: 152–154, pl. 3, fig. 6), Menke (1843: 5, as *diemensis*), Hubendick (1945b: 22, 70, figs. 23, 28, 29; 1946: 38–39, pl. 2, figs. 14–17; 1955: 130, 131), McAlpine (1952: 40, 42, fig. 2), Galindo (1977: 416, as *diemensis*), Jenkins (1983: 28–30, 1984: 113, 116–117), and Wilson (2002: 172, 173). According to Hutton (1878: 41), Hutton's (1873) specimens of *diemenensis* were a misidentification of *obliquata*, something with which Suter (1909b: 33, 1913: 599) and Hubendick (1946: 24) agreed. Hutton (1878: 10, 42) also listed *denticulata* as a synonym of *diemenensis*, but he was not sure whether *diemenensis* inhabited New Zealand. According to Oliver (1915: 546), Suter's (1907) specimens of *diemenensis* were a misidentification of *raoulensis*.

***diemensis*.** — Incorrect subsequent spelling (Anton 1839: 26; Paetel 1873: 117; 1883: 178; 1889: 428; Menke 1843: 5; Galindo 1977: 416) of *diemenensis*.

elatior **Schrenck, 1867**: 306–308, *Siphonaria*, Philippinen [Philippines], [leg. unknown]. — The name *elatior* was created by Schrenk for a forma of *sipho*, and should now be ranked as a subspecies (ICZN Article 45.6.4). Hubendick (1946: 48) mentioned the existence of *elatior* but did not provide any comment on its status.

elegans **Iredale, 1940**: 441, pl. xxxiv, figs. 3–4, *Planesiphon*, Keppel Bay, Queensland [Australia], leg. H. Bernhard. — Regarded as valid by Hubendick (1945b: 29, 72, figs. 44 and 47; 1946: 56–57, pl. 4, figs. 32–34). However, after McAlpine (1952: 42) compared the conchology and anatomy of *elegans* and *bifurcata*, Hubendick (1955: 129–130) decided that *elegans* was a synonym of *zelandica*. Jenkins (1983: 4–5, 28) agreed with this synonymy. Morrison (1972: 57) thought that Hubendick's (1946) specimens of *elegans* were as a misidentification of *laciniosa*.

eumelas **Iredale, 1940**: 439, pl. xxxiv, figs. 5–6, *Mestosiphon*, Snapper Island, North Queensland [Australia], [leg. unknown]. — Regarded as a synonym of *atra* by Hubendick (1946: 52, 1955: 128) and of *laciniosa* by Morrison (1972: 57).

exigua **Martini** *in* **Sowerby, 1823**: pl. 143, fig. 4, *Siphonaria*, [no type locality indicated], [leg. unknown]. — In the figure caption for his plate 143, Sowerby (1823) gives "Lepas exigua, *Martini*" for the name of the shell illustrated on the figure 4, indicating that Sowerby regarded Martini as the author of *exigua*. To date, it is unclear to what publication and species Sowerby refers. Martini (1769) cited several times *Lepas exigua*, but always in the context of polynominal (non-Linnaean) combinations: e.g. *Lepas exigua aurantia* (p. 131), *Lepas exigua cornea striata* (p. 148), *Lepas exigua Laevis neritoides* (p. 161). As a result, Sowerby's (1823) mention of *exigua* should be regarded as the first publication of the name. Hanley (1858b: 151) cited Sowerby as the author for *exigua*, but acknowledged Martini. Reeve (1856: Species 9, pl. II, figs. 9a–9b), Schrenk (1867: 306), Hutton (1880: 36), Adam and Leloup (1939: 7) regarded *exigua* as a synonym for *sipho*. Regarded as valid by Sowerby (1825: 32), Blainville (1827: 295), Anton (1839: 26), Catlow and Reeve (1845: 100), Mörch (1852: 148) [also acknowledged Martini], Adams and Adams (1855: 271), Frauenfeld (1869: 878), Paetel (1873: 117, 1883: 178, 1889: 428), Schepman (1913: 460), Oostingh (1931: 222), and Galindo (1977: 416). Hubendick (1945b: 29) listed *exigua* as a

variety of *sipho* and then (Hubendick, 1946: 47–48, pl. 3, fig. 16) as a variety of *laciniosa*. According to Morrison (1972: 52), *exigua* was a synonym of *javanica*.

exulorum. — Incorrect subsequent misspelling (Hanley, 1858b: 152; Paetel, 1889: 428; Iredale, 1940: 438) of *exulum*.

***exulum* Hanley, 1858a**: 25, *Siphonaria*, Norfolk Island [Australia], [leg. unknown]. — Hanley (1858b: 152), Paetel (1889: 428), and Iredale (1940: 438) regarded *exulum* as valid. Hubendick (1946: 38) listed both *exulum* and *exulorum* as synonyms of *diemenensis*.

***ferruginea* Reeve, 1856**: Species 26, pl. V, fig. 26, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Regarded as valid by Hanley (1858b: 152), Liénard (1877: 59, from Mauritius), Deshayes (1863: 41), Martens (1880: 310), Paetel (1873: 117, as *feruginea*; 1883: 178; 1889: 428, as *feruginea* from Reunion Island), Dall (1886: 288, from Vera Cruz, Mexico; 1890: 299, from Brazil); Ihering (1915: 141), Hubendick (1945b: 29; 1946: 53–54, pl. 4, figs. 16–19), and Galindo (1977: 416). Morrison (1963: 8) listed *ferruginea* as a synonym of *alternata*. Hubendick (1946: 54, 64) considered that Dall's (1886) *ferruginea* was a misidentification of *hispida*. Finally, Morrison (1972: 56) listed *ferruginea* as a synonym of *laciniosa*.

feruginea. — Incorrect subsequent mispelling (Hanley 1858b: 152; Paetel 1873: 117; 1889: 428; Iredale 1940: 438) of *ferruginea*.

***flemingi* Powell, 1955**: 121–122, pl. 5, fig. 44, *Kerguelenella*, bay south of Crozier Point, Auckland Islands [New Zealand], leg. C. A. Fleming. — Regarded as valid by Morton and Miller (1968: 380) and Galindo (1977: 416), and as a synonym of *innominata* by Powell (1979: 293).

***fuliginata* Reeve, 1856**: Species 34, pl. VII, figs. 34a–b, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Regarded as valid by Hanley (1858b: 152), Paetel (1883: 178; 1889: 429), and Galindo (1977: 416), and as a *nomen nudum* by Hubendick (1946: 67), who probably meant *nomen dubium* because *fuliginata* cannot be a *nomen nudum*.

***funiculata* Reeve, 1856**: Species 6, pl. II, figs. 6a–b, *Siphonaria*, Van Diemen's Land [Tasmania], [leg. unknown]. — Reeve (1856: Species 35, pl. VII, figs. 35a–35b) erroneously labeled Species 35 as *funiculata* instead of *lirata* according to Reeve's

erratum in the appendix. Regarded as valid by Hanley (1858b: 152), Angas (1867: 232), Hutton (1873: 55), Paetel (1889: 428), Tate and May (1902: 419), Pritchard and Gatliff (1903: 220–221), May (1921: 88), Adam and Leloup (1939: 9, pl. II, fig. 2), Hubendick (1945b: 12, 15, 16, 66, figs. 3, 12, 58; 1946: 23, pl. 1, figs. 15–17), Galindo (1977: 416), and Jenkins (1981: 1–13, figs. 2–3, pl. 1, figs. a–l, pl. 2, figs. a–k, pl. 3, figs. a–h, 1983: 29). Tenison-Woods (1877: 58) regarded *funiculata* as a variety of *diemenensis*. Hutton (1878: 42) listed it as a synonym of *laeviuscula*. Hedley (1915: 751, 752; 1917b: 96) thought that Angas's (1867) *funiculata* was a misidentification of *virgulata* and argued that Angas erroneously recorded *funiculata* from New South Wales. According to Hubendick (1946: 23), *funiculata* from both Angas (1867) and Adam and Leloup (1939) was a misidentification of *virgulata*.

***gareensis* Mittre**. — This species name appears only in Fulton (1924: 7) as a valid species name of *Siphonaria*. To date, an original publication could not be found. Hubendick (1946: 67) rightly regarded it as a *nomen nudum*, but suggested that, because the spelling of *gareensis* is close to Gorée, it might refer to a species from Gorée Island. Senegal, and thus could be a synonym of *pectinata*. However, another explanation is that it is an incorrect subsequent spelling of *goreensis*, as in *Patella goreensis* Gmelin, 1791, although the species referred to by Gmelin (1791: 3694), which is Adanson's (1757: pl. 2, fig. 10) Jenae, does not belong to *Siphonaria*.

***gigas* Sowerby, 1825**: vi, *Siphonaria*, Panama [Pacific coast], [leg. unknown]. — Regarded as valid by many authors (e.g. Anton 1839: 26; Jay 1839: 39; Reeve 1842: 20, pl. CXXXVIII, fig.6; Catlow and Reeve 1845: 100; Mörch 1852: 148; Reeve 1856: Species 3, pl. I, figs. 3a–b; Adams and Adams 1855: 271; Hanley 1858b: 152; Keen 1858: 509, fig. 1031; Mörch 1861: 116; Dall 1870: 39; Paetel 1873: 117; 1883: 178; 1889: 428; Stearns 1894: 405, 429; Fischer and Crosse 1900: 107; Dall 1909: 205; Dall and Ochsner 1928: 155; Boone 1928: 10; Pilsbry and Lowe 1932: 108; Boone 1938: 299–300, pl. 115; Burch 1945: 16; Hubendick 1945b: 22, 24, 25, 70, 72, figs. 27, 32, 38; 1946: 39–40, pl. 6, figs. 23–29; Morrison 1963: 8; Galindo 1977: 416). *S. gigas* is distributed in the tropical eastern Pacific, from the Gulf of California to northern Peru, including oceanic islands from the

region (Galapagos); according to Hubendick (1946: 39), it also is found off Conception, Chile, which is outside the tropical eastern Pacific.

godeffroyi Crosse. — Paetel (1873: 117; 1883: 178; 1889: 428) mentioned *godeffroyi* as a valid species of *Siphonaria*. To date, no original description could be found. Hubendick (1946: 68) came to the same conclusion and rightly regarded *godeffroyi* as a *nomen nudum*.

grisea Gmelin, 1791: 3727, *Patella*, Africa, [leg. unknown]. — Gmelin created *Patella grisea* with a reference to Adanson's (1757: 34–35, pl. 2, fig. 5) description of a species that Adanson called Le Mouret. Gmelin refer to it as "*Adans. Seneg. I., t. 2. f. 5.*" Thus, *mouretus* and *adansonii*, both created by Blainville in 1824 in reference to Adanson's Le Mouret (see *mouretus* and *adansonii*), are objective synonyms of *grisea*, which has precedence. Africa was the type locality given by Gmelin, but "l'isle de Gorée" was the type locality provided by Adanson. Menke (1853: 68) transferred *grisea* into *Siphonaria*, and regarded it as valid, along with Iredale (1921: 206–207), Galindo (1977: 416), and Paetel (1889: 428). However, Hanley (1858b: 152), Hubendick (1946: 31), and Morrison (1972: 53) regarded it as a synonym of *pectinata*.

guamensis Quoy and Gaimard, 1833: 343, pl. 25, figs. 15–16, *Siphonaria*, port d'Humata [Guam], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Catlow and Reeve (1845: 100), Adams and Adams (1855: 271), Hanley (1858b: 152), Paetel (1889: 428), Hubendick (1945b: 25, 27, 72, figs. 33 and 37; 1946: 41–42, pl. 6, figs. 30–32), Tan (2000: 115), and Tan and Kastoro (2004: 50) regarded *guamensis* as valid.

gussoni. — Incorrect subsequent spelling (Dall 1879: 285–289, pl. XIII, figs. 1–2) of *gussonii*.

gussonii Costa, 1829: 10–11, *Ancyclus* ?, [no type locality indicated, but in an article describing species from Pantelleria Island, Italy], [leg. unknown]. — By mistake, all authors cited below refer to *gussonii* as *gussoni*, except Bucquoy et al. (1886) and Dautzenberg (1900). Dall (1879: 285–289, pl. XIII, figs. 1–2) transferred *gussonii* to *Siphonaria* and Bucquoy et al. (1886: 481, pl. 51, figs. 14–15) into *Williamia*. Paetel (1889: 428) regarded *gussonii* as a valid species of *Siphonaria*, and Dieuzeide (1935: 16, 17–18) as a valid species of the section *Williamia* of the genus *Siphonaria*. Dautzenberg (1900: 155) and Hubendick (1946: 70–71, pl. 6, figs. 34–35, 37) considered *gussonii* to be a valid species of *Williamia*. Galindo

(1977: 416) listed *gussonii* as a valid species, but attributed authorship to both Sowerby and Costa.

***henica* Verrill and Bush, 1900**: 524, pl. LXV, fig. 8, *Siphonaria*, Bailey Bay [Bermuda Islands], [leg. unknown]. — Considered valid by Davis (1904: 127), Hubendick (1946: 29–30), Abbott (1974: 335), and Galindo (1977: 416, as *hernica*).

hernica. — Incorrect subsequent spelling (Galindo, 1977: 416) of *henica*.

hispida. — Incorrect subsequent spelling (Smith *in* Ridley 1890: 497) of *lepida*.

***hispida* Hubendick, 1946**: 64, pl. 5, figs. 32–34, Fernando Noronha, Brazil, [leg. unknown]. — Smith (1890: 497, pl. XXX, figs. 4–4b) described a variety of *picta*, but did not create any new name for it but mentioned that it appeared to be the same species as "*S. hispida*, Gould" from Rio Janeiro. However, as pointed out by Hubendick (1946: 64), Gould's species name from Rio Janeiro was *lepida*, and *hispida* was an incorrect subsequent spelling. However, Hubendick (1946: 64, pl. 5, figs. 32–34) decided to adopt *hispida* to refer to a species for which he recognized several potential synonyms: *picta*, *subrugosa*, and *rugosa*. Secondary records of *picta* are also regarded as part of *hispida* by Hubendick, including that of Adams and Adams (1855: 270, 271, pl. LXXXIV, figs. 10–10a) and the variety of *picta* illustrated by Smith (1890: 497, pl. XXX, figs. 4–4b). Hubendick decided to adopt a new name instead of using *picta* because he thought that d'Orbigny's (1834: pl. LVI, figs. 7–11) original illustrations were too confusing. However, it is unclear whether the creation of a new name was necessary, especially given that Hubendick's *hispida* referred to a different species than Gould's *lepida*, which Smith *in* Ridley referred to as *hispida*. Marcus and Marcus (1960: 107–130, pl. 1, figs. 1–8, pl. 2, figs. 9–12, pl. 3, figs. 13–17, pl. 4, 18–22) regarded *hispida* as valid.

***incerta* Deshayes, 1863**: 81–82, pl. XXXIV [Conchyliologie pl. 7], figs. 16–17, *Siphonaria*, [no type locality indicated, but in an article describing species from Reunion Island], [leg. unknown]. — Liénard (1877: 59), Martens (1880: 310), Paetel (1889: 428), and Dautzenberg (1932: 10) considered *incerta* valid. Hubendick (1946: 47) listed *incerta* as a possible synonym of *laciniosa*. Morrison (1972: 56) regarded it as a synonym of *laciniosa*.

***inculta* Gould, 1848**: 153, *Siphonaria*, New Zealand, [leg. unknown]. — Regarded as valid by Gould (1852: 358–359, figs. 465–465b), Adams and Adams (1855: 271), Hanley

(1858b: 152), Hutton (1878: 7), and Paetel (1889: 428). Regarded as a synonym of *sipho* by Hutton (1880: 36), of *zelandica* by Suter (1913: 600), and of *australis* by Hubendick (1946: 49) and Jenkins (1983: 12, 13, 18, 28).

innocuous. — Incorrect subsequent spelling (Morrison 1972: 57) of *innocuus*.

innocuus **Iredale, 1940**: 439, pl. xxxiv, figs. 9–10, *Parellsiphon*, Norfolk Island [Australia], [leg. unknown]. — Regarded as a synonym of *australis* by Hubendick (1946: 49), but Jenkins (1983: 29) disagreed with that synonymy. Morrison (1972: 57, as *innocuous*) listed it as a synonym of *laciniosa*.

innominata **Iredale, 1915**: 478, *Kerguelenia*, subantarctic islands of New Zealand [Antipodes Island, Auckland Islands, Campbell Island, and Macquarie Island, according to Suter (1913: 602)] [no leg. mentioned by Iredale, but Captain Bollous (Campbell Island), and A. Hamilton (Macquarie Island) according to Suter (1913: 602)]. — Iredale created this name for shells that Suter (1913: 602) had originally misidentified as *lateralis*. Suter (1913: 602) gave the dimensions of four shells, one shell from each of the following islands: Antipodes Island, Auckland Islands, Campbell Island, and Macquarie Island. Given that Iredale did not specify, he supposedly referred to all of them as *innominata*. Hubendick (1945b: 66) regarded *innominata* as valid, but later suggested that it was a possible synonym of either *lateralis* or *stewartiana* (Hubendick 1946: 26–27, 28). Regarded as valid by Odhner (1924: 55) and Powell (1979: 293, pl. 54, figs. 16–17). However, Hubendick (1946: 28) thought that Odhner's *innominata* was a misidentification of *stewartiana* and Powell (1955: 121) thought it was a misidentification of *flemingi*.

intermedia **Davis, 1904**: 127, pl. IV, fig. 16, *Siphonaria*, [no type locality indicated, but in an article describing species from the Bermuda Islands], [leg. unknown]. — The name *intermedia* was created by Davis for a variety of *alternata*, and should now be regarded as a subspecific name (ICZN Article 45.6.4). Hubendick (1946: 45) considered *intermedia* a valid variety of *alternata*, whereas Morrison (1963: 8) simply regarded it as a synonym of *alternata*. However, *intermedia* Davis, 1904 is available but permanently invalid because it is preoccupied by *intermedia* Schrenk, 1867.

intermedia **Schrenck, 1867**: 307–308, *Siphonaria*, Philippinen [Philippines], [leg. unknown]. — The name *intermedia* was created by Schrenk for a forma of *sipho*, and should now be ranked as a subspecies (ICZN Article 45.6.4). Hubendick (1946: 48) mentioned the existence of *intermedia* but did not provide any comment on its status.

japonica **Donovan, 1824**: plate LXXIX, *Patella*, Japan, leg. Dr. Stutzer. — Transferred to *Siphonaria* by Hanley (1858b: 152). Paetel (1889: 428), Pilsbry (1921: 141), Hirase (1934: 94, pl. 121, fig. 12), Abe (1940: 59–95), Hubendick (1945b: 25, 27, 61, 63, figs. 34, 36, 39, 41; 1946: 42–43, pl. 2, figs. 29–32), Kira (1962: 201, pl. 69, fig. 8), Galindo (1977: 416), Hasegawa et al. (2001: 29), Hylleberg and Kilburn (2003: 133), and Zhongyan (2004: 198, pl. 108, fig. E) considered *japonica* valid. Hubendick (1946: 43) regarded Pilsbry's (1921: 141) conclusion that *japonica* was an earlier name for *cochleariformis* as erroneous.

javanica **Lamarck, 1819**: 333, *Patella*, les côtes de Java [Indonesia], leg. Leschenault. — In the original description, Lamarck pointed out the similarity between *javanica* and *leucopleura*. Transferred to *Siphonaria* by Blainville (1827: 294). Regarded as valid by several authors (Adams and Adams 1855: 271; Hanley 1858b: 152; Anton 1839: 26; Paetel 1873: 117; 1883: 178; 1889: 428; Morrison 1972: 52; Dharma 1992: 78, pl. 17, fig. 1; Tan 2000: 116; Hasegawa et al. 2001: 28; Hylleberg and Kilburn 2003: 13; Tan and Kastoro 2004: 50). Hanley (1858b: 152) thought it was a possible synonym of *exigua*. According to Hubendick (1946: 38), *javanica* could not be a synonym of *diemenensis* because the latter is distributed in temperate southern waters.

jeanae **Jenkins, 1984**: 114–116, text figs. 1–2, pl. 1, figs. a–j, pl. 2, figs a–i, *Siphonaria*, Ceduna, S.A. [South Australia], leg. B. B. Collette and J. R. Paxton.

jonasi. — Incorrect subsequent spelling (Paetel, 1873: 117; 1883: 178; 1889: 428; Morrison, 1972: 53) of *jonasii*.

jonasii **Dunker, 1846**: 25, *Siphonaria*, Loandam [Luanda, Angola], [leg. unknown]. — Regarded as valid by Dunker (1853: 3, pl. I, figs. 7–12), Adams and Adams (1855: 271), Hanley (1858b: 152), and Paetel (1873: 117; 1883: 178; 1889: 428; all as *jonasi*). Hubendick (1946: 33) listed *jonasii* as a synonym of *capensis* and Morrison (1972: 53, as *jonasi*) as a synonym of *pectinata*.

koreensis. — Incorrect subsequent spelling (Dunker 1861: 33) of *coreensis*.

***kowiensis* Turton, 1932**: 10, pl. II, fig. 84, *Siphonaria*, [no type locality indicated, but in an article describing new species from the Port Alfred, South Africa], [leg. unknown]. — Hubendick (1945b: 66) regarded *kowiensis* as valid, but he also thought that it could be a synonym of *lessonii* or *tristensis* (Hubendick 1946: 24). Turton's description was based on a heavily-eroded shell and both Hubendick (1946: 24) and Allanson (1958: 159) discussed the difficulty of determining the status of *kowiensis* given the poor quality of Turton's illustration and type specimen.

***kraussi* Hubendick, 1946**: 33–34, pl. 2, figs. 1–4, *Siphonaria*, Tafelbai [Table Bay, South Africa], [leg. unknown]. — Hubendick (1946: 33) created *kraussi* for a forma of *capensis*, and it should now be regarded as a subspecific name (ICZN Article 45.6.4). Hubendick actually created it as a new replacement name for the variety name *lineolata* Krauss, 1848, preoccupied by *lineolata* Sowerby, 1835.

***kurracheensis* Reeve, 1856**: Species 20, pl. V, fig. 20, *Siphonaria*, Kurrachee, Scinde [Karachi, Pakistan], [leg. unknown]. — Regarded as valid by several authors (Hanley 1858b: 152; Issel 1869: 153, 316–317, 318–319; MacAndrew 1870: 445, as *kurrachensis*; Paetel 1873: 117; Paetel 1883: 178; Cooke 1886a: 133, as *kurrachensis*; Cooke 1886b: 383, as *kurrachensis*; Paetel 1889: 428; Melvill and Standen 1901: 457; Pallary 1926: 28, pl. 3, figs. 3.1–3.5; Moazzo 1939: 131–132, pl. XXXVIII, fig. 2; Thorson 1940: 227–229, fig. 32; Hubendick 1945b: 29, 32, 72, fig. 51; Galindo 1977: 416, as *kurrachensis*; Jenkins 1983: 28, 29–30; Jenkins 1984: 116, 117; Bosch et al. 1995: 185, fig. 862; Hylleberg and Kilburn 2003: 133). Adcock (1893: 11, as *kurrachensis*) listed it as a synonym of *luzonica* and Tomlin (1927: 291, as *kurrachensis*) as a synonym of *savignyi*. Hubendick (1946: 54–55, pl. 2, figs. 36–40) regarded *kurracheensis* as valid, and listed five conchological varieties: *kurracheensis* (typical form), *zebra*, *siquijorensis*, *luzonica*, and *depressa*. According to Hubendick (1946: 34), Moazzo's (1939) *kurracheensis* was a misidentification of *belcheri*. According to Morrison (1972: 57), Hubendick's (1946: 54–55, pl. 2, figs. 36–40) *kurracheensis* was a misidentification of *laciniosa*.

kurrachensis. — Incorrect subsequent spelling (MacAndrew 1870: 445; Cooke 1886a: 133; Cooke 1886b: 383; Adcock 1893: 11; Tomlin 1927: 291; Galindo 1977: 416) of *kurracheensis*.

***laciniata* Dunker**. — Paetel (1873: 117; 1883: 178; 1889: 428) listed *laciniata* as a valid name of *Siphonaria*, with no description or illustration. However, no original description by Dunker could be found. Hubendick (1946: 68) regarded *laciniata* as a *nomen nudum* and suggested that it could be an incorrect subsequent spelling of *laciniosa*. It is not an available name.

***laciniosa* Linné, 1758**: 781, *Patella*, India, [leg. unknown]. — Transferred to *Siphonaria* by Hubendick (1946: 47–48, pl. 3, figs. 16–19). Considered valid by Hubendick (1946: 47–48, pl. 3, figs. 16–19; 1955: 132), Morrison (1972: 54–60), Galindo (1977: 416), Abbott (1991: 87, pl. 41, fig. 7), Fukuda (1994: 50, 65, pl. 75, fig. 805), Hasegawa et al. (2001: 29, as *lanciniosa*), and Hylleberg and Kilburn (2003: 133–134). According to Morrison (1972: 52), Hubendick's (1946: 47–48, pl. 3, figs. 16–19) *laciniosa* was a misidentification of *javanica*.

***laevis* Philippi, 1846**: 51, *Siphonaria*, Chili [Chile], [leg. unknown]. — Regarded as valid by Hanley (1858b: 152) and Paetel (1889: 428), and as a synonym of *lessonii* by Hubendick (1946: 21) and Forcelli (2000: 132).

***laeviscula*.** — Incorrect subsequent spelling (Galindo 1977: 416) of *laeviuscula*.

***laeviuscula* Sowerby, 1835**: 7, *Siphonaria*, Valparaiso [Chile], leg. G. B. S. [i.e. G. B. Sowerby]. — The name in the original description is l*æviuscula*, which should now be spelled *laeviuscula* (ICZN Article 27). Reeve (1856: Species 5, pl. I, figs. 5a–5b) listed *laeviuscula* as a valid species, but erroneously attributed authorship to Blainville, as pointed out by Watson (1886: 675). Following Reeve, several authors have incorrectly cited Blainville as the author of this species (Hutton 1878; Paetel 1873, 1883, 1889; Galindo 1977). Regarded as valid by Catlow and Reeve (1845: 100), Adams and Adams (1855: 271, as *leviuscula*), Hanley (1858b: 152), Paetel (1873: 117; 1883: 178; 1889: 428), Köhler (1894: 23–27, fig. B, pl. 2, figs. 22–25, pl. 5, fig. 5), Dall (1909: 205), Hubendick (1945b: 12, 66, figs. 5 and 13; 1946: 20, pl. 1, figs. 4–8), Galindo (1977: 416, as *laeviscula*), and Forcelli (2000: 132, fig. 422). Regarded by d'Orbigny (1854: 50) as a synonym of *lessonii*. Listed as a synonym of *funiculata* by Hutton (1878: 42), but Hubendick (1946: 23) thought that Hutton's (1878: 42) *laeviuscula* was a misidentification of *funiculata*. Strebel (1907: 172, pl. 3, fig. 34) considered *laeviuscula* a variety of *tristensis*. According to Hubendick (1946: 20), *laeviuscula* inhabits South America from Valparaiso southwards to the Strait of Magellan but is absent from New

Zealand, based on records by Paetel (1889) and Suter (1915); however, Suter (1913, 1915) does not mention *laeviuscula*, and Hubendick possibly may have been referring to *lateralis* instead.

lanciniosa. — Incorrect subsequent spelling (Hasegawa et al. 2001: 29) of *laciniosa*.

lateralis Couthouy *in* Gould, 1848: 153–154, *Siphonaria*, Burnt Island, Orange Harbor [Nassau Bay, Argentina], [leg. unknown]. — Several authors considered *lateralis* valid and attributed authorship to Couthouy: Gould (1852: 363–364, figs. 462–462b), Rochebrune and Mabille (1889: 29), Pelseneer (1903: 9–10), Strebel (1907: 172–173, pl. 3, figs. 27–29a; 1908: 8), and Suter (1909b: 33–34). Others regarded *lateralis* as valid, but attributed authorship to Gould: Adams and Adams (1855: 271), Hanley (1858b: 152), Frauenfeld (1869: 878), Paetel (1889: 428), Suter (1913: 601–602; 1915: pl. 49, fig. 10), Hubendick (1945b: 17, 19, 66, 67, figs. 15 and 59; 1946: 26–27, pl. 1, figs. 22–25), Morrison (1963: 8), Dell (1964: 290–292), Powell (1979: 293, pl. 54, figs. 18–19), and Forcelli (2000: 132, fig. 423). It was regarded as a synonym of *redimiculum* by Smith (1879: 182) and of *innominata* by Watson (1886: 675). The identification of *lateralis* by Suter (1913) has remained problematic: Odhner (1924: 55) thought it was a misidentification of *innominata*; Hubendick (1946: 28) thought it was a misidentification of *stewartiana*; Powell (1955: 121) thought it was, in part, a misidentification of *flemingi* and, in part, of *lateralis macquariensis*; Powell (1979: 293) also regarded it as a misidentification of *innominata*. Powell (1955: 122) regarded Hubendick's (1946: 26–27, pl. 1, figs. 22–25) identification of *lateralis* as a misidentification of *lateralis macquariensis*, but later (Powell 1979: 293) listed *lateralis macquariensis* as a synonym of *lateralis*.

lecamium. — Incorrect subsequent spelling (Galindo 1977: 416) of *lecanium*.

lecania. — Unjustified emendation (Strong and Hanna 1930: 21; Burch 1945: 16) of *lecanium*, because *lecanium* is a Latinized greek substantive, not an adjective. According to ICZN Article 33.2.3, *lecania* is a junior objective synonym of *lecanium*.

lecanium Philippi, 1846: 51, *Siphonaria*, Mazatlan [Mexico], [leg. unknown]. — Carpenter (1857a: 182–183, 1864: 676), Hanley (1858b: 152), Binney (1867: 154), Dall (1870: 39), Paetel (1873: 117, as *leoanium*; 1883: 178; 1889: 428); Stearns (1895: 166–169), Fischer and Crosse (1900: 107), Melvill and Standen (1901: 457), Pilsbry and Lowe (1932: 108), Morrison (1963: 8), and Galindo (1977: 416, as *lecamium*)

regarded *lecanium* as valid. Strong and Hanna (1930: 21) and Burch (1845: 16) regarded it as a variety (as *lecania*) of *maura*. Hubendick (1946: 40) and Keen (1958: 510) listed *lecanium* as a synonym of *maura*. Melvill and Standen (1901) recorded *lecanium* from Karachi but Hubendick (1946: 52) thought this was a misidentification of *atra*.

***lentulus* Iredale, 1940**: 439, pl. xxxiv, figs. 14–15, *Mestosiphon*, Lord Howe Island [Australia], [leg. unknown]. — Regarded as a synonym of *australis* by Hubendick (1946: 49) and Jenkins (1983: 29), and as a synonym of *laciniosa* by Morrison (1972: 57).

leoanium. — Incorrect subsequent spelling (Paetel 1873: 117) of *lecanium*.

***lepida* Gould, 1848**: 154, *Siphonaria*, Rio Janeiro [Brazil], [leg. unknown]. — Regarded as valid by Gould (1852: 360–361, figs. 466a–466c), Adams and Adams (1855: 271), Hanley (1858b: 152), Paetel (1889: 429), and Hubendick (1946: 64–65, pl. 5, figs. 23–24), but regarded as a synonym of *alternata* by Morrison (1963: 8). According to Hubendick (1946: 43, 65), *lepida* from Fujita (1895: 89–93, pl. XIV, figs. 1–10) was a misidentification of *cochleariformis*.

lessoni. — Incorrect subsequent spelling (multiple authors, see below) of *lessonii*.

***lessonii* Blainville, 1827**: 296, *Siphonaria*, îles Malouines [Falkland Islands], leg. MM. Lesson et Garnot [Expedition of *la Coquille*]. — There has been a great deal of confusion in the literature about the date of publication of *lessonii* as well as about the spelling (i.e. *lessoni* or *lessonii*). The correct date of publication is 1827, although all authors who have mentioned a date selected 1824. Blainville (1827: 296) published a written description of *lessonii* in the article on the *Siphonaire* in the 49th volume of the *Dictionnaire des Sciences Naturelles*. In the same year, Blainville (1827: pl. 44, figs. 2–2a) also published an illustration of what he referred to as "Siphonaire de Lesson," in the *Atlas* of his *Manuel de Malacologie et de Conchyliologie*. Blainville's *Manuel* was published in two volumes: in the first volume, which only contains the text, Blainville (1825) did not mention *S. lessonii*, which was only mentioned in the second volume with the plates. Thus, the correct reference for *S. lessonii* is Blainville's (1827: 296) article on *Siphonaire* in the *Dictionnaire des Sciences Naturelles* in which the binomial "*S.* [for *Siphonaria*] *lessonii*" clearly appears as a correct Linnean binomial. The original spelling was *lessonii*. Therefore, according to ICZN Article 33.4, *lessoni*

is an incorrect subsequent spelling and only *lessonii* should be regarded as the correct spelling, although most authors have used *lessoni* instead of *lessonii*, with a few exceptions (e.g. Potiez and Michaud 1838: 55; d'Orbigny 1841: 469; Catlow and Reeve 1845: 100; Hupé 1854: 249–250; d'Orbigny 1854: 50; Paetel 1873: 117). According to Dall (1909: 205), *lessonii* was first published by Blainville in the "Dict. Sci. Nat., vol. 32, p. 267, pl. 44, fig. 2." Blainville (1824a: 267–268) mentioned the genus *Siphonaria* in the article on *Mollusques* published in the 32nd volume of the *Dictionnaire des Sciences Naturelles*, but he did not mention *lessonii*. Also, Dall's (1909) citation was confusing because "pl. 44, fig. 2" does refer to another book than the *Dictionnaire*, i.e. the *Atlas* of Blainville's (1827) *Manuel*. Several authors cited Blainville as an author, without specifying any date (Jay 1839: 39; Catlow and Reeve 1845: 100; Mörch 1852: 148; Hupé 1854: 249–250; d'Orbigny 1854: 50; Adams and Adams 1855: 271; Paetel 1873: 117; 1883: 178; 1889: 429; Pelseneer 1903: 9; Hubendick 1945b: 12, 15, 16, 64, 66, figs. 2, 7–9, 56; Galindo 1977: 416). Hanley (1858b: 152" cited "Blainville, Malac.," likely to refer to Blainville's (1827) *Atlas* of the *Manuel*. Gould (1852: 361–362) also provided Blainville's *Atlas* as "Malacol., pl. 44, fig. 2" as a reference for *lessonii*. However, as indicated above, the name used in Blainville's (1827: pl. XLIV, figs. 2–2a) was invalid ("Siphonaire de Lesson"). Several authors (Burch 1945: 16; Morrison 1963: 7) cited "Blainville, 1824" as authorship without any explanation or reference. D'Orbigny (1834: pl. LVI, figs. 12–14; 1841: 469;) provided a wrong date ("Blainv., 1825, Malacologie, pl. 44, fig. 2"), as did Rochebrune and Mabille (1889: 28–29), because 1825 was the publication date of the first volume of Blainville's *Manuel*, but the date of the *Atlas* is 1827. Potiez and Michaud (1838: 55, pl. X, figs. 15–17) cited De Boissy as an author, which was a mistake. Lamarck (1839: 207) is one of the few authors who gave a nearly correct citation for *lessonii* as "De Blainv., Malac. pl. 44, f. 2. Dict. Sc. Nat. t. 49, p. 296." According to Reeve (1856: Species 23, pl. V, figs. 23a–23b), Dall (1870: 33, 1876: 45), Watson (1886: 675), and Strebel (1907: 170), *lessonii* is a synonym of *tristensis*. Most other authors have accepted *lessonii* as a valid species. According to Hubendick (1946: 21, as *lessoni*), *lessonii* is distributed on the West coast (from about 12° S) and the East coast (up to Uruguay) of South America through the Tierra del Fuego, including the Falkland Islands (type

locality). Dall (1909) also considers *lessonii* to be present in Nicaragua, which may not be part of its natural distribution.

leucopleura **Gmelin, 1791**: 3699, *Patella*, [no type locality indicated], [leg. unknown]. — Regarded as a valid name of *Patella* by Lamarck (1819: 332), but transferred to *Siphonaria* by Blainville (1827: 293). Hanley (1858b: 152) provided an erroneous authorship (Blainville), but Blainville (1827: 293) only mentioned *leucopleura* as a valid name of *Siphonaria*. Regarded as a valid species by many authors (e.g. Anton 1839: 26; Jay 1839: 39; Catlow and Reeve 1845: 100; Martens 1874: 127, 141; Paetel 1873: 117; 1883: 178; 1889: 429). According to Hubendick (1946: 31), Arango's (1878: 230) record of *leucopleura* from the Caribbean Islands was a misidentification of *pectinata*. According to Dall (1886: 288), Arango's (1878: 230) *leucopleura* was a misidentification of *lineolata*. According to Hubendick (1946: 58), Paetel's (1883: 178) record of *leucopleura* from Viti (Fiji Islands) was a misidentification. Hubendick (1946: 58) also discussed a possible synonymy of *leucopleura* with *concinna*.

leviuscula. — Incorrect subsequent spelling (Adams and Adams 1855: 271) of *laeviuscula*.

lineata. — Incorrect subsequent spelling (Krebs 1864: 75) of *lineolata*.

lineata **Lamarck, 1819**: 331–332, *Patella*, [no type locality indicated], [leg. unknown]. — Paetel (1889: 429) listed "*lineata* Lm." in a checklist of *Siphonaria* species names. However, to our knowledge, he is the only author who ever regarded *lineata* as a species of *Siphonaria*.

lineolata **Krauss, 1848**: 58, pl. IV, fig. 2, *Siphonaria*, Tafelbai [Table Bay, South Africa], [leg. unknown]. — The name *lineolata* was created by Krauss for a variety of *capensis* which should now be regarded as a subspecific name (ICZN Article 45.6.4). Regarded as a valid variety name of *capensis* by Martens (1874: 127), Sowerby (1892: 54), Bartsch (1915: 10), Turton (1932:10), and Hubendick (1945b: 19, 1946: 33). However, *lineolata* Krauss, 1848 is available, but permanently invalid because it is preoccupied by *lineolata* Sowerby, 1835. Hubendick (1946: 33) created *kraussi* as a new replacement name.

lineolata **d'Orbigny, 1841**: 232–233, [1842: pl. XVII, figs. 13 and 15], *Siphonaria*, près de la Havane [Havana, Cuba], leg. de la Sagra et Auber. — The *Histoire Physique, Politique et Naturelle de l'Ile de Cuba* was initially printed in parts from 1841 to 1853: the written description of *lineolata* was published in 1841, and

plate XVII in 1842. Regarded as valid by Krebs (1864: 75, as *lineata*), Dall (1886: 288, 1902: 501), Smith (1890: 497), Dautzenberg (1900: 154), and Ihering (1915: 141), as a synonym of *leucopleura* by Arango (1878: 230), and as a synonym of *pectinata* by Hubendick (1946: 31) and Morrison (1963: 9; 1972: 53–54). However, *lineolata* d'Orbigny, 1841 is available but permanently invalid because it is preoccupied by *lineolata* Sowerby, 1835.

lineolata **Sowerby, 1835**: 6, *Siphonaria*, Insulam Chiloe Chilensium [Chiloé Island, Chile], leg. G. B. S. [i.e. G. B. Sowerby]. — Regarded as valid by d'Orbigny (1846: 682), Catlow and Reeve (1845: 100), Reeve (1856: Species 11, pl. III, figs. 11a–11b), Adams and Adams (1855: 271), Paetel (1873: 117; 1883: 178; 1889: 429), Dall (1909: 205), Pilsbry and Lowe (1932: 108), Burch (1945: 16), and Galindo (1977: 416). Regarded as a synonym of *costata* by Hanley (1858b: 152) and as a synonym of *leucopleura* by Arango (1878: 230). According to Hubendick (1946: 68), Reeve's (1856) record of *lineolata* was a misidentification. Philippi (1860: 181) thought it might be a synonym of *tenuis*. Hubendick (1946: 21, 31, 68) thought *lineolata* could be a synonym of *lessonii* or of the variety *venosa* of *pectinata*, but listed it as a *nomen nudum*, although he actually meant that it was a *nomen dubium*. Dall (1870: 32) classified *lineolata* in the section (subgenus) *Liriola*, along with *lateralis*, *lessonii*, *macgillivray*i, *redimiculum*, *thersites*, and *tristensis*.

lirata **Reeve, 1856**: Species 35, pl. VII, figs. 35a–35b, *Siphonaria*, [no type locality indicated], [leg. unknown]. — According to Reeve's *erratum* on the same page as the appendix (no pagination), the name of Species 35 should read *lirata* instead of *funiculata*. Hanley (1858b: 152), Brazier (1888: 1001), and Galindo (1977: 416) regarded *lirata* as valid. Both Hubendick (1946: 23) and Jenkins (1981: 2) regarded it as a synonym of *funiculata*.

luzonica **Reeve, 1856**: Species 29, pl. VI, figs. 29a–29b, *Siphonaria*, Puteao, Island of Luzon, Philippines, [leg. unknown]. — Considered valid by Hanley (1858b: 152), Angas (1865: 190), Paetel (1889: 429), Adcock (1893: 11), Dautzenberg (1910a: 25), Hubendick (1955: 128, fig. 3), and Galindo (1977: 416). Köhler (1894: 43–45, pl. 4, fig. 52, pl. 6, figs. 13–15) regarded *luzonica* as a variety of *stellata*. Cooke (1886a: 133) and Hubendick (1946: 54–55, pl. 2, fig. 36) regarded *luzonica* as a variety of *kurracheensis*. It was regarded as a synonym of *sipho* by Adam and Leloup (1939: 7) and a synonym of *laciniosa* by Morrison (1972: 56).

***macauleyensis* Oliver, 1915**: 547, pl. XII, figs. 42–42a, *Siphonaria*, Macauley Island [Kermadec Islands, New Zealand], [leg. unknown]. — Hubendick (1946: 38) considered *macauleyensis* a synonym of *diemenensis*.

***macgillivrayi* Reeve, 1856**: Species 25, pl. V, figs. 25a–25b, *Siphonaria*, Island of St. Paul's [Indian Ocean], [leg. unknown]. — Considered valid by Hanley (1858b: 152), Paetel (1873: 117; 1883: 178; 1889: 429), Rochebrune and Mabille (1889: 28), Hubendick (1945b: 17, 19, 67–68, figs. 16–18, 57; 1946: 28–29, pl. 6, figs. 4–6), and Galindo (1977: 416). Forcelli (2000: 132, fig. 423) listed it as a synonym of *lateralis*.

***macquariensis* Powell, 1939**: 238, pl. 49, figs. 9–10, *Kerguelenia*, Macquarie Island [Australia], [leg. unknown]. — Powell (1946: 91) regarded it as valid. Powell (1955: 122) and Galindo (1977: 416, as *macquerensis*) thought it was a subspecies of *lateralis*. Ultimately, Powell (1979: 239) agreed with Hubendick (1946: 26) that it was a synonym of *lateralis*.

***macquerensis*. —** Incorrect subsequent spelling (Galindo 1977: 416) of *macquariensis*.

***madagascariensis* Odhner, 1919**: 20, pl. I, figs. 10–12, *Siphonaria*, Majunga [Madagascar], [leg. W. Kaudern]. — Dautzenberg (1923: 24) and Hubendick (1945b: 29, 30, fig. 50; 1946: 55–56, pl. 4, figs. 20–24) regarded it as valid, although Hubendick also mentioned that it could be a synonym of *kurracheensis*. Morrison (1972: 57) listed it as a synonym of *laciniosa*.

***magellanica* Philippi, 1856**: 100, *Siphonaria*, [no type locality indicated, but in an article describing shells from the Strait of Magellan], [leg. unknown]. — Note that the article that contains the original description of *magellanica* was published twice by Philippi (1856, 1857). Considered valid by Hanley (1858b: 152) and Paetel (1889: 429). Smith (1879: 182) listed *magellanica* as a possible synonym of *redimiculum*. Strebel (1907: 174) regarded it as a synonym of *tristensis*, and Hubendick (1946: 26) as a synonym of *lateralis*.

***mamillaris*. —** Incorrect subsequent spelling (Anton 1839: 26; Menke 1853: 68) of *mammillaris*.

***mammillaris* Linné, 1758**: 782, *Patella*, M. Mediterraneo [Mediterranean Sea], [leg. unknown]. — Anton (1839: 26, as *mamillaris*) transferred *mammillaris* to *Siphonaria*. Menke (1853: 68, as *mamillaris*) agreed it was a *Siphonaria* but thought it probably was a valid name for *leucopleura*. However, Iredale (1940:

437) and Hubendick (1946: 73–74) regarded *mammillaris* as a species of *Trimusculus* (which they referred to as *Gadinia*). Subsequently designated as the type species of *Trimusculus* by Rehder (1940: 68).

***marza* Iredale, 1940**: 438, pl. xxxiv, figs. 1–2, *Ellsiphon*, Keppel Bay [Queensland, Australia], leg. H. Bernhard. — Regarded as valid by Galindo (1977: 416) and Hubendick (1946: 61, pl. 5, figs. 27–28) who added Port Jackson, Sydney, New South Wales, as another locality.

***maura* Sowerby, 1835**: 7, *Siphonaria*, Panamam [Panama], [leg. unknown]. — Regarded as valid by Catlow and Reeve (1845: 100), Reeve (1856: Species 36, pl. VII, figs. 36a–36b), Adams and Adams (1855: 271), Hanley (1858b: 152), Dall (1870: 39, 1909: 205), Paetel (1883: 178; 1889: 429), Pilsbry and Lowe (1932: 108), Burch (1945: 16), Hubendick (1946: 40–41, pl. 2, figs. 18–28), Keen (1958: 510, figs. 1032–1032b), Morrison (1963: 8), and Galindo (1977: 416).

***melanoleuca* Gmelin, 1791**: 3713, *Patella*, [no type locality indicated], [leg. unknown]. — In addition to a brief written description, Gmelin (1791: 3713) referred to previous illustrations: "Martin. Conch. I, *t. 7, f. 56. 57.*," which refers to a shell illustrated by Martini (1769: 110–111, pl. VII, figs. 56–57) according to whom it is similar to Adanson's (1757: pl. 2, fig. 5) "mouret" from Senegal. Martens (1874: 127) regarded *melanoleuca* as a synonym of *variabilis*. According to Hubendick (1946: 58), the record of *melanoleuca* by Martens (1874) was a misidentification of *concinna*, and *variabilis* was a synonym of *concinna*. However, Hubendick (1946: 58) did not comment on Gmelin's original description. Morrison (1972: 53) regarded *melanoleuca* as a synonym of *pectinata*. Given the absence of type locality, it probably should be regarded as a *nomen dubium*.

***melanozonias* Gmelin, 1791**: 3703, *Patella*, [no type locality indicated], [leg. unknown]. — Transferred to *Siphonaria* by Mörch (1852: 148). Regarded as valid by several authors (Mörch 1852: 148; Adams and Adams 1855: 271; Martens 1874: 127). However, Tryon and Pilsbry (1891: 160) thought it just referred to an unidentifiable limpet, which may or may not belong to *Siphonaria*. Also, Hubendick (1946: 68) argued that it should be regarded as a *nomen nudum* or simply be rejected, because insufficiently described. It cannot be a *nomen*

nudum because Gmelin did provide a brief description. However, it should probably be a *nomen dubium*, especially given the lack of type locality.

milneedwardsi **Locard, 1898**: 99–100, pl. IV, figs. 19–21, *Siphonaria*, La Praja (Cap–Vert) [Praia, Cape Verde, collected during the expedition of *le Talisman*], [leg. unknown]. — It was originally created as *milne-edwardsi*, but should now be spelled without the hyphen (ICZN Article 32.5.2.4). Hubendick (1946: 31) regarded it as a possible synonym of *pectinata*.

minor **Pallary, 1900**: 243, *Siphonaria*, Oran [Algeria], [leg. unknown]. — The name *minor* was created by Pallary for a variety of a species he referred to as *Siphonaria mouret* (Adanson, 1757) which he thought was a synonym of *S. algesirae*. According to ICZN Article 45.6.4, *minor* is to be regarded as a subspecific name. Dieuzeide (1935: 29, 30) and Hubendick (1946: 32) considered *minor* a variant form of *pectinata*.

mirificus **Iredale, 1940**: 440–441, pl. xxxiv, figs. 28–29, *Legosiphon*, Magnetic Island, near Townsville, Queensland [Australia], leg. A. F. Basset Hull. — Regarded as a possible synonym of *ferruginea* by Hubendick (1946: 53), although Hubendick's (1946: pl. 4, figs. 16–19) illustrations of *ferruginea* do not resemble those from Iredale. However, Hubendick (1946: 61) also considered that *mirificus* may be a valid species or even the corroded shell of another species, such as *acmaeoides*.

monticulus **Iredale, 1940**: 441, pl. xxxiv, figs. 11 and 13, *Hebesiphon*, Lifu, Loyalty Islands, New Caledonia, [leg. unknown]. — Regarded as valid by Hubendick (1945b: 29; 1946: 45–46, pl. 3, figs. 7–9) who added Wijnkoops Bay, Java, as another locality.

mouret **Adanson, 1757**: 34–35, pl. 2, fig. 5, *Lepas*, isle de Gorée [Gorée Island, Dakar, Senegal], [leg. unknown]. — Several authors (e.g. Sowerby 1825: 32; Menke 1853: 68; Pallary 1900: 242–243) have treated *Siphonaria mouret* as an available name, with authorship to Adanson. However, the specific name *mouret* is not available according to the current Code because it was published before 1758 and because Adanson was not using consistently a Latin binominal nomenclature. In fact, Adanson referred to the species discussed here with a French vernacular name, Le Mouret, which explains that Hanley (1858b: 152) referred to it as "*Le Mouret*," and Paetel (1889: 429) selected *Lemouret* as a specific name instead of *mouret*. The fact that authors have attributed the

authorship to Adanson for his "mouret" throughout the 19th century is easily understood: 1758 was adopted as the starting date for application of the concept of priority only in 1892 (see Dayrat 2010), which means that before 1892 authors could use names that had been created before 1758. Sowerby (1825: 32), Paetel (1889: 429, as "*lemouret*"), and Pallary (1900: 242–243) regarded *mouret* as valid. Menke (1853: 68) and Iredale (1921: 207) thought it was a synonym of *Patella grisea* Gmelin, 1791, which Menke (1853: 68) also rightly transferred to *Siphonaria*. Indeed, *grisea* was created by Gmelin specifically to replace Adanson's (1757: 34–35, pl. 2, fig. 5) Le Mouret. As a result, *grisea* is an objective synonym of both *adansonii* and *mouretus* (see these specific names), also created with a reference to Adanson's description of Le Mouret. Dautzenberg (1889: 164; 1910b: 55 [1910c: 9]) and Dieuzeide (1935: 18) listed *mouret* as a synonym of *algesirae*. Hubendick (1946: 31) and Morrison (1972: 53, 54) listed *mouret*, *mouretus*, and *le mouret* as synonyms of *pectinata*. However, for the reasons given above, *mouret* is not available under the current Code and thus cannot be valid, nor can it be a synonym.

mouretus **Blainville, 1824a**: 267–268, *Siphonaria*, [no type locality indicated, but "Isle de Gorée, Dakar, Senegal, according to Adanson], [leg. unknown, but based on an earlier description by Adanson who collected his own specimens in Senegal]. — Blainville created *mouretus* to refer to a species described by Adanson (1757: 34–35, pl. 2, fig. 5) as "Le Mouret" and placed in the genus *Lepas*. A year later, Blainville (1825: 475) published the same comment on Adanson's description. However, Blainville (1824b: 162) also introduced *Mouretus adansonii* to refer to the same species description by Adanson (see *adansonii*). Later on, Blainville (1827: 295) listed "*le Mouret*" as a synonym of *Siphonaria adansonii*. Thus, *Siphonaria mouretus* Blainville, 1824a and *Mouretus adansonii* Blainville, 1824b are objective synonyms because they are based on the same type material (i.e. the material described and originally illustrated by Adanson). There is a third objective synonym: *Patella grisea*, created by Gmelin (1791: 3727) with a reference to Adanson's description of Le Mouret. Only one of these three names could potentially be valid, which naturally is *grisea*. However, for the time being, they are all regarded as synonyms of *pectinata*. Hubendick (1946: 31) and

Morrison (1972: 53, 54) listed *mouretus* as a synonym of *pectinata* (see also *adansonii*, *grisea*, *mouret*, and *pectinata*).

***natalensis* Krauss, 1848**: 61, pl. IV, fig. 6, *Siphonaria*, In litore natalensi [Natal, South Africa], [leg. unknown]. — Regarded as valid by Adams and Adams (1855: 271), Hanley (1858b: 152), Paetel (1883: 178), Paetel (1889: 429), Sowerby (1892: 54), Dautzenberg (1923: 24), Turton (1932: 10), Hubendick (1946: 59–60, pl. 5, fig. 18), and Galindo (1977: 416, as *nataliensis*). Cooke (1886a: 133) thought that *natalensis* was a synonym of *kurracheensis*. Regarded as a synonym of *aspera*, by Allanson (1958: 169, 171) and Kilburn and Rippey (1982: 135), and as a synonym of *serrata* by Chambers and McQuaid (1994a: 264, 265).

***nataliensis*.** — Incorrect subsequent spelling (Galindo 1977: 416) of *natalensis*.

***naufragum* Stearns, 1873b**: 23–24, *Siphonaria*, Amelia Island, east coast of Florida, leg. Col. E. Jewett and Dr. William Stimpson. — Regarded by Dall (1886: 288; 1902: 501) as a synonym of *lineolata*, and by Hubendick (1946: 31) and Morrison (1972: 54) as a synonym of *pectinata*.

***nereis* Iredale, 1940**: 441–442, *Talisiphon*, Port Fairy, Victoria [Australia], [leg. unknown]. — Iredale created *nereis* as a subspecies of *Talisiphon tasmanicus*. Hubendick (1946: 22) regarded *tasmanica* as valid but did not comment on *nereis*.

***nigerrima* Smith, 1903**: 356, pl. XV, figs. 4–5, *Siphonaria*, Umhlali, Natal [South Africa], leg. Burnup. — Regarded as valid by Hubendick (1945b: 19, 20, 70). Hubendick (1946: 35) and Kilburn and Rippey (1982: 134) considered *nigerrima* a synonym of *carbo*. However, Chambers and McQuaid (1994a: 264, 265, fig. 1M) argued that *carbo* is found in the Caribbean and thus regarded *nigerrima* as valid.

***nigra* Pallary, 1900**: 243, *Siphonaria*, Oran [Algeria], [leg. unknown]. — The name *nigra* was created by Pallary for a variety of a species he referred to as *Siphonaria mouret* (Adanson, 1757) which he thought was a synonym of *S. algesirae*. According to ICZN Article 45.6.4, *nigra* is to be regarded as a subspecific name. Dieuzeide (1935: 30) and Hubendick (1946: 32) considered *nigra* a variant form of *pectinata*.

***normalis* Gould, 1848**: 154, *Siphonaria*, Sandwich Islands [Hawaii], [leg. unknown]. — Gould (1852: 359–360, figs. 468a–b), Adams and Adams (1855: 271), Paetel (1883: 178;

1889: 429), Hubendick (1946: 63; 1947: 4, figs. 3–4), Cernohorsky (1972: 210, pl. 60, fig. 2), Galindo (1977: 416), and Jenkins (1984: 117) considered *normalis* valid.

nuttali. — Incorrect subsequent misspelling (Paetel 1883: 178; Hubendick 1946: 17, 50, 51–52, 63, pl. 4, figs. 1–4) of *nuttallii*.

***nuttallii* Hanley, 1858b**: 153, *Siphonaria*, Insularum Sandvicensium [Hawaii], leg. Dr. Frick. — Regarded as valid by Paetel (1873: 117; 1883: 178, as *nuttali*; 1889: 429) and Hubendick (1945b: 73; 1946: 51–52, pl. 4, figs. 1–4, as *nuttali*).

***obliquata* Sowerby, 1825**: vii, *Siphonaria*, Van Diemen's Land [Tasmania], [leg. unknown]. — According to the original description, the type locality is Tasmania. However, according to Reeve (1856), the distribution of *obliquata* is New Zealand, and most authors have followed him. Regarded as valid by most authors: Reeve 1842: 20, pl. CXXXVIII, figs. 4–5; Catlow and Reeve 1845: 100; Reeve 1856: Species 12, pl. III, figs. 12a–12b; Hanley 1858b: 152; Hutton 1873: 56; Paetel 1873: 117; 1883: 178; 1889: 429; Hutton 1880: 36; 1883: 141–142, pl. XVII, figs. A–D; Moss 1908: 41, pl. IX, fig. 24; Suter 1909b: 33; 1913: 599–600; 1915, pl. 48, fig. 9; Cottrell 1911: 582–594, figs. 1–8, pl. XXVIII, figs. 1–7, pl. XXIX, figs. 1–3; 1912: 374–379, figs. 1–4; Iredale 1915: 478; Odhner 1924: 55; Powell 1939: 217; 1946: 91; 1979: 293, pl. 54, figs. 12–13; Hubendick 1945b: 17, 66, figs. 11 and 14; 1946: 24; Borland 1950: 385–393; Morton and Miller 1968: 302, 336, 338, 354, 378, figs. 121–122, pl. 19, fig. 10; Galindo 1977: 416; Jenkins 1983: 28, 30; Morley 2004: 130; Bucknill 1924: 82, pl. III, figs. 15–15a. Hutton (1878: 41) regarded it as a synonym of *diemenensis*.

***oblivirgulata* Hubendick, 1945a**: 4–5, figs. 2 and 6, *Siphonaria*, Port Jackson, Australien [Sydney, New South Wales, Australia], leg. Eugenie Expedition. — Regarded as valid by Hubendick (1945b: 66) and thought to represent a transition between *obliquata* and *virgulata*, hence its name (Hubendick 1946: 25–26, pl. 1, figs. 26–27). So far, endemic to Sydney Harbor.

***oblonga* Sowerby**. — This name was only mentioned by Paetel (1883: 178; 1889: 429) and no original description could be found. Hubendick (1946: 68) rightly regarded it as a *nomen nudum*.

***oblongata* Yokoyama, 1926**: 288, pl. XXXIV, fig. 14, *Acmaea*, Sawané Formation [Sado Island, Japan Sea], leg. Y. Ozawa. — Although *oblongata* was originally

described from the Pliocene, Habe (1958: 35–36, pl. 2, figs. 3–4) discovered an extant population he identified as *oblongata* living on eelgrass at the entrance of Lake Akkeshi, Japan. Habe (1958: 35–36, pl. 2, figs. 3–4; 1964: 144, pl. 44, fig. 15) transferred *oblongata* into a new genus, *Siphonacmea*. Toyohara et al. (2001: 27–35) detailed the population dynamics and life history of *oblongata* living in Ostuchi Bay, Honshu, Japan.

oculus **Krauss, 1848**: 58–59, pl. IV, fig. 3, *Siphonaria*, In sinu tabulari [Table Bay, South Africa], [leg. unknown]. — Regarded as a valid by Adams and Adams (1855: 271), Hanley (1858b: 152), Paetel (1889: 429), Sowerby (1892: 54), Bartsch (1915: 11), Turton (1932: 10), Hubendick (1946: 59, pl. 5, figs. 7–8), Allanson (1958: 163–166; 1963: 70), Galindo (1977: 416), Kilburn and Rippey (1982: 134, pl. 32, fig. 11), and Chambers and McQuaid (1994a: 265, fig. 1G).

opalescens **Davis, 1904**: 127, pl. IV, fig. 15, *Siphonaria*, Hungry Bay [Bermuda Islands], [leg. unknown]. — The name *opalescens* was created by Davis for a variety of *alternata*, and is now regarded as a subspecific name (ICZN Article 45.6.4). Hubendick (1946: 45) regarded *opalescens* as a valid variety name, but Morrison (1963: 8) regarded it as a synonym of *alternata*.

oppositus **Iredale, 1940**: 440, *Mallorisiphon*, Keppel Bay [Queensland, Australia], many places in Queensland [no more detail provided], Facing Island, Port Curtis, Fiji, leg. H. Bernhard [for specimens collected from Keppel Bay]. — Iredale mentioned several localities without specifying one of them as the type locality. As a result, all localities are regarded as type localities. Hubendick (1946: 52) regarded it as a variant form of *atra* and Morrison (1972: 57) as a synonym of *laciniosa*.

optivus **Iredale, 1940**: 440, pl. xxxiv, figs. 26–27, *Legosiphon*, Magnetic Island, Queensland [Australia], [leg. unknown]. — Regarded as a synonym of *laciniosa* by Hubendick (1946: 47; 1954: 132).

pallida **Allanson, 1958**: 171–173, pls. III–IV, figs. 8 and 17, *Siphonaria*, Langebaan Lagoon, Saldanha Bay [South Africa], leg. J. H. Day. — The name *pallida* was created by Allanson for a variety of *aspera* and is now regarded as a subspecific name (ICZN Article 45.6.4). Regarded as a synonym of *aspera* by Kilburn and Rippey (1982: 135).

palmata **Carpenter, 1857a**: 183, *Siphonaria*, Mazatlan [Mexico], [leg. unknown]. — The name *palmata* was created by Carpenter for a variety of *lecanium* and is now regarded as a subspecific name (ICZN Article 45.6.4). Hubendick (1945b: 22, 24, 72, fig. 31; 1946: 40, plate 2, figs. 18–25) regarded *palmata* as a valid variety name of *lecanium* but determined that *lecanium* was a synonym of *maura*, thereby using the name *maura* var. *palmata*. Several other authors regarded it as a valid variety name of *maura* (Strong and Hanna 1930: 21; Pilsbry and Lowe 1932: 108, as *palmula*; Burch 1945: 16; Keen 1958: 510, fig. 1032a; Galindo 1977: 416, as both *palmata* and *palmula*). However, according to Stearns (1895: 166–168), it is a synonym of *lecanium*. Finally, some authors treated *palmata* as a specific name and not a variety (Dall 1870: 39; Morrison 1963: 8; Galindo 1977: 416) although Dall (1870: 39) also acknowledged that *palmata* may just be a variety name.

palmula. — Incorrect subsequent spelling (Pilsbry and Lowe 1932: 108; Galindo 1977: 416) of *palmata*.

palpebra. — Unjustified emendation (Hanley 1858b: 152) of *palpebrum*, because *palpebrum* is a Latin noun (Article 34.2.1.), although the correct word is *palpebra* –*palpebrae* as plural). According to ICZN Article 33.2.3, *palpebra* is a junior objective synonym of *palpebrum*.

palpebrum **Reeve, 1856**: Species 18, pl. IV, figs. 18a–18b, *Siphonaria*, Lisbon [Portugal], [leg. unknown]. — It is regarded as valid by Paetel (1873: 117; 1883: 178; 1889: 429, all as *palpetrum*) and Galindo (1977: 416), as a synonym of *algesirae* by Petit de la Saussaye (1869: 92, as *palpilabrum*) and Burnay and Monteiro (1977: 19), as a synonym of *pectinata* by Hanley (1858b: 152, as *palpebra*) and Morrison (1972: 53), and as a synonym of *lineolata* by Dautzenberg (1900: 154). According to Hubendick (1946: 31–32, pl. 1, figs. 30–31), *palpebrum* was a variety of *pectinata*.

palpetrum. — Incorrect subsequent spelling (Paetel 1873: 117; 1883: 178; 1889: 429) of *palpebrum*.

palpilabrum. — Incorrect subsequent spelling (Petit de la Saussaye 1869: 92) of *palpebrum*. According to Hubendick (1946: 31), Petit de la Saussaye (1869: 92) used the incorrect spelling *papilabrum* (instead of *palpilabrum*).

parcicostata **Deshayes, 1863**: 82, pl. XXXIV [Conchyliologie pl. VII], figs. 18–19, *Siphonaria*, [no type locality indicated, but in an article describing species from Reunion Island], [leg. unknown]. — Regarded as valid by Liénard (1877: 59), Martens (1880: 310), Paetel (1889: 429), and Hubendick (1945b: 29, 32, 72; 1946: 46, pl. 3, figs. 13–15).

parma **Hanley, 1858a**: 24–25, *Siphonaria*, Africa Occidentali [west Africa], [leg. unknown]. — Hanley (1858b: 152) and Paetel (1889: 429) recorded *parma* on their lists of valid species of *Siphonaria*. Hubendick (1946: 31) and Morrison (1972: 53) considered *parma* a synonym of *pectinata*.

parmelas **Iredale, 1940**: 437, *Mestosiphon*, Ponerihouen, east coast New Caledonia, leg. A. F. Basset Hull. — Regarded as a synonym of *atra* by Hubendick (1946: 52) and as a synonym of *laciniosa* by Morrison (1972: 57).

pascua **Rehder, 1980**: 97, pl. 12, figs. 4–7, *Siphonaria*, Easter Island [Chile], [leg. unknown]. — There is no other mention of this name in the literature.

pectinata **Linné, 1758**: 783, *Patella*, M. Mediterraneo [Mediterranean Sea], [leg. unknown]. — Krauss (1848: 57), Hanley (1858b: 152), Martens (1874: 141), Paetel (1889: 429), Köhler (1894: 3–23, fig. A, pl. 1, figs. 1–15, pl. 2, figs. 16–21, pl. 3, fig. 44, pl. 5, figs.1–2), Hubendick (1945b: 19, 20, 70, fig. 25; 1946: 31–33, pl. 1, figs. 30–39), Voss (1959: 84–98), Warmke and Abbott (1961:154), Allanson (1963: 70), Morrison (1963: 8–9; 1972: 53–54), Abbott (1974: 335, fig. 4111), Galindo (1977: 416), Hylleberg and Kilburn (2003: 134), and Ardovini and Cossignani (2004: 44, 249) regarded *pectinata* as valid.

peltoides **Carpenter, 1864c**: 474, *Nacella*, [no type locality indicated, but from a publication describing shells from Mazatlan, western coasts of Mexico], [leg. unknown]. — Carpenter referred to a former description of an unnamed species, "*Nacella*, sp. ind., Maz. Cat. No. 262, p. 202," from his own *Catalogue of the Reigen Collection of Mazatlan Mollusca, in the British Museum* (Carpenter, 1857a). Regarded as a valid name of *Nacella* by Carpenter (1864b: 545), of *Siphonaria* (Dall 1870: 37; Stearns 1894: 384), of *Liriola* (Dall 1878: 70; Fischer and Crosse 1900: 108), and of *Williamia* by Hubendick (1946: 72).

percea **Iredale, 1940**: 437, *Torquisiphon*, Rarotonga [Cook Islands], leg. G. P. Whitley. — Regarded as valid by Hubendick (1946: 63–64).

***perplexa* Oliver, 1915**: 547–548, pl. XII, figs. 43–43a, *Siphonaria*, Sunday Island [Kermadec Islands, New Zealand], [leg. unknown]. — The name *perplexa* was created by Oliver for a variety of *macauleyensis*, and is now regarded as a subspecific name (ICZN Article 45.6.4). Hubendick (1946: 38–39) regarded *macauleyensis* as a synonym of *diemenensis* and *perplexa* as a valid variety of *diemenensis*.

***peruviana* Sowerby, 1835**: 6, *Mouretia*, Peruviæ (Cobija) [Cobija, Chile], [leg. unknown]. — D'Orbigny (1841: 470) transferred *peruviana* to *Siphonaria*, and later (d'Orbigny, 1854: 50) to *Gadinia*. Hupé (1854: 250–251) and Galindo (1977: 416) regarded *peruviana* as a *Siphonaria*, but Hubendick (1946: 75–76) regarded it as a *Gadinia*.

***pica* Sowerby, 1835**: 6, *Siphonaria*, Acapulco [Mexico], [leg. unknown]. — Regarded as valid by Catlow and Reeve (1845: 100), Reeve (1856: Species 16, pl. IV, figs. 16a–16b), Adams and Adams (1855: 271), Hanley (1858b: 152), Dall (1870: 39), Paetel (1873: 117; 1883: 178), Heilprin (1889: 176, as *picta*), Fischer and Crosse (1900: 107), Odhner (1921: 248), Pilsbry and Lowe (1932: 108), Lamy (1938: 142), Morrison (1963: 8), and Galindo (1977: 416). Stearns (1895: 166) listed *pica* as a possible synonym of *lecanium*. Hubendick (1945b: 72) thought that *maura* and *pica* referred to the same species. Later, Hubendick (1946: 40, 41, 66) determined that *pica* was either a "probable" synonym of *maura* or valid. Regarded as a variety of *maura* by Keen (1958: 510, fig. 1032b) and Galindo (1977: 416). According to Pilsbry (1900: 505, as *picta*), Heilprin's (1889: 176, as *picta*) record of *pica* was a misidentification of *brunnea*, and according to Peile (1927: 87, as *picta*) it was a misidentification of *alternata*. Finally, according to Rehder (1980: 97), Odhner's (1921) and Lamy's (1938) records of *pica* were misidentifications of *pascua*.

***pica*.** — Incorrect subsequent spelling (Paetel 1889: 429) of *picta*, because the authorship was attributed to d'Orbigny.

***picta*.** — Incorrect subsequent spelling (Pilsbry 1900: 505; Heilprin 1889: 176; Peile 1927: 87) of *pica*, because the authorship was attributed to Sowerby.

***picta* d'Orbigny, 1834**: pl. LVI, figs. 7–11, *Siphonaria*, [no type locality indicated], [leg. unknown]. — The *Voyage dans l'Amérique Méridionale* was printed in parts; the plate LVI was published in 1834 and the written description of *picta* in 1841.

According to ICZN Article 12.2.7, the publication date for *picta* is 1834 because the illustrations of *picta* were published in association with a binomial. Regarded as valid by d'Orbigny (1841: 469; 1841 [Cuba]: 231–232; 1854: 50), Catlow and Reeve (1845: 100), Adams and Adams (1855: 270, 271, pl. LXXXIV, figs. 10–10a), Hanley (1858b: 152), Krebs (1864: 75), Arango (1878: 230), Paetel (1883: 178; 1889: 429, as *pica*), Dall (1886: 288), Smith (1890: 497, pl. XXX, figs. 4–4b), Pilsbry (1900: 505), Ihering (1915: 140–141), and Galindo (1977: 416). Regarded as a possible synonym of *atra* by Reeve (1842: 20), as a possible synonym of *alternata* by Dall (1902: 501, 502), and as a possible synonym of both *alternata* and *hispida* by Hubendick (1946: 44, 45, 64).

pisangensis **Hubendick, 1947**: 1–4, figs. 1–2, *Siphonaria*, Isle of Pisang, New Guinea [Pisang Islands, West Papua], [leg. unknown, but collected during the "voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique"]. — Hubendick (1947: 3) noted that plate II, figure 2 in Adam and Leloup (1939) is an objective synonym of *pisangensis*. There is no other mention of this species in the literature.

placentula **Menke, 1853**: 69, *Siphonaria*, [no type locality indicated, but in an article describing shells from St. Vincent, Lesser Antilles], [leg. unknown]. — Regarded as valid by Adams and Adams (1855: 271), Hanley (1858b: 152), and Paetel (1889: 429), and as a possible synonym of the variant form *kraussi* of *capensis* by Hubendick (1946: 33).

plana **Quoy and Gaimard, 1833**: 345–346, pl. 25, figs. 21–22, *Siphonaria*, environs du port Louis, Ile-de-France [Mauritius], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Anton (1839: 26), Catlow and Reeve (1845: 100), Adams and Adams (1855: 271), Hanley (1858b: 152), Deshayes (1863: 83), Paetel (1873: 117; 1883: 178; 1889: 429), Martens (1880: 310), and Galindo (1977: 416) considered *plana* valid. Regarded as a synonym of *lineolata* by Reeve (1856), despite the difference in type localities (*lineolata* was described from Chile and Central America), and as synonym of *laciniosa* by Morrison (1972: 56). Hubendick (1946: 69) thought that *plana* resembled *kurracheensis* var. *luzonica* or *kurracheensis* var. *zebra*, but regarded it as a *nomen nudum* (although he likely meant *nomen dubium*), due to insufficient information in the original description.

***plicata* Quoy and Gaimard, 1833**: 346–347, pl. 25, figs. 26–27, *Siphonaria*, Hifo, Tonga–Tabou [Hihifo, Tonga], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Regarded as valid by Anton (1839: 26), Catlow and Reeve (1845: 100), Adams and Adams (1855: 271), Hanley (1858b: 152), Paetel (1873: 117; 1883: 178; 1889: 429), and Galindo (1977: 416). Regarded as a synonym of *sipho* by Reeve (1856: Species 9, pl. II, figs. 9a–d), Schrenk (1867: 306), Hutton (1880: 36), and Adam and Leloup (1939: 7). Finally, regarded as a synonym of *laciniosa* by Hubendick (1946: 47).

***promptus* Iredale, 1940**: 438, pl. xxxiv, figs. 24–25, *Parellsiphon*, North West Island, Capricorn Group [Queensland, Australia], [leg. unknown]. — Regarded as a probable synonym of *acmaeoides* by Hubendick (1946: 30–31, 63), as a synonym of *laciniosa* by Morrison (1972: 57).

***propria* Jenkins, 1983**: 23–28, figs. 5a–f, *Siphonaria*, S. side of Kaikoura Peninsula, E. coast, S. Island, New Zealand, [leg. unknown]. — There is no other mention of this name in the literature.

***punctata* Quoy and Gaimard, 1833**: 341–342, pl. 25, figs. 13–14, *Siphonaria*, port Louis de l'Ile-de-France [Mauritius], [leg. unknown]. — Regarded as valid by Catlow and Reeve (1845: 100), Adams and Adams (1855: 271), Hanley (1858b: 152), Martens (1880: 310), Paetel (1889: 429), and Galindo (1977: 416); as a synonym of *sipho* by Reeve (1856: Species 9, pl. II, figs. 9a–d), Schrenk (1867: 306), and Hutton (1880: 36). Regarded as a synonym of *laciniosa* by Hubendick (1946: 47).

***punctulata*. — Incorrect subsequent spelling (Paetel 1889: 429) of *punctata*. Paetel, 1889 cites "Rv. Ic. Siph. 35." as the source of this name. However, Reeve (1856) did not mention *punctulata* which appears to be a combination of *punctata* and *funiculata*, which is Reeve's (1856) Species 35. Hubendick (1946: 47) listed *punctulata* as a synonym of *laciniosa,* although it is clearly not available.

***radians* Adams and Adams, 1855**: 271, *Siphonaria*. — This is a new replacement name for *radiata* Adams and Reeve, 1848, which is an available but permanently invalid name, because it is preoccupied by *radiata* Blainville, 1827. Regarded as valid by Paetel (1889: 429), Hubendick (1946: 43), who also thought it could be a variant of *japonica*, and Hylleberg and Kilburn (2003: 134).

***radiata* Adams and Reeve, 1848**: 69, pl. XIII, figs. 2a–b, *Siphonaria*, China Sea, [leg. unknown].— Regarded by Adams and Adams (1855: 271) and Hubendick (1946: 43) as a synonym of *radians* Adams and Adams, 1855. However, *radiata* Adams and Reeve, 1848 is available but permanently invalid because it is preoccupied by *radiata* Blainville, 1827. A new replacement name, *radians*, was created by Adams and Adams (1855: 271). Regarded as valid by Paetel (1889: 429).

***radiata* Blainville, 1827**: 294, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Blainville (1827: 294) published a written description of *radiata* in the article on the *Siphonaire* in the 49th volume of the *Dictionnaire des sciences naturelles*. In the same year, Blainville (1827: pl. II, figs. 4–4a) also published an illustration of what he referred to as "Siphonaire radiée" in the *Atlas* of his *Manuel de malacologie et de conchyliologie*. Blainville's *Manuel* was published in two volumes: in the first volume, which only contains the text, Blainville (1825) did not mention *S. radiata*, which was only mentioned in the second volume, the *Atlas* with the plates. Thus, the original publication for *radiata* is Blainville's (1827: 294) article on *Siphonaire* in which the Linnaean binomial "*S.* [for *Siphonaria*] *radiata*" appears. Several authors regarded this species as valid (e.g. Jay 1839: 39; Catlow and Reeve 1845: 100; Adams and Adams 1855: 271; Hanley 1858b: 152; Paetel 1889: 429; Galindo 1977: 416). Regarded as a synonym of *australis* by Hubendick (1946: 49) and Jenkins (1983: 12, 18), and as a synonym of *javanica* by Morrison (1972: 52). Jenkins further concluded that *radiata* was a *nomen dubium* because the types are lost, the type locality is unknown, and the original description and figures were inadequate.

***radiata* Sowerby, 1835**: 6, *Siphonaria*, Occidentalia Africæ (Gambia) [Gambia, Western Africa], [leg. unknown]. — Catlow and Reeve (1845: 100), Paetel (1883: 178), and Hanley (1858b: 152) regarded it as valid. Hubendick (1946: 31, 43) and Morrison (1972: 53) regarded it as a synonym of *pectinata* and pointed out that *radiata* Sowerby, 1835 was a junior, primary homonym of *radiata* Blainville, 1827. Indeed, *radiata* Sowerby, 1835 is available but permanently invalid because it is preoccupied by *radiata* Blainville, 1827.

***raoulensis* Oliver, 1915**: 546, pl. XII, figs. 40–40a, *Siphonaria*, Sunday Island [Kermadec Islands, New Zealand], [leg. unknown]. — Regarded as a synonym of *diemensis* by Hubendick (1946: 38).

redimicula. — Unjustified emendation (Galindo 1977: 416) of *redimiculum* because the latter is a noun, and not an adjective (Article 31.2.1). According to ICZN Article 33.2.3, *redimicula* is a junior objective synonym of *redimiculum*.

***redimiculum* Reeve, 1856**: Species 24, pl. V, figs. 24a–b, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Hanley (1858b: 152), Smith (1879: 182–183, from Kerguelen Island), Hutton (1880: 36; 1883: 143–144, pl. XVII, figs. N–R, from Auckland Islands), Rochebrune and Mabille (1889: 28, from Orange Bay, Cape Horn), Köhler (1894: 28–37, figs. C–D, pl. 3, figs. 31–43, pl. 4, figs. 53–56, pl. 5, fig. 8, pl. 6, figs. 9–10), Dautzenberg (1896: LXV, from Strait of Magellan), Hedley (1916: 61–62, from Macquarie Island), and Galindo (1977: 416, as *redimicula*, from New Zealand) regarded *redimiculum* as valid. Regarded as a synonym of *tristensis* by Watson (1886: 675) and Tate and May (1902: 419), as a subspecies or a synonym of *lateralis* by Strebel (1908: 8), as a synonym of *lateralis* by Suter (1909b: 34, 1913: 601) and Hubendick (1946: 21, 22, 26–27). Hanley (1858a: 25) described an unnamed variety of *redimiculum* and Paetel (1889: 429) erroneously attributed the authorship of *redimiculum* to Hanley.

***reticulata* Sowerby, 1835**: 6, *Mouretia*, Valparaiso [Chile], [leg. unknown]. — Transferred to *Siphonaria* by d'Orbigny (1846: 682) and then to *Gadinia* by Hubendick (1946: 76).

***rosea* Hubendick, 1945a**: 1–2, figs. 1 and 5, *Siphonaria*, Inseln Kharg, Persischer Meerbusen [Kharg Island, Iran, Persian Gulf], leg. G. Thorson. — Regarded as a valid species by Hubendick (1945b: 29, 32, 72; 1946: 53, pl. 4, figs. 12–15) and Galindo (1977: 416), and as a synonym of *laciniosa* by Morrison (1972: 57).

***rucuana* Pilsbry, 1904**: 36, pl. VI, figs. 60–60b, *Siphonaria*, Riukiu Island [Japan], leg. Y. Hirase. — Regarded as valid by Hirase (1934: 94, pl. 121, fig. 14), Hubendick (1946: 62; 1955: 132), and Fukuda (1994: 50), and as a subspecies of *laciniosa* by Habe (1964: 144, pl. 44, fig. 16).

rugosa. — Paetel (1873: 117; 1883: 178; 1889: 429) mentioned the existence of *rugosa* from Brazil, with authorship attributed to d'Orbigny. As Hubendick (1946: 69)

suggested, Paetel likely got confused with *subrugosa* Sowerby, 1835, also from Brazil. In any case, *rugosa* is a *nomen nudum* and is not available.

***savignyi* Philippi *in* Krauss, 1848**: 61, *Siphonaria*, [no type locality indicated, but likely the Red Sea], [leg. unknown]. — Philippi created *savignyi* for a species of *Siphonaria* illustrated by Savigny (1817: pl. 1, figs. 1.1–1.4). Hanley (1858b: 152) considered *savignyi* a synonym of *crenata*. Listed as a synonym of *kurracheensis* by Issel (1869: 153). Paetel (1873: 117; 1883: 178; 1889: 429). Hubendick (1945b: 29, 72; 1955: 127, 129; 1946: 55, pl. 4, figs. 25–29) regarded it as valid. Tomlin (1927: 291) considered *savignyi* a valid species, but commented that the specimen collected from the Suez Canal during the 1924 Cambridge Expedition may also be either *sipho* or *basseinensis*. Moazzo (1939: 131) regarded Tomlin's (1927: 291) *savignyi* as a synonym of *kurracheensis*. Morrison (1972: 56, 57, 60, figs. 3–4) regarded *savignyi* as a valid forma of *laciniosa*. Hubendick (1946: 55) cited 1826 as the year Philippi published a description of *savignyi*; this is an erroneous year since the first mention of this name occurs in Krauss, 1848, which was also noted by Morrison (1972: 60).

***scabra* Reeve, 1856**: Species 2, pl. I, figs. 2a–b, *Siphonaria*, Port Jackson [Sydney, New South Wales], Australia, [leg. unknown]. — Regarded as valid by Hanley (1858b: 152), Angas (1865: 190; 1867: 232), Paetel (1883: 178; 1889: 429), Hedley (1917a: 715, pl. L, fig. 32; 1917b: 95), and Galindo (1977: 416). Regarded as a synonym of *diemenensis* by Pritchard and Gatliff (1903: 220), Suter (1907: 265), Verco (1907: 103), and McAlpine (1952: 40–42), and as a subspecies of *diemenensis* by Hubendick (1946: 38–39, pl. 2, fig. 14). According to McAlpine (1952: 40, 42), Hedley's (1917) record of *scabra* was a misidentification of *denticulata* (as *Ellsiphon denticulatus*).

***scutella*.** — Unjustified emendation (Burch 1945: 16) of *scutellum* because the latter is a Latin noun (Article 34.2.1.), although the correct word is *scutella –scutellae* as plural). According to ICZN Article 33.2.3, *scutella* is a junior objective synonym of *scutellum*.

***scutellum* Deshayes, 1841**: pl. 35, *Siphonaria*, Ile Chatam [Chatham Island, New Zealand], [leg. unknown]. — Regarded as valid by Catlow and Reeve (1845: 100), Hutton (1873: 55), Paetel (1889: 429), Dall (1870: 39, with Blainville as author), Burch (1945: 16, as *scutella*), and Galindo (1977: 416). Regarded as a synonym of *obliquata*

by Reeve (1856: Species 12, pl. III, figs. 12a–12b), Hanley (1858b: 152), Hutton (1880: 36; 1883: 141), Stearns (1894: 405, 430), Suter (1909b: 33; 1913: 599), Hubendick (1946: 24), and Jenkins (1983: 28), and as a synonym of *australis* by Hubendick (1946: 49). Regarded as a synonym of *zelandica* by Hutton (1878: 41). In fact, according to Jenkins (1983: 5), Hutton's (1878) record of *scutellum* was a misidentification of *zelandica*.

***sedimaculina* Reeve**. — Galindo (1977: 416) mentioned *sedimaculina* as a valid name, with authorship to Reeve. However, no original description could be found and *sedimaculina* is a *nomen nudum*.

***serrata* Fischer, 1807**: 116, *Patella*, [no type locality indicated], [leg. unknown]. — Placed in the family Siphonariidae by Ivanov et al. (1993: 81, pl. 2, figs. 3–6) and later transferred to *Siphonaria* by Chambers and McQuaid (1994: 264–265, figs. 1B–1D, 1J). Hubendick (1946) made no mention of *serrata* in his monograph. Considered valid by Ivanov et al. (1993: 81, pl. 2, figs. 3–6), as well as Chambers and McQuaid (1994: 264–265, figs. 1B–1D, 1J) who thought that Fischer likely collected the types of *serrata* near the Cape of Good Hope.

sinus. — Incorrect subsequent spelling (Galindo 1977: 416) of *sirius*.

***sipho* Sowerby, 1823**: pl. 143, fig. 1, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Regarded as valid by Blainville (1827: 294), Anton (1839: 26), Catlow and Reeve (1845: 100), Gray (1847: 181), Reeve (1856: Species 9, pl. II, figs. 9a–d), Adams and Adams (1855: 270, 271, pl. LXXXIV, fig. 10b), Hanley (1858b: 152), Brazier (1878: 135), Hutton (1880: 36), Paetel (1883: 178; 1889: 429), Boettger (1892: 168), Melvill and Standen (1901: 457), Sykes (1903: 137, 138), Tillier and Bavay (1905: 176), Hedley (1909: 369), Hirase (1934: 94, pl. 121, fig. 11), Adam and Leloup (1939: 7–9, fig. 1, pl. II, figs. 1a–1d), Thorson (1940: 225–227, fig. 31), Hubendick (1945b: 29, 72), Galindo (1977: 416), and Jenkins (1983: 28, 1984: 113). Regarded as a variety of *laciniosa* by Hubendick (1946: 47–48, pl. 3, figs. 17 and 19), and as a synonym of *laciniosa* by Morrison (1972: 51, 52, 57). Several misidentifications have also been mentioned: according to Morrison (1972: 51, 52, 57), Thorson's record of *sipho* is a misidentification of *laciniosa*; according to Moazzo (1939: 131) and Hubendick (1946: 54), the record of *sipho* by Tiller and Bavay (1905) is a synonym of *kurracheensis*; according to Jenkins (1983: 13), Reeve's (1856) and Hutton's

(1880) records of *sipho* are misidentifications of *australis*; according to Hubendick (1946: 49, 46), Hutton's (1880) record of *sipho* is a misidentification of *acervus*; according to Hubendick (1946: 34), Thorson's (1940) *sipho* is a misidentification of *belcheri*. In addition, Hubendick (1946: 48) noted that "many authors" misidentified *stellata* as *sipho*, but did not cite any specific reference.

siquijorensis **Reeve, 1856**: Species 27, pl. VI, figs. 27a–b, *Siphonaria*, Island of Siquijor, Philippines, [leg. unknown]. — Regarded as valid (Hanley 1858b: 152; Brazier 1878: 135; Paetel 1873: 117; 1883: 178; 1889: 429; Hedley 1909: 369; Galindo 1977: 416, as *siquoyorensis*; Fukuda, 1994: 51), as a synonym of *kurracheensis* by Cooke (1886a: 133) and Hubendick (1946: 54), as a variety of *kurracheensis* by Hubendick (1945b: fig. 52, as *siquiorensis*; 1946: 55, pl. 2, fig. 38), and, finally, as a synonym of *laciniosa* by Morrison (1972: 56).

siquiorensis. — Incorrect subsequent spelling (Hubendick, 1945b: fig. 52) of *siquijorensis*.

siquoyorensis. — Incorrect subsequent spelling (Galindo, 1977: 416) of *siquijorensis*.

sirius **Pilsbry, 1894a**: 9–10, *Siphonaria*, Sagami and Kashiurazaki, Boshiu, Japan, leg. Frederick Stearns. — Pilsbry (1895: 5–6, pl. VI, figs. 23–28) published again the original description. Regarded as valid by Hirase (1934: 94, pl. 121, fig. 16), Hubendick (1945b: 29; 1946: 50–51, pl. 3, figs. 24–27), Kira (1962: 201, pl. 69, fig. 12), Galindo (1977: 416), Dharma (1992: 78, pl. 17, fig. 2), and Hylleberg and Kilburn (2003: 134).

soranus **Iredale, 1940**: 441, pl. xxxiv, figs. 20–21, *Planesiphon*, Townsville, Queensland [Australia], [leg. unknown]. — Regarded as a probable synonym of *acmaeoides* by Hubendick (1946: 30–31, 63).

sowerbyi **Adams and Adams, 1855**: 271. — This is a new replacement name for *radiata* Sowerby, 1835, available but permanently invalid because preoccupied by *radiata* Blainville, 1827. Hubendick (1946: 31) and Morrison (1972: 53) regarded *sowerbyi* as a synonym of *pectinata*. However, *sowerbyi* Adams and Adams, 1855 is preoccupied by *sowerbyi* Michelin, 1832, and is thus available but permanently invalid.

sowerbyi **Michelin, 1832**: Classe V, pl. 17, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Regarded as valid by Guérin-Méneville (1844: 30, pl. 15, figs. 10a–b), Anton (1839: 26), Hanley (1858b: 152), and Paetel (1889: 429), and as a synonym of *laciniosa* by Morrison (1972: 56). Due to the lack of type locality and

information in the original description, Hubendick (1946: 69) concluded that *sowerbyi* was a *nomen nudum*. It cannot be a *nomen nudum*, but it could certainly be a *nomen dubium*.

spinosa **Reeve, 1856**: Species 32, pl. VII, figs. 32a–b, *Siphonaria*, New Zealand, [leg. unknown]. — Hanley (1858b: 152), Hutton (1873: 56; 1878: 42; 1880: 36), Paetel (1873: 117; 1883: 178; 1889: 429), and Galindo (1977: 416) regarded *spinosa* as valid. Hubendick (1946: 60–62) discussed that *spinosa* may be valid, or a synonym of *aspera*. According to Jenkins (1983: 29), who examined the type material, *spinosa* is a synonym of *aspera* and has been incorrectly recorded from New Zealand.

stella **Petit *in* Jay, 1839**: 39, *Siphonaria*, Peru, [leg. unknown]. — Regarded as valid by Catlow and Reeve (1845: 100) and Paetel (1889: 429). However, *stella* is not accompanied by a description or reference to a previous illustration or description. Therefore, *stella* was rightly regarded as a *nomen nudum* by Hubendick (1946: 69) and is not available.

stellata **de Roissy *in* Blainville, 1827**: 295, *Siphonaria*, [no type locality indicated], [leg. unknown]. — Regarded as valid by Hanley (1858b: 153), Paetel (1889: 429, with authorship to Blainville), and Hubendick (1945b: 29, 30, 32, 72, figs. 42 and 53; 1946: 48), and as a synonym of *laciniosa* by Morrison (1972: 56). However, *Siphonaria stellata* de Roissy *in* Blainville, 1827 became a junior secondary homonym when Martens (1869: 235) transferred *Patella stellata* Helbing, 1779 to *Siphonaria*. Therefore, de Roissy *in* Blainville, 1827 is invalid but remains available.

stellata **Helbling, 1779**: 109–110, pl. I, fig. 11, *Patella*, [no type locality indicated], [leg. unknown]. — Transferred to *Siphonaria* by Martens (1869: 235) who thought it referred to the same species as *exigua*. Regarded as a synonym of *luzonica* by Adcock (1893: 11), and of *laciniosa* by Hubendick (1946: 48).

stewartiana **Powell, 1939**: 237–238, pl. 49, figs. 7–8, *Kerguelenia*, Aker's Point, Stewart Island [New Zealand], leg. R. H. Harrison. — Regarded as valid by Hubendick (1945b: 17, 67; 1946: 28, pl. 6, figs. 4–6), Powell (1946: 91; 1979: 293–294, pl. 54, figs. 14–15), Knox (1955: 85–86, fig. 1), Morton and Miller (1968: 379, 380, fig. 109), and Galindo (1977: 416). Hubendick (1946: 28) also noted that *stewartiana* may refer

to the same species as *stowae*. According to Powell (1955: 121), the record of *stewartiana* by Hubendick is a misidentification of *flemingi*. However, Powell (1979: 293) later decided that Hubendick's record of *stewartiana* was actually a misidentification of *innominata*.

***stowae* Verco, 1906**: 223–224, pl. VIII, figs. 3–8, *Siphonaria*, Pondolowie Bay, Spencer Gulf and King's Point, Encounter Bay [South Australia], leg. Miss Stow [specimens from King's Point]. — It is spelled *stowæ* in the original description, but should now be spelled *stowae* (ICZN Article 27). Regarded as valid by Verco (1907: 105), Hedley (1917b: 96), May (1921: 89), Iredale (1924: 276–277), Cotton and Godfrey (1932: 155, pl. 3, fig. 5), Hubendick (1945b: 70; 1946: 29), and Galindo (1977: 416). Hubendick (1946: 29) thought that *stowae* may refer to the same species as *stewartiana*.

striatocompressa. — Incorrect subsequent spelling (Pallary 1900: 242–243) of *striatocostata*. Hubendick (1946: 33) regarded *striatocompressa* as a synonym of *striatocostata*, and Morrison (1972: 54) regarded it as a synonym of *pectinata*, but it strictly speaking only is an incorrect spelling.

***striatocostata* Dunker, 1846**: 24–25, *Siphonaria*, Benguela [Angola], [leg. unknown]. — It is spelled *striato-costata* in the original description, but should now be spelled *striatocostata* (ICZN Article 32.5.2.4). Regarded as valid by Dunker (1853: 3, pl. I, figs. 1–6), Adams and Adams (1855: 271), Hanley (1858b: 153); Weinkauff (1862: 335), Paetel (1873: 117; 1883: 178; 1889: 429), Hubendick (1946: 33), and Galindo (1977: 416). Regarded as a synonym of *algesirae* by Weinkauff (1866: 237) and as a synonym of *pectinata* by Morrison (1972: 53). Pallary (1900: 242–243, as *striatocompressa*) regarded it as a likely synonym of *Siphonaria mouret*, which is not an available name although it refers to the same species as *pectinata*. Weinkauff (1862: 335) and Petit de la Saussaye (1863: 142) erroneously attributed the authorship to Deshayes and Philippi, respectively, but Weinkauff (1863: 233) later acknowledged his mistake and attributed authorship to Dunker. According to Kobelt (1888: 272), the record of *striatocostata* from Weinkauff (1862) was a misidentification of *algesirae*.

striatopunctata. — Incorrect subsequent spelling of *striatocostata*. Petit de la Saussaye (1869: 92), Kobelt (1888: 272), Paetel (1889: 429), and Locard (1898: 98) mentioned *striatopunctata* (with authorship attributed to Weinkauff) as a synonym

of *algesirae*. Kobelt (1888: 272) specifically cited "Weinkauff J.C. X p. 334," i.e. page 334 of an article by Weinkauff in the 10th volume of the *Journal de Conchyliologie*. These authors were referring to *striatocostata* Dunker, 1846, which Weinkauff (1862: 335) correctly cited as *striatocostata* and not as *striatopunctata*. The latter is thus a *nomen nudum*, although Hubendick (1946: 31) and Morrison (1972: 54, with authorship to Weinkauff) regarded it as a synonym of *pectinata*.

***striatula* Gmelin, 1791**: 3699, *Patella*, [no type locality indicated], [leg. unknown]. — Regarded as valid by several authors (Mörch, 1852: 148; Adams and Adams, 1855: 271; Paetel, 1889: 429). Mörch (1852: 148) cited Africa as the distribution of *striatula* and *algesirae* as a synonym. However, Hubendick (1946: 69) argued that *striatula* could not even be identified as a *Siphonaria*. Given the lack of type locality and the brief original description, *striatula* should probably be regarded as a *nomen dubium*.

***subaquitalis*.** — Galindo (1977: 416) mentioned *subaquitalis* as a valid name. However, there is no other occurrence of this name in the literature which should be regarded as a *nomen nudum*.

***subatra* Pilsbry, 1904**: 36, pl. VI, figs. 61–61b, *Siphonaria*, Chichijima, Ogasawara [Japan], leg. Y. Hirase. — Regarded as valid by Hirase (1934: 94, pl. 121, fig. 13), Hubendick (1945b: 29; 1946: 51, pl. 3, figs. 32–35), Kira (1962: 201, pl. 69, fig. 10), Galindo (1977: 416), Fukuda (1994: 50–51, pl. 42, fig. 808), Hylleberg and Kilburn (2003: 134), and as a synonym of *laciniosa* by Morrison (1972: 56).

***subrugosa* Sowerby, 1835**: 6–7, *Siphonaria*, Brasilæ [Brazil], G. B. S. [G. B. Sowerby]. — Regarded as valid by Catlow and Reeve (1845: 100), Adams and Adams (1855: 271), Hanley (1858b: 153), Frauenfeld (1869: 878), Paetel (1889: 429), and Köhler (1894: 27–28, pl. 2, figs. 27–29, pl. 5, fig. 6) and as a possible synonym of *hispida* by Hubendick (1946: 64). In addition, according to Hubendick (1946: 21), the record of *subrugosa* from Köhler was a misidentification of *lessonii*.

***subspiralis* Carpenter, 1866**: 213 [of the volume III publication in 1868], *Nacella*, Catalina Island, 10-20 fathoms [18 to 36 meters depth, California, United States], leg. J. G. Cooper. — The species description of *subspiralis* was initially published in February 1866 [Part III] as an individual article; the volume III of the *Proceedings of the California Academy of Natural Sciences* combined individual articles from

the years 1863 to 1867 [Parts I–IV] and was published in 1868. Carpenter (1864b: 612, 650) mentioned *subspiralis* earlier, but with no description or reference to a previous description or illustration. Carpenter (1866: 213) was unsure of the generic identity of this new species and stated the shell was insufficient to prescribe a genus. Regarded as a valid name of *Nacella* by Cooper (1867: 23) and Dall (1878: 70). Previously, Dall (1870: 37, 38) had mentioned *subspiralis* as a synonym of *Siphonaria peltoides*, thus indirectly transferring it to *Siphonaria*. Fischer and Crosse (1900: 108) transferred it to *Liriola*, and then Hubendick (1946: 72) to *Williamia* (as a synonym of *Williamia peltoides*).

tasmanica Tenison-Woods, 1877: 54–56, *Siphonaria*, [no type locality indicated, but in an article describing species from Tasmania], [leg. unknown]. — The name *tasmanica* was created by Tenison-Woods for a variety of *denticulata*, and now must be regarded as a subspecific name (ICZN Article 45.6.4). Regarded as a synonym of *zonata* by Pritchard and Gatliff (1903: 221) and Verco (1907: 105), and as a valid species name by Iredale (1924: 276), Cotton and Godfrey (1932: 154), Hubendick (1945b: 66; 1946: 22–23, pl. 1, figs. 12–14), Galindo (1977: 416), and Jenkins (1983: 29, 1984: 113, 117). Transferred (as a valid species name and as *tasmanicus*) to the genus *Talisiphon* by Iredale (1940: 442).

tenuicostulata Smith, 1903: 356, pl. XV, figs. 14–15, *Siphonaria*, Umhlali, Natal [South Africa], leg. H. Burnup. — Considered valid by Hubendick (1945b: 19, 20, 70, fig. 25; 1946: 35, pl. 6, figs. 18–19), Kilburn and Rippey (1982: 134), Bosch and Bosch (1989: 75, unnumbered figure), and Chambers and McQuaid (1994a: 264, 265, fig. 1N). Allanson (1958: 166–167) listed *tenuicostulata* as a possible synonym of *anneae*.

tenuis Philippi, 1860: 181–182, *Siphonaria*, Ganzen chilenschen Küste vor der Mündung des Rio bueno im Süden bis Isla blanca [37° S, off Chilean coast], [leg. unknown]. — According to Philippi, *tenuis* is closely related to *lineolata*, *concinna*, and *lessoni*. Regarded as a valid species by Dall (1909: 205) and Burch (1945: 16), and as a synonym of *lessoni* by Hubendick (1946: 21).

thersites Carpenter, 1864a: 425–426, *Siphonaria*, Neeah Bay [Washington, USA], leg. [J. G.] Swan. — Regarded as a valid name by many authors (Carpenter 1864b: 627, 647, 676; Stearns 1867a: 334; Dall 1870: 33, 39, pl. 4, fig. 8, pl. 5, fig. 2; 1905: 111; 1921: 66; 1925: 26, pl. 33, figs. 2–3; Paetel 1883: 178; Aurivillius 1885: 374, pl. 12, figs. 19–

20, pl. 13, fig. 16; Oldroyd 1927: 57; Burch 1945: 16; Hubendick 1945b: 12, 15, 64, figs. 1 and 55; 1946: 19; Morrison 1963: 7; Abbott 1974: 335, fig. 4113; Galindo 1977: 416).

***tongensis* Hubendick, 1945a**: 6, figs. 4 and 8, *Siphonaria*, Foua, Tonga-Inseln [Tonga], leg. Eugenie Expedition. — Regarded as valid and endemic to Tonga Islands by (Hubendick 1946: 63, pl. 5, figs. 29–31), and as a synonym of *laciniosa* by Morrison (1972: 57).

***tristensis* Leach *in* Sowerby, 1823**: pl. 143, fig. 3, *Patella*, [no type locality indicated], [leg. unknown]. — The label given by Sowerby for the figure 3 is "*Siphonaria Tristensis*, Patella Tristensis, *Leach*" which indicates that Sowerby attributed authorship to Leach who had originally combined *Tristensis* with *Patella*. To date, no original description of *tristensis* by Leach has been located (Watson, 1886: 675). Sowerby (1825: 32) mentioned *tristensis* as a valid name of *Siphonaria*; however, he placed a question mark after the specific name and did not mention Leach as the author. Several authors regarded *tristensis* as valid and attributed the authorship to Leach: Reeve (1856: Species 23, pl. V, figs. 23a–23b), Hanley (1858b: 153), Dall (1870: 33–37, pl. 4, fig. 9, pl. 5, figs. 1, 3, 4, 6, 7; 1876: 45), Watson (1886: 675), Paetel (1889: 429), Strebel (1907: 170–172, pl. 3, figs. 31–33), Strebel (1908: 8), and Hubendick (1945b: 12, 15, 66, figs. 4, 6, 10; 1946: 22, pl. 1, figs. 9–11). Other authors regarded *tristensis* as valid but attributed the authorship to Sowerby: Blainville (1827: 296), Paetel (1873: 117, 1883: 178), Tate and May (1902: 419), and Galindo (1977: 416). Some misidentifications have been mentioned: according to Smith (1879: 182), Dall's (1876) record of *tristensis* is a misidentification of *redimiculum*; according to Pritchard and Gatliff (1903: 221) and Verco (1907: 105), the record of *tristensis* from Tate and May (1902) is a misidentification of *zonata*; according to Suter (1909b: 34; 1913: 601), Watson's (1886) record of *tristensis* is a misidentification of *lateralis*. Finally, according to Forcelli (2000: 132, fig. 423), *tristensis* is a synonym of *lateralis*.

***turritus* Iredale, 1940**: 442, *Talisiphon*, Macquarie Harbour [Tasmania, Australia], leg. A. F. Basset Hull. — The name *turritus* was created by Iredale for a variety of *tasmanicus*, and should now be regarded as a subspecific name (ICZN Article 45.6.4). Hubendick (1946: 22) regarded *tasmanicus* as a synonym of *tasmanica* Tenison-Woods, 1878, but did not mention of *turritus*.

***umbonata* Menke, 1853**: 69, *Siphonaria*, [no type locality indicated, but in an article describing shells from St. Vincent, Lesser Antilles], [leg. unknown]. — Regarded as valid by Adams and Adams (1855: 271), Hanley (1858b: 153), and Paetel (1889: 429), and as a synonym of *pectinata* by Hubendick (1946: 31) and Morrison (1972: 53).

***variabilis* Krauss, 1848**: 59–60, pl. IV, fig. 4a, *Siphonaria*, In sinu tabulari et in litore natalensis [Table Bay and Natal, South Africa], [leg. unknown]. — Regarded as valid by several authors (Mörch 1852: 148; Dunker 1853: 4; Adams and Adams 1855: 271; Paetel 1873: 117; Martens 1874: 127; Martens 1880: 310; Paetel 1889: 429; Sowerby 1892: 54; Dautzenberg 1923: 24; Turton 1932: 10; Galindo 1977: 416), and as a synonym of *concinna* by Hanley (1858b: 153) and Hubendick (1946: 58).

***venosa* Reeve, 1856**: Species 10, pl. III, figs. 10a–b, *Siphonaria*, Cape Coast [Ghana], [leg. unknown]. — Regarded as valid by Hanley (1858b: 153), Paetel (1873: 117; 1883: 178; 1889: 429), and Galindo (1977: 416), as a synonym of *capensis* var. *lineolata* by Sowerby (1892: 54), as a synonym of *capensis* var. *kraussi* by Hubendick (1946: 33), and as synonym of *pectinata* by Morrison (1972: 53). Hubendick (1946: 31–32, pl. 1, figs. 36–37) also referred to some specimens from Valparaiso, Chile, as *pectinata* var. *venosa*, although the type locality of *pectinata* is in the Mediterranean Sea.

***vernalis* Dall *in* Stearns, 1867b**: 346, *Nacella*, [no type locality indicated, but in an article describing shells from the Purissima and Lobitas Creeks, San Mateo County, California, United States], leg. Dr. Newcomb and R. E. C. Stearns. — The original description was published in September 1867 in the Part IV of the *Proceedings of the California Academy of Natural Sciences*, although the volume III of the *Proceedings of the California Academy of Natural Sciences*, combining Parts I to IV, appeared in 1868. Regarded by Dall (1870: 37, 38) as a synonym of *Siphonaria peltoides*, thus indirectly transferring *vernalis* to *Siphonaria*. Later regarded as a valid species of *Nacella* by Dall (1878: 70) and as a valid species of *Williamia* by Hubendick (1945b: 32–33, 73, fig. 54; 1946: 71–72, pl. 6, figs. 33 and 36).

***virgulata* Hedley, 1915**: 751–752, pl. lxxxv, figs. 96–98, *Siphonaria*, Terrigal, Sydney, and Twofold Bay [New South Wales, Australia], [leg. unknown]. — Regarded as valid by

Hedley (1917b: 95), Hubendick (1945b: 12, 15, 16, 17, 66; 1946: 23–24, pl. 1, figs. 18–21; 1955: 126–127), and Galindo (1977: 416), and as a variant form of *funiculata* by Iredale (1924: 275–276) and Jenkins (1981: 1–3, 13, pl. 2, figs. a–c, e, f, h, j).

viridis **Quoy and Gaimard, 1833**: 332–333, pl. 25, figs. 30–31, *Siphonaria*, rade d'Amboine, aussi la Nouvelle-Guinée [Ambon, Maluku Islands, Indonesia, and New Guinea], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Regarded as valid by Catlow and Reeve (1845: 100), Adams and Adams (1855: 271), Hanley (1858b: 153), and Paetel (1889: 430), as a synonym of *sipho* by Adam and Leloup (1939: 7), and as a synonym of *laciniosa* by Hubendick (1946: 47).

williamsi **Berry, 1969**: 166, *Siphonaria*, Cove inside Flat Rock, south end of Natividad Id., Baja California, leg. M. W. Williams. — Regarded as valid by Abbott (1974: 336) and Galindo (1977: 416).

zanda **Iredale, 1940**: 438, pl. xxxiv, figs. 7–8, *Parellsiphon*, Low Isles, North Queensland [Australia], [leg. unknown]. — Regarded as valid by Hubendick (1945b: 29; 1946: 52–53, pl. 4, figs. 8–11) with a distribution from southern Japan to Madagascar, but regarded by Morrison (1972: 57) as a synonym of *laciniosa*.

zealandiae. — Incorrect subsequent spelling (Paetel, 1889: 430) of *zelandica*.

zealandica. — Incorrect subsequent spelling (Hutton 1873: 55; 1880: 36; 1883: 143, pl. XVII, figs. H–M; Hubendick 1946: 36, 47; 1955: 129–132;) of *zelandica*.

zebra **Reeve, 1856**: Species 21 [Species 22], pl. V, fig. 21, *Siphonaria*, Philippine Islands [Port Jackson, Australia (see below)], [leg. unknown]. — According to Jenkins (1983: 28), who examined relevant type material, the descriptions of *zebra* and *bifurcata* have been mixed up in Reeve's *Monograph* so that *zebra* is actually the Species 22 with figure 21 (instead of Species 21 with figure 21), and *bifurcata* is actually the Species 21 with figure 22. As a result, the type locality of *zebra* is Port Jackson instead of the Philippines Islands. Iredale (1924: 276) had also noted this possible confusion and thought that *zebra* referred to the same species as *baconi*. Hanley (1858b: 153), Paetel (1883: 178, 1889: 430), Hedley (1917b: 95), and Galindo (1977: 416) regarded *zebra* as valid. Originally, Hubendick (1946: 54–55, pl. 2, fig. 37) regarded it as a variety of *kurracheensis*, and later (Hubendick 1955: 129) as a synonym of *zelandica*. Finally, according to

Hubendick (1946: 37), Hedley's (1917b) record of *zebra* was a misidentification of *bifurcata*.

zelandica Quoy and Gaimard, 1833: 344–345, pl. 25, figs. 17–18, *Siphonaria*, Nouvelle Zélande et Nouvelle Hollande [New Zealand and Australia], [leg. unknown, but collected during the expedition of *l'Astrolabe*, under the command of Dumont d'Urville]. — Regarded as valid by Catlow and Reeve (1845: 100), Adams and Adams (1855: 271), Hanley (1858b: 153), Hutton (1873: 55, as *zealandica*; 1878: 41; 1883: 143, pl. XVII, figs. H–M, as *zealandica*), Paetel (1889: 430, as *zealandiae*), Suter (1913: 600–601; 1915: pl. 24, fig. 8), Iredale (1915: 478), Bucknill (1924: 82–83, pl. III, figs. 16–16a), Odhner (1924: 55), Powell (1933: 186; 1939: 217; 1946: 91; 1979: 292, pl. 54, fig. 10), Hubendick (1955: 129–132, as *zealandica*), Knox (1955: 86), Morton and Miller (1968: 300, 302, pl. 19, fig. 8), Galindo (1977: 416), Jenkins (1983: 1–2, 4–11, 28–30, fig. 3, pl. 1, figs. a–h, pl. 2, figs. a–h; 1984: 116, 117), and Wilson (2002: 172, 173). Regarded as a synonym of *sipho* by Reeve (1856: Species 9, pl. II, figs. 9a–d), Schrenk (1867: 306), and Hutton (1880: 36, as *zealandica*), and as a synonym of *australis* by (Hubendick, 1946: 49). Misidentifications were also mentioned: according to Hubendick (1946: 36, 47, as *zealandica*), Hutton's (1883) record of *zelandica* is a misidentification of *cookiana*, and Reeve's (1856) record is a misidentification of *laciniosa*; according to Jenkins (1983: 13), the records of *zelandica* by Hutton (1878), Suter (1913, 1915), Iredale (1915), Powell (1939, 1946, 1979), Knox (1955), and Morton and Miller (1968) are all misidentifications of *australis*.

zonata Tenison-Woods, 1878: 99–100, *Siphonaria*, South Tasmanian coast [Tasmania] and near Queenscliff, at the entrance of Port Phillip [Victoria, Australia], [leg. unknown, but likely Tenison-Woods himself]. — This name was created for a taxon that Tenison-Woods (1877: 54–56) had previously described as the variety *tasmanica* of *denticulata*. Iredale (1924: 276) and Hubendick (1946: 22) rightly pointed out that *zonata* was a synonym of *tasmanica*. Regarded as valid by Pritchard and Gatliff (1903: 221), Verco (1907: 105), May (1921: 89), and Galindo (1977: 416), and a synonym of *funiculata* by Tate and May (1902: 419).

Type Localities of *Siphonaria* Species-group Names by Biogeographic Region

A list of all type localities is provided below because information on type localities is critical in any systematic work. Type localities are organized by biogeographic region. Only the available names are considered here (available but permanently invalid names are excluded, too). The abbreviation 'ssp.' precedes subspecific names. Note that more than one type locality may exist for a name (in cases of syntypes from different localities, and no particular type locality was subsequently selected). Information from the secondary literature regarding the name status is also included: in bold = authors consider the name to be valid; (name) = authors consider the name to be synonymous; no symbol = authors consider the name to be valid or synonymous; * = authors consider the name to be valid, synonymous, or of doubtful application (*nomen dubium*).

Type Locality Unknown. — *alternicosta*, (*angulata*), **belcheri**, *blainvillei*, **carbo**, *characteristica*, *concinna*, *conica*, *crenata*, *deflexa**, *exigua*, *ferruginea*, *fuliginata**, *leucopleura*, **lineata**, *lirata*, (*melanoleuca*), *melanozonias**, (*mouretus*), *picta*, *radiata**, *redimiculum*, *savignyi*, **serrata**, *sipho*, *sowerbyi**, (*stellata*), *striatula**, *tristensis*.

European Eastern Atlantic and Mediterranean. — *algesirae*, ssp. **minor**, ssp. **nigra**, *palpebrum*, **pectinata**.

Eastern Atlantic. — Angola: *jonasii*, *striatocostata*. — Cape Verde: (*milneedwardsi*). — Western Africa: (*adansonii*), *grisea*, *parma*, *venosa*.

South Africa. — ssp. *adjecans*, ssp. *albofasciata*, **anneae**, *aspera*, *becki*, **capensis**, **compressa**, *cyaneomaculata*, *kowiensis*, ssp. **kraussi**, *natalensis*, *nigerrima*, **oculus**, (ssp. *pallida*), *tenuicostulata*, *variabilis*.

Caribbean. — Bermuda Islands: *brunnea*, **henica**, ssp. *opalescens*. — Florida: **alternata**, *naufragum*. — Lesser Antilles: *placentula*, *umbonata*.

Western Atlantic. — Brazil: *brasiliana*, **hispida**, *lepida*, *subrugosa*.

Southwestern Atlantic. — Argentina: *lateralis*. — Falkland Islands: *lessonii*.

Tierra del Fuego. — Strait of Magellan. — *magellanica*. — Cape Horn. — *antarctica*.

Southeastern Pacific. — Chile: *laevis*, *laeviuscula*, *lineolata**, *tenuis*. — Easter Island: **pascua**.

Tropical Eastern Pacific. — Baja California: **williamsi**. — Central America: *costata*. — Mexico: *aequilorata*, *lecanium*, ssp. *palmata*, *pica*. — Panama: **gigas**, **maura**.

Northeastern Pacific. — *amara**, **brannani**, **thersites**.

Northwestern Pacific. — <u>Japan</u>: **acmaeoides**, ssp. **depressior**, **japonica**, **rucuana**, **sirius**, *subatra*. — <u>Korea</u>: *coreensis*.

Southwestern Pacific. — <u>Australia</u>: *zelandica* (see New Zealand). — <u>Australia (Macquarie Island)</u>: *macquariensis*. — <u>Australia (South Australia)</u>: **jeanae**, **stowae**. — <u>Australia (Tasmania)</u>: **diemenensis**, *funiculata*, *obliquata*, ssp. *tasmanica*, ssp. **turritus**, *zonata* (see Australia, Victoria). — <u>Australia (Victoria)</u>: ssp. **nereis**, *zonata* (see Australia, Tasmania). — <u>New Zealand</u>: (*amphibia*), *australis*, *cancer*, (*cheesemani*), *cookiana*, *flemingi*, *incluta*, *innominata*, (*macauleyensis*), ssp. **perplexa**, **propria**, (*raoulensis*), *scutellum*, *spinosa*, **stewartiana**, *zelandica* (see Australia).

Tropical and Subtropical Indo-West Pacific. — <u>Australia (New South Wales)</u>: ssp. **comita**, **oblivirgulata**, *scabra*, **virgulata**, *zebra*. — <u>Australia (Queensland)</u>: **currumbinensis**, *densatus*, *elegans*, (*eumelas*), **marza**, *mirificus*, *oppositus*, (*optivus*), (*promptus*), (*soranus*), *zanda*. — <u>Australia (Western Australia)</u>: *baconi*, *denticulata*. — <u>China</u>: **alterniplicata**, *cochleariformis*. — <u>China Sea</u>: **radians**. — <u>Cook Islands</u>: **percea**. — <u>Eastern Africa</u>: **dayi**. — <u>Guam</u>: **guamensis**. — <u>Hawaii</u>: **normalis**, **nuttallii**. — <u>India</u>: *basseinensis*, **laciniosa**. — <u>Indian Ocean</u>: *macgillivrayi*. — <u>Indonesia</u>: *javanica*, *viridis* (see New Guinea). — <u>Java Sea</u>: *alba*. — <u>Lord Howe Island</u>: (*lentulus*). — <u>Madagascar</u>: *madagascariensis*. — <u>Mauritius</u>: *plana**, *punctata*. — <u>New Caledonia</u>: **acervus**, (*commixtus*), **monticulus**, (*parmelas*). — <u>New Guinea</u>: **pisangensis**, *viridis* (see Indonesia). — <u>Norfolk Island</u>: *exulum*, *innocuus*. — <u>Pacific Islands</u>: *depressa*. — <u>Pakistan</u>: *kurracheensis*. — <u>Papua New Guinea</u>: *albicante* (see Solomon Islands). — <u>Persian Gulf</u>: **ashgar**, *rosea*. — <u>Philippines</u>: *bifurcata*, *cornuta*, *corrugata*, ssp. **elatior**, ssp. **intermedia**, *luzonica*, *siquijorensis*. — <u>Reunion Island</u>: *incerta*, **parcicostata**. — <u>Solomon Islands</u>: *acuta* (see Sulawesi), *albicante* (see Papua New Guinea), *atra*. — <u>Sulawesi</u>: *acuta* (see Solomon Islands). — <u>Tonga</u>: *plicata*, *tongensis*.

Conclusion

The analysis of all the secondary taxonomic literature that could be found on *Siphonaria* in the context of the present study shows that authors have agreed on the status of only few species-group names. Indeed, of all the 204 names that are available and not permanently invalid, there are only 44 specific and 10 subspecific names that all authors consider to be valid, and only 17 specific and 1 subspecific names that all authors consider to be synonymous. However, there are 96 specific and 5 subspecific names that authors consider to be valid or synonymous, and 9 specific names that authors consider to be valid, synonymous, or of doubtful application (*nomina dubia*). One of the reasons for this lack of general agreement likely is that, so far, taxa have mainly been delineated using shell morphology, which is quite plastic. Therefore, *Siphonaria* clearly is in need of a taxonomic revision, which could take place at different scales, locally, regionally, or globally.

The tropical Indo-West Pacific is the biogeographic region that hosts by far the highest diversity, or at least the highest number of species-group names of *Siphonaria* that are potentially valid. Based on our analysis of the secondary literature, in the tropical Indo-West Pacific there are: 17 specific and 3 subspecific names regarded as valid by all authors; 7 specific names regarded as synonymous by all authors; 33 specific names regarded as valid or synonymous by authors; and 1 name regarded as valid, synonymous, or of doubtful application by authors. Also, the tropical Indo-West Pacific may prove especially problematic when determining the number of valid species. Several species are linked via transitional forms that may be natural variants or distinct species (Hubendick 1946). To address this issue, Hubendick (1955) suggested the examination of speciation mechanisms and the collection of large populations in order to understand the degree of intraspecific variation. Obviously, DNA sequence data would also be useful in delineating species in the tropical Indo-West Pacific and, more broadly, worldwide.

Acknowledgments

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Table 1

Classification of *Siphonaria* proposed by Hubendick (1946).

Genus *Siphonaria*

    Subgenus *Liriola*

        Sectio *Liriola*

        Sectio *Pachysiphonaria*

        Sectio *Benhamina*

        Sectio *Kerguelenia*

        Sectio *Patellopsis*

Subgenus *Siphonaria*

    Sectio *Siphonaria*

    Sectio *Sacculosiphonaria*

    Sectio *Heterosiphonaria*

    Sectio *Ductosiphonaria*

    Sectio *Simplisiphonaria*

CHAPTER 3: Molecular phylogeny of siphonarians

Inferring species-level phylogenies of the *Siphonaria*: molecular vs. shell morphology

Abstract

Shell morphology of limpets in the genus *Siphonaria* is highly plastic and exhibits a dearth of characteristics that can make identifying individuals to species difficult. To address this difficulty, portions of the COI, 12S, and 16S mitochondrial genes were sequenced for 159 specimens of *Siphonaria* then analyzed using Maximum Likelihood and Bayesian Inference methods. Forty-four clusters were identified on the resulting phylogenetic tree and ultimately 35 ESUs were recognized. High species diversity of

siphonarians in the Indo-West Pacific was confirmed. The tree also revealed three species complexes based on shell morphology: *S. laciniosa*, *S. normalis*, and *S. subatra*. Five clusters, most of which contained only one individual, were not able to be identified to the specific level. The ancestral mode of development was determined to be planktotrophic and the origin of siphonarians appears to be the tropical west coast of the Americas. The percentage of sequence divergence was a helpful tool in demarcating species and the threshold for this data set of siphonarians is approximately 5.9%. More specimens need to be collected and added to this set of morphological descriptions and molecular sequences before a complete pattern of speciation processes can be determined for siphonarians.

Introduction

Historically, systematic studies of gastropods have been based upon morphological characters (e.g. internal anatomy, radula structure, shell morphology), some of which can demonstrate a high degree of plasticity depending upon environmental stressors (Teske et al. 2007). Shell morphology has been the primary method for distinguishing species in the genus *Siphonaria*, a group of limpet-like pulmonate gastropods; this has lead to numerous novel species descriptions that are not valid. Hubendick (1946) alleviated much of this nomenclatural clutter with his monograph of the Patelliformia (or Siphonarioidea), a group consisting of species in the genera *Siphonaria*, *Williamia*, and *Trimusculus* (formerly *Gadinia*). However, since the synonymies in Hubendick's monograph were based entirely on morphological data, the likelihood remains great that there continues to be a number of invalid siphonarian species names. Molecular sequence data would be an additional data set that could elucidate the number of valid species in *Siphonaria*, as well as their phylogenetic relationships. This research utilized portions of three mitochondrial genes: cytochrome oxidase I (COI), 12S, and 16S.

Molecular sequence data has already demonstrated that the classification system used to delineate species of siphonarians may be fallible. A group of South African scientists have been researching the systematics of the siphonarians located in that region over the past 15 years. In the mid-90s, they looked at the various modes of reproduction (planktotrophic vs. direct development) of siphonarians (Chambers and McQuaid 1994)

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and later used protein electrophoresis to detect genetic variability between South African species that demonstrated different modes of reproduction (Chambers et al. 1996). The authors then used randomly amplified polymorphic DNA (RAPD) to elucidate the phylogeny of nine South African species and the evolutionary pattern of their modes of reproduction (Chambers et al. 1998). While Chambers et al. (1998) were able to address some taxonomic issues at the level of sectia (they designate these as subgenera), the results of this analysis suggested that direct development could be the ancestral mode of reproduction, which is opposite of their earlier findings in 1996; therefore, Chambers et al. (1998) concluded that more detailed molecular techniques, such as sequencing mitochondrial DNA, would be needed to provide further resolution.

In 2007, Teske et al. used partial sequence data from COI and the intron-containing nuclear gene adenosine triphosphate synthase β-subunit (ATPSβ) to address the taxonomy of four sympatric species of *Siphonaria* located on the east coast of South Africa: *Siphonaria nigerrima*, *Siphonaria tenuicostulata*, Siphonaria *anneae*, and *Siphonaria dayi*. These four species, all members of the *Patellopsis* sectia, are similar in their reproductive strategy (direct development) and habitat distribution; the only character that can clearly distinguish each species is the shell morphology: size, thickness, color, and the number and shape of the ribs (Teske et al. 2007). Instead of producing a tree in which each of the four species was well delineated, the analysis of Teske et al. (2007) produced a tree that had only two lineages, each comprised of more than one species. Of particular interest, the division of the two lineages was associated with a geographic boundary between the subtropical east coast and the south coast that occurs near Cape St. Lucia. The difficulty faced by Teske et al. (2007) was explaining how these four species were genetically indistinguishable and yet had such striking differences in shell morphology. Biotic and abiotic factors can alter how the genotype is expressed, thus altering the phenotype; however, these four species are sympatric and are exposed to the same environmental factors. The only hypothesis provided by Teske et al. (2007) is that the different shell morphotypes evolved prior to the divergence of the northern and southern lineages. Molecular sequence data can clarify the relationships of siphonarians and in doing so can also create even more questions when unexpected results are produced.

Another aspect of Hubendick's monograph that was addressed with molecular sequence data is the phylogenetic status of the two subgenera and ten sectia (five sectia per subgenus) he established under the genus *Siphonaria*. The two subgenera, *Liriola* and *Siphonaria*, are delineated by the presence of either muscle or connective tissue in the epiphallus duct, absence or presence of longitudinal folds in the epiphallus duct, absence or presence of a flagellum, and characteristics of the spermatophore (Hubendick 1946). In general, species in the subgenus *Liriola* are centrally distributed on the west coasts of Africa and the Americas and around the polar region of the southern hemisphere, whereas species in *Siphonaria* have their distribution centered in the Indo-West Pacific (Hubendick 1946) (Figure 1). Further division of the subgenera into sectia is based primarily on morphology of the reproductive system, intestinal coils, and radula; structure of the shell; and the position of the kidney in relation to the gill vessel (Hubendick 1946). The five sectia under the subgenus *Liriola* are *Liriola*, *Pachysiphonaria*, *Benhaminia*, *Kerguelenia*, and *Patellopsis*; the five sectia under the subgenus *Siphonaria* are *Siphonaria*, *Sacculosiphonaria*, *Heterosiphonaria*, *Ductosiphonaria*, and *Simplisiphonaria*. Again, the supra-specific classification of siphonarians has been based on morphological characters and molecular sequence data can be used to check the soundness of this classification.

Partial sequence data from the three mitochondrial genes may also provide useful information about the ancestral mode of reproduction and insight into the evolutionary history of siphonarians. Various authors have hypothesized about the origin of siphonarians (see Hodgson 1999); some propose that their terrestrial ancestors began inhabiting the upper shores of the tidal zone, others a marine ancestry. In relation to the ancestral mode of reproduction, there are two basic scenarios. If siphonarians had a terrestrial ancestor, the ancestral mode of reproduction would be direct development and the lecithotrophic larvae would hatch with the ability to crawl. If the ancestor was marine, the planktotrophic larvae would emerge as swimming veligers. The reproductive strategy of the species in the earliest branch produced by phylogenetic analyses could be equated to the ancestral mode of reproduction. The majority of siphonarians exhibit planktotrophic larval development, but there are variations (e.g. pelagic egg ribbons or juveniles with both swimming velum and crawling foot) and strategies are not known for every species (Chambers and McQuaid 1994, Hodgson 1999).

Methods and Materials

Specimens of *Siphonaria* were acquired from the Australian Museum (AM), British Museum of Natural History (BMNH), California Academy of Sciences (CAS), Florida Museum of Natural History (UF), and Museo de La Plata (MLP) (Table 1). DNA was extracted using the phenol-chloroform extraction protocol with cetyltrimethyl-ammonium bromide (CTAB). Portions of the three mitochondrial genes (COI, 12S, 16S) were amplified using the following universal primers: COIF (5'-3') GGT CAA CAA ATC ATA AAG ATA TTG G, COIR (5'-3') TAA ACT TCA GGG TGA CCA AAR AAY CA by Folmer et al. (1994); 12SF (5'-3') AAA CTA GGA TTA GAT ACC CTA TTA T, 12SR (5'-3') GAG GGT GAC GGG CGG TGT GT by Palumbi et al. (1991); and 16SF (5'-3') CGC CTG TTT ATC AAA AAC AT, 16SR (5'-3') CCG GTC TGA ACT CAG ATC ATG T by Palumbi et al. (1991). The 25 μl PCR reactions contained 10.9 μl of water, 2.5 μl of 10X PCR Buffer, 2 μl of 25 mM MgCl$_2$, 1 μl of each 10 μM primer, 2 μl of dNTP Mixture, 0.2 μl (1 unit) of TaKaRa Taq (Code No. R001A), 5 μl of 20 ng/μl template DNA, and 0.4 μl of 100X BSA. In some short PCR reactions the BSA was replaced with 5 μl of 5X Qiagen Q-Solution (water added to these reactions was 6.3 μl). The thermoprofile used for 12S was five minutes at 94°C; 40 cycles of 40 seconds at 94°C, 1 minute at 46°C, and 1 minute at 72°C; and 10 minutes at 72°C. The thermoprofile used for cox1 and 16S was five minutes at 94°C; 30 cycles of 40 seconds at 94°C, 1 minute at 46°C, and 1 minute at 72°C; and 10 minutes at 72°C. The PCR products were cleaned with Qiagen QIAquick PCR Purification Kit (Cat. No. 28106) prior to sequencing. Sequences of all three genes were not obtained for some specimens; those specimens used in the phylogenetic analyses had sequences from two or all three of the genes. Sequences from cox1, 12S, and 16S were first aligned individually, cox1 sequences using MUSCLE (Edgar 2004) and 12S and 16S sequences using MAFFT (Katoh et al. 2002). Each alignment was minimally cropped on either end and then sequences were concatenated. The concatenated alignment was not adjusted manually nor were any variable sites removed.

The model for nucleotide substitution of the concatenated sequences was determined by Topali version 2.5 (Milne et al. 2004); utilizing the Akaike Information Criterion (AIC),

the model selected for both the maximum likelihood (ML) analysis and the Bayesian inference (BI) analysis was GTR+I+G. The ML analysis of the nucleotide sequence was run using PhyML in Topali with bootstrap support values based on 100 replicates. The BI Metropolis-coupled Markov chain Monte Carlo (MCMC) analysis was performed with MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001) for the nucleotide sequence (two parallel analyses, 11,850,000 generations, sampled every 100 generations, 25% burn-in). Pairwise distance analyses were also completed using MEGA version 4.1 (Beta) (Tamura et al. 2007) and the default settings except for the model (Kimura 2-parameter) and the rate among sites (gamma distribution).

Morphological characteristics of the shells (e.g. height of shell, position of apex, ridge pattern, coloration of muscle scar, etc.) were analyzed for each "cluster" of individuals that occurred on the tree produced by the phylogenetic analyses. Shell size was determined based on the length of the shell (length: >30mm = large, 15 to 30mm = medium, <15mm = small) and shell height was also correlated to the length of the shell (>1/2 of length = high, 1/4 to 1/2 of length = medium, <1/4 of length = low). The external location of the apex was roughly mapped onto an X-Y graph and given coordinates in the anterior-posterior axis (Y) and the left-right axis (X). Shell measurements given in Table 1 were taken at the widest portion of each shell.

Results

Identical tree topologies were produced by both the ML (-LnL = 46520.02) and BI (-LnL = 46375.02) analyses with the exception of Clusters 12 and 13 (Figure 2). In the ML analysis, Cluster 12 is sister to Clusters 13 and 14+15 (weakly supported) and in the BI analysis, Cluster 12 is sister to Cluster 13 (highly supported). The siphonarians formed a well-supported monophyletic clade and forty-four clusters were identified based on the tree topology. Descriptions of the shell morphology, dorsal and lateral pictures of the individual shells, and distribution for each of the clusters are given below (see Table 1 for shell measurements).

Eighteen species of siphonarians were easily identified based on shell morphology and location: *acmaeoides*, *alternata*, *ashgar*, *atra*, *belcheri*, *cf. compressa* (Oman), *denticulata*, *gigas*, *japonica*, *laciniosa*, *lateralis*, *lessonii*, *maura*, *normalis*, *pascua*, *pectinata*, *savignyi*, *sirius*, and *subatra*. *Siphonaria funiculata* was also easy to identify, but the two clusters (13 and 14) identified as that species were not reciprocally monophyletic. Cluster 13 is sister taxon to Cluster 12 in the BI tree and sister to the clade containing Clusters 13, 14, and 15 in the ML tree. In both the ML and BI tree, Cluster 14 is sister taxon to the *S. lessonii* clade (Cluster 15). Two species complexes were identified that contain cryptic species based on shell morphology: *laciniosa* and *normalis*; *S. subatra* may also be a species complex. Five clusters were unidentified and may be undescribed species. Given below are the physical descriptions of the shells of specimens in each cluster, pictures of the dorsal and lateral views of each shell, and a map of the specimens' collection localities.
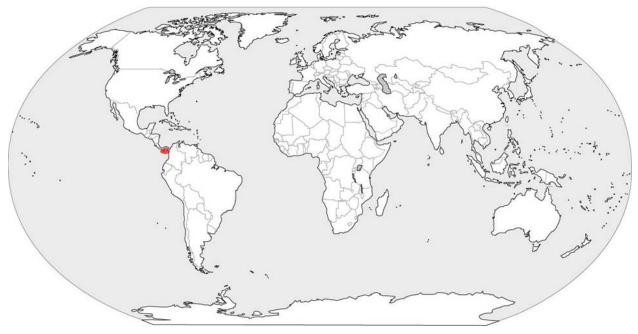
Cluster 1 – *Siphonaria gigas* Sowerby, 1825 (Heterosiphonaria)

As the biggest siphonarian, this species has a large shell size, medium to high shell height, and robust shell thickness. The periphery of the shell demonstrates bilateral symmetry, is oval in shape with the anterior end of the shell narrower than the posterior end, and has scalloped edges. There is no projection of the shell at the siphon. Typically, the shell has one to seven finer ridges interspersed between 10 distinct ridges. In the anterior-posterior axis, the apex is central to slightly anterior (0 to 0.5) and in the left-right axis, the apex is central (0). The apex is not hooked and points upward. Coloration of the shell's inner side is white to mottled white and brown at the apex and dark brown at the margin. Some shells have white rays visible at the margin of the shell that can extend past the muscle scar. The muscle scar lacks any specific coloration, but the shell may be slightly darker at that position.

UF359682   UF359645

CLUSTER 1

Cluster 2 – *Siphonaria maura* Sowerby, 1835 (Heterosiphonaria)

Like *S. gigas*, *S. maura* is located in the eastern Pacific from Baja California south to Chile. However, this distinctly flattened species is smaller, typically medium in size, with a medium to low height. The general overall shape of the shell is a bilateral oval with the anterior end of the shell being narrower than the posterior end. The edges of the robust shell are scalloped due to the presence of ridges on the shell's surface. There are approximately 10 to 12 distinct ridges (typically white and can be somewhat broad) with one to five fine ridges in between each distinct ridge. Two distinct ridges mark the location of the siphon; there is a tendency to have more fine ridges anterior and

posterior of these distinct ridges and few fine ridges in between the two. The apex is centrally (0, 0) located in both the anterior-posterior and left-right axes, is not hooked, and the tip points posteriorly. The inner side of the shell is entirely dark brown except for the white rays at the margin. These rays do not extend beyond the muscle scar. The muscle scar is indicated by a slight darkening the shell, but lacks pigmentation.

UF359679

UF141401

UF351511

UF359623

UF359681

UF371626

UF371937

UF371950
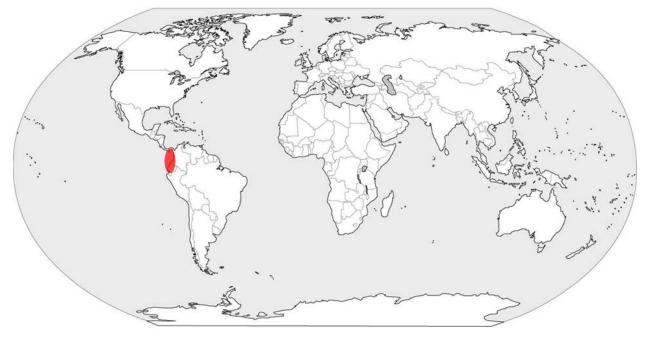
UF371957

CLUSTER 2

Cluster 3 – *Siphonaria ashgar* Biggs, 1958

Typically, these fragile shells are small, but some may reach a medium size and the height ranges from low to medium. The anterior end of the shell is narrower than the posterior end, thus the shell is oval-shaped and has bilateral symmetry. There is a slight projection of the shell where the siphon is located that is more vertical in nature than lateral. The edges are finely scalloped due to the presence of ridging; there are several distinct ridges (approximately 30) with one to two fine ridges between each distinct ridge. The apex of the shell is not hooked, points upward, is central to slightly posterior (0 to -0.5) in the anterior-posterior axis, and is central (0) in the left-right axis. Dark brown is the coloration of the inner side of the shell and the margins have white rays. The inner side margin rays may be patches of white alternating with patches of brown and some shells may have more white than brown. The rays do not extend beyond the white muscle scar. This species occurs in the Persian Gulf and is distinct due to its light coloration.
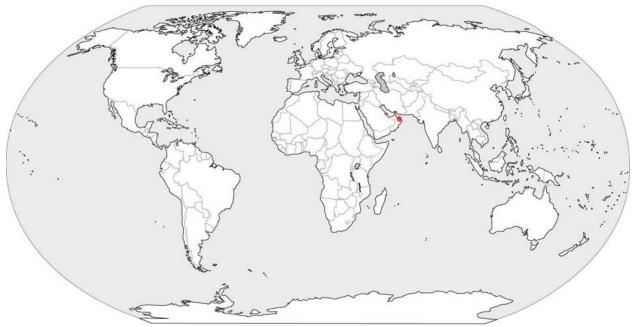
UF368014

UF296019

CLUSTER 3

Cluster 4 – *Siphonaria pectinata* (Linné, 1758) (Patellopsis)

This species occurs in the Mediterranean, the Atlantic Ocean from Portugal to Cameroon with a break at the Gulf of Guinea, Florida, the Gulf of Mexico, and the Caribbean. *Siphonaria pectinata* originated in the Mediterranean and East Atlantic then spread to the West Atlantic. These small to medium-sized shells are easily identifiable due to the thin dark and light alternating rays. Shell height is low to medium and while the shells exhibit bilateral symmetry and are generally oval in shape, the anterior end may or may not be narrower than the posterior end. The edges of these fragile shells are not scalloped since the ridges [rays] are not raised and there is no projection of the shell at the siphon. The apex is slightly posterior (-0.5) in the anterior-posterior axis, is central (0) in the left-right axis, is not hooked, and points posteriorly. The coloration of the shell's apex on the inner side is white and the margins are brown with white rays. These rays do not extend beyond the muscle scar, which lacks any distinct coloration.

UF382817

UF54117

UF79313
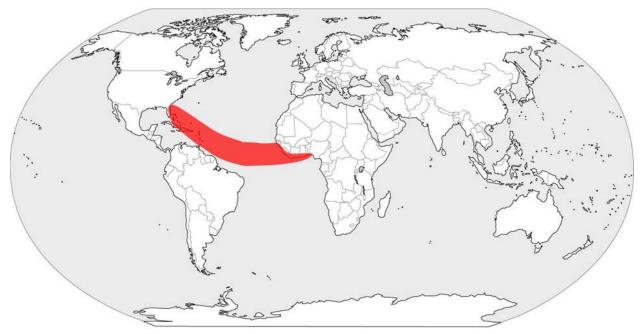
UF254828

BMNH20080071

CLUSTER 4
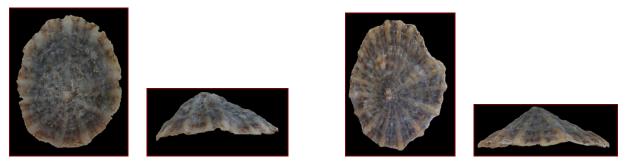
Cluster 5 – *Siphonaria japonica* (Donovan, 1824) (Sacculosiphonaria)

These small to medium-sized shells have a low to medium height and are located in Japan, Taiwan, and Hong Kong. In general, the fragile shell is bilaterally symmetrical and oval in shape, but the siphonal projection extends all the way to the posterior end of the shell instead of narrowing back to the width anterior to the siphon. The siphonal groove is associated with 2 closely-spaced distinct ridges. Typically, the anterior end of the shell is narrower than the posterior end, but this may not always be the case. There are approximately 15 to 19 distinct ridges with each having one to four fine ridges in between. Due to the ridging, the edge of the shell is scalloped. The position of the apex is also a defining characteristic of this species; it is slightly posterior (-0.5) in the anterior-posterior axis and left of center (-0.5) in the left-right axis. The apex is not hooked and the tip points posteriorly. The coloration of the entire inner side of the shell is dark brown and white rays are present at the margin; some may have more white than brown at the shell margin. The muscle scar may be slightly darker, but has no distinct color and the rays do not extend beyond it.

UF350544

UF350553

UF310519
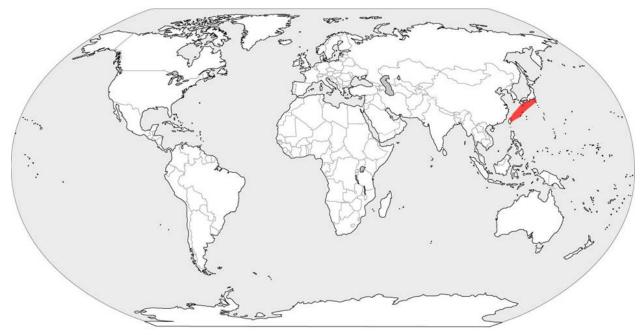
UF368383

Extraction 892-1

CLUSTER 5
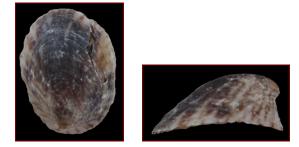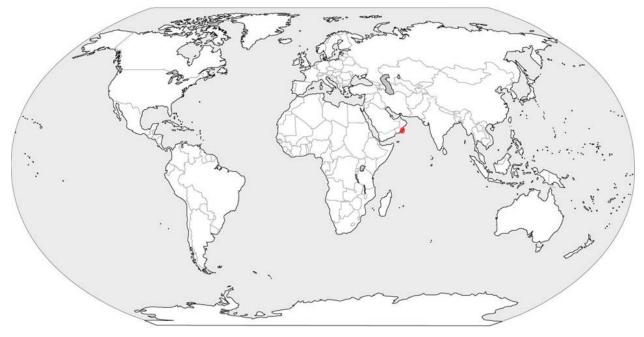
Cluster 6 –*Siphonaria cf. compressa* Allanson, 1958 (Sacculosiphonaria)

These small, extremely fragile shells were collected in Oman and are likely the undescribed species mentioned by Bosch et al. (1995). The bilaterally symmetrical shells are medium to high in height and are mostly oval in shape although the anterior end may or may not be narrower than the posterior end of the shell. All of the ridges on the surface of the shell appear to be the same size, but this is difficult to determine due to the small shell size. There is no siphonal projection and the edges are not scalloped. The apex is located at the posterior end of the shell (-2), is left of center (-1) in the left-right axis, is hooked, and points posteriorly. Interior coloration reflects the external coloration, white or brown, and if rays are present, they do extend beyond the muscle scar. The muscle scar has no distinctive color.
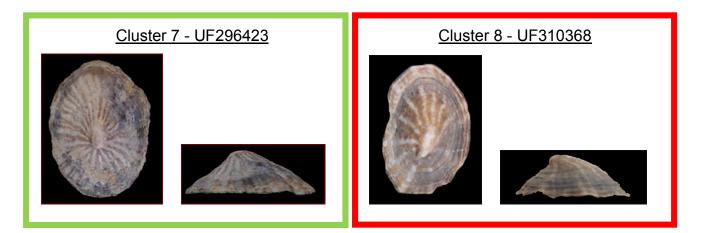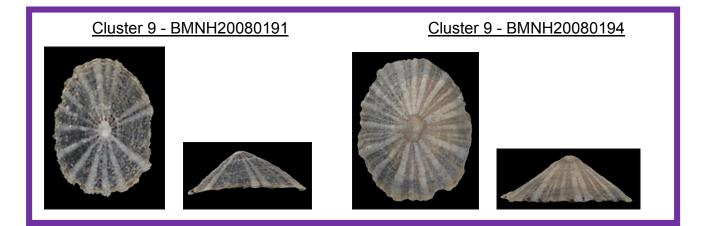
CLUSTER 6
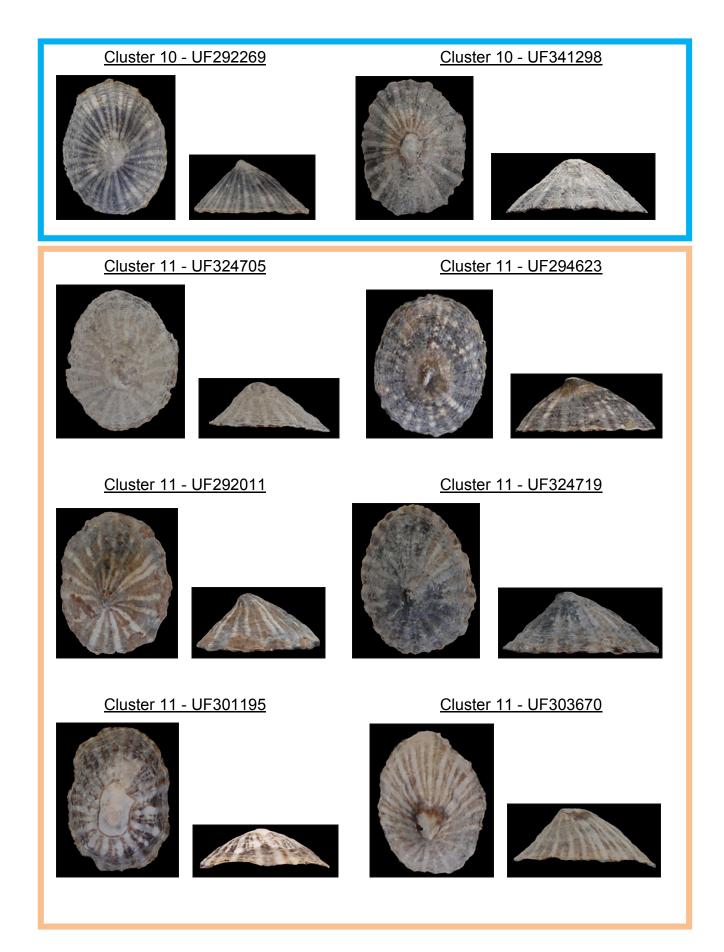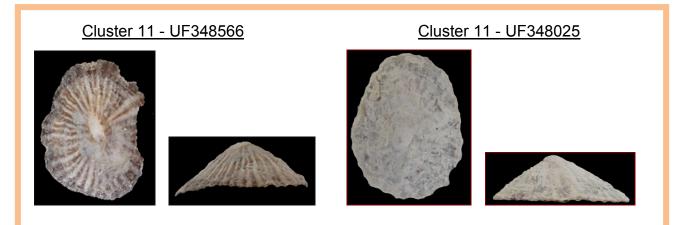
Clusters 7 - 11 – *Siphonaria normalis* Gould, 1848 species complex

The majority of individuals are small and fragile, but some may reach a medium size and have a more robust shell. Typically, the shells are medium in height although some specimens may be low. The shell symmetry is bilateral and oval in shape although the anterior end may or may not be narrower than the posterior end. Ridges are present on the shells, usually alternating distinct and fine ridges, but appear more as light-colored rays on a darker background. The shell edge may or may not be scalloped and there is either a slight or no projection of the shell at the siphon. Typically associated with the siphonal groove are two, closely-spaced distinct ridges that may have one fine ridge in

between them. The location of the apex is central to slightly posterior (0 to -0.5) in the anterior-posterior axis and central (0) in the left-right axis. The apex is not hooked and the tip points posteriorly. White is the typical color of the apex on the inner side of the shell, but the apex may also be dark blackish-brown or even a mottling of white and brown. The inner side margin is brown with white rays and the rays typically do not extend beyond the colorless muscle scar. The type locality of *S. normalis* is Hawaii [Sandwich Islands] and this species' distribution extends from the Pacific Ocean into the Indian Ocean. Cluster 11 contains a specimen from Hawaii and the localities of the other specimens included in this species complex are Caroline Islands, Thailand, Singapore, Fiji, Samoa Islands, Nauru, Guam, Society Islands, Gambier Islands, Marquesas Island, and Cocos (Keeling) Islands. Since Cluster 11 contains a specimen from the type locality, individuals of this cluster are *S. normalis*. Possible names for individuals in Clusters 7-10 are: *acervus*, *acuta*, *albicante*, *baconi*, *bifurcata*, *corrugata*, *elatior*, *intermedia*, *javanica*, *luzonica*, *monticulus*, *pisangensis*, *siquijorensis*, or *viridis*.

Cluster 7 - UF296423

Cluster 8 - UF310368

Cluster 9 - BMNH20080191

Cluster 9 - BMNH20080194

Cluster 10 - UF292269

Cluster 10 - UF341298

Cluster 11 - UF324705

Cluster 11 - UF294623

Cluster 11 - UF292011

Cluster 11 - UF324719

Cluster 11 - UF301195

Cluster 11 - UF303670

Cluster 11 - UF348566

Cluster 11 - UF348025

Cluster 11 - UF400391

Cluster 11 - UF392234
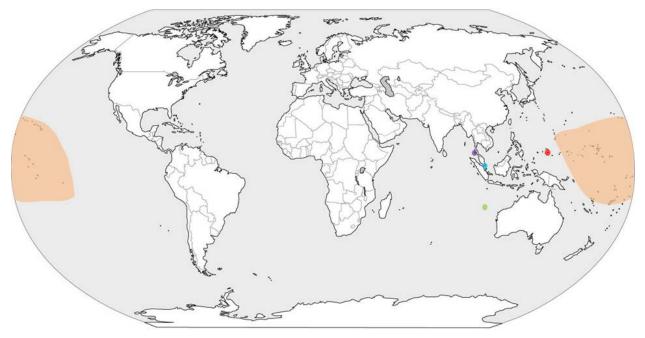
Cluster 11 - BMNH20080069

Cluster 12 – *Siphonaria lateralis* Couthouy *in* Gould, 1848 (Kerguelenia)

The small to medium-sized shells are fragile and medium in height. While most shells are generally oval in shape, the anterior end may or may not be narrower than the posterior end. The overall symmetry of the shell is bilateral, but some individuals have a flattened left side that forms a straight line, whereas the right side of the shell angles outwards towards the location of the siphon and then back in towards the shell's posterior. Shells may or may not have a projection at location of the siphon and there are no ridges that mark the location either. Ridges are present on the shells, but some shells have more elevated ridges than others; those shells with elevated ridges have edges that are scalloped. Some shells have ridges that appear equal in size, others have both distinct and fine ridges with one to two fine ridges in between each distinct ridge. The location and structure of the apex are distinct characteristics of this species. The hooked apex is posterior (-1.5 to -2) in the anterior-posterior axis, left of center (-1) in the left-right axis, and points posteriorly. The inner side of the shell is entirely brown with white rays at the margin that do not extend past the muscle scar. Some shells have a white muscle scar and in others the muscle scar is not white, but lighter in color than

the shell's interior. This species' range includes the Falkland Islands, South Georgia, Kerguelen Islands, Tasmania, Macquarie Island, Auckland Islands, Campbell Island, Antipodes Islands, Strait of Magellan, and Patagonia, Argentina.

MLP13170

MLP13163
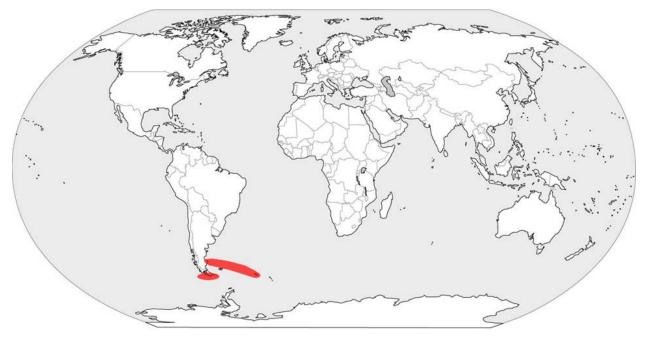
BMNH1994092

CLUSTER 12
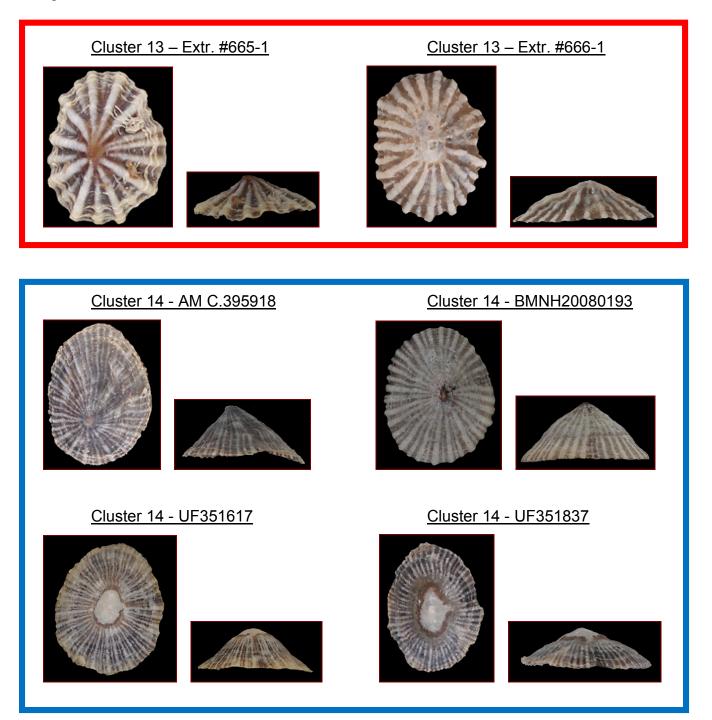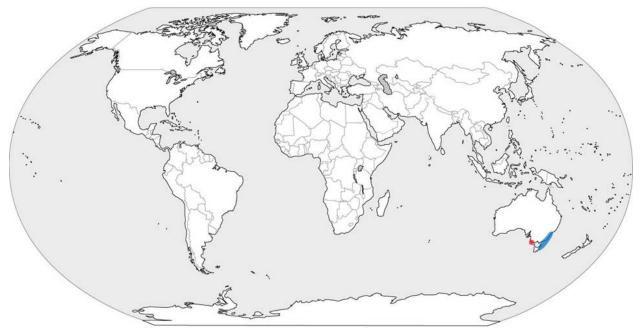
Clusters 13 - 14 – *Siphonaria funiculata* Reeve, 1856 [species complex?] (Pachysiphonaria)

This species inhabits New South Wales, Victoria, and Tasmania (Australia) and has shells that range in size from small to large and height of low to medium. The smaller shells are fragile and as they increase in size, the shell becomes more robust. Symmetry is bilateral and the shell is oval in shape due to the anterior end being narrower than the posterior end. When the specimens are smaller, the ridges are more elevated, the ridge pattern is distinct alternating with fine, and there is a slight projection of two adjacent distinct ridges that marks the location of the siphon. Larger specimens have a smoother surface, one to five fine ridges in between a pair of distinct ridges, and no external indication of the siphonal groove. There are, on average, approximately 15 distinct ridges on each shell and the edge of the shell is scalloped. The apex is centrally located in both the anterior-posterior (0) and left-right (0) axes, not hooked, and points posteriorly. Interior coloration at the apex is white and the margin is brown with white rays that may or may not extend beyond the muscle scar. Larger specimens have a

muscle scar that is white outlined by brown; the muscle scar in small specimens is lighter but without a distinct color.

Cluster 13 – Extr. #665-1

Cluster 13 – Extr. #666-1

Cluster 14 - AM C.395918

Cluster 14 - BMNH20080193

Cluster 14 - UF351617

Cluster 14 - UF351837

CLUSTERS 13 - 14

Cluster 15 – *Siphonaria lessonii* Blainville, 1827 (Pachysiphonaria)

This well known species found on the west coast of South America from Peru to the Strait of Magellan, the east coast of South America from Uruguay to Tierra del Fuego, and the Falkland Islands, is small to medium in size and has a medium to high shell height. The fragile shell is oval in shape with the anterior end narrower in width than the posterior end. In general, the edge of the shell is bilaterally symmetrical although the right side of the shell can gradually slope outwards to form a slight projection at the location of the siphon. The shell edge is not scalloped. Light and dark rays [ridges] alternate on the surface of the shell with some shells having every other dark ray darker in color. There are approximately 30 dark rays and these rays are unique to this species. The apex is posterior (-1 to -1.5) in the anterior-posterior axis, left of center (-0.5) in the right-left axis, not hooked, and points posteriorly. The coloration of the inner side is brown with white rays at the margin that do not extend beyond the muscle scar. Small specimens have a colorless muscle scar while larger specimens have a muscle scar that is lighter in color.

MLP13164

MLP13165

MLP13166

MLP13168

MLP13169
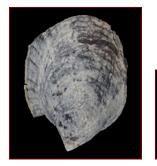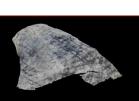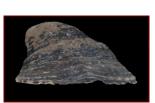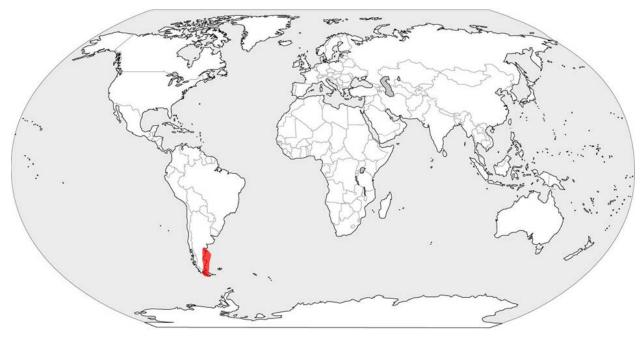
MLP13167

CLUSTER 15
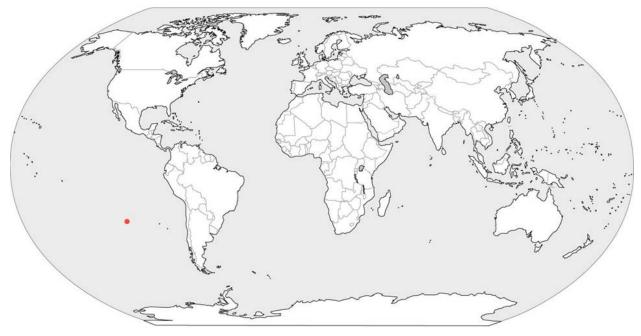
Cluster 16 – *Siphonaria pascua* Rehder, 1980

This fragile, small-shelled species that is low in height has only been reported from Easter Island. The shell is bilaterally symmetrical, oval in shape with the anterior end narrower than the posterior end, and there is no projection of the shell at the siphonal groove. Due to the presence of ridging (approximately 14 distinct ridges), the edge of the shell is scalloped. Typically, the distinct and fine ridges alternate, but there may be two to three fine ridges in between two distinct ridges or distinct ridges that are adjacent to one another without a fine ridge in between. At the location of the siphon, there are two adjacent distinct ridges. The apex is central (0, 0) in both the anterior-posterior and left-right axes, points to the posterior, and is not hooked. The inner side of the shell is entirely dark brown with white rays at the margin. These marginal rays do not extend past the colorless muscle scar.

CLUSTER 16
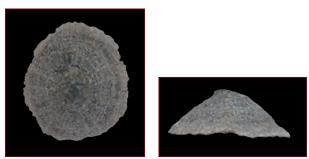
<u>Cluster 17</u> – *Siphonaria* sp.
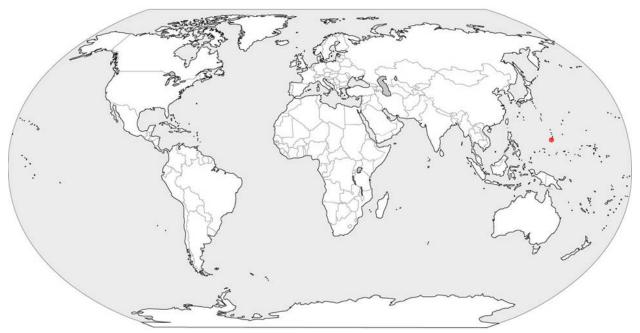
Collected from Saipan, Northern Mariana Islands, the shell of this siphonarian is small in size, fragile, and low to medium in height. The anterior end of the shell is typically narrower than the posterior end which results in the shell appearing oval in shape. There is no projection of the shell the siphon, the shell is bilaterally symmetrical, and the edge is not scalloped. There are numerous, fine, raised ridges that appear to be all the same size and this ridge morphology is a unique characteristic of this species. The apex is slightly posterior (-0.5) in the anterior-posterior axis, central (0) in the left-right axis, not hooked, and points posteriorly. The inner side of the shell is dark brown with white

rays at the margin. These rays extend beyond the muscle scar that may be colorless or slightly darker than the interior of the shell. This individual may be *S. guamensis*, but further anatomical research needs to be completed before species designation.

<u>UF400392</u>
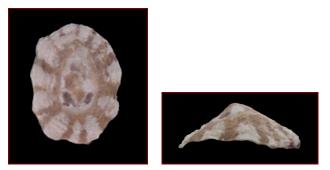
CLUSTER 17
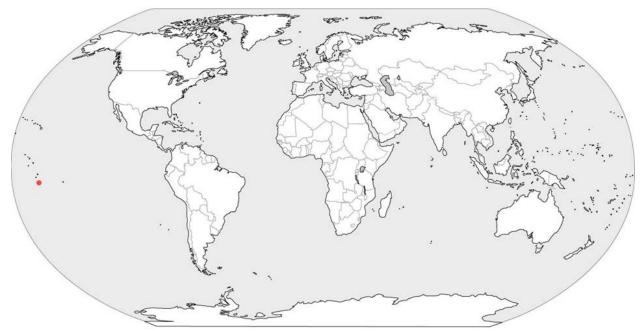
Cluster 18 – *Siphonaria* sp.

The fragile shell of the specimens collected in Rarotonga, Cook Islands is small in size and low to medium in height. There is no siphonal projection so the shell is bilaterally symmetrical and generally oval in shape, but the anterior end may or may not be narrower than the posterior end. While the shell edge is not scalloped, the ridge pattern

consists of approximately 13 broad, light-colored, distinct ridges separated by single dark rays. At the location of the siphon, there are two distinct ridges that are more closely spaced together than those on the rest of the shell. The ridge morphology is a unique characteristic of this shell. The apex is slightly posterior (-0.5) in the anterior-posterior axis, central (0) in the left-right axis, not hooked, and points posteriorly. Coloration of the inner side apex is mottled brown and white and the margin is brown with white rays. These white rays extend beyond the colorless, but slightly darker, muscle scar.

UF291950

CLUSTER 18

Cluster 19 – *Siphonaria* sp.
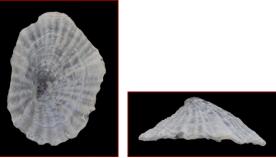
Specimens were collected from a lagoon on Wake Island and each of their shells is small in size with a medium height. The fragile shell is oval, bilaterally symmetrical with the anterior end narrower than the posterior end. There is a slight projection of the shell at the siphon and the edge of the shell is scalloped. Two distinct ridges indicate the location of the siphon, which is typical, but the pattern of ridge thickness is not. On the anterior end of the shell, the ridges are all the same size, whereas on the posterior end of the shell, the ridges alternate between distinct and fine. There are approximately 20 distinct ridges. The apex is slightly posterior (-0.5) in the anterior-posterior axis, central (0) in the left-right axis, not hooked, and points towards the posterior end of the shell. The interior of the shell is entirely dark brown with white rays at the margin. These rays extend beyond the colorless muscle scar, which may be slightly lighter than the shell's interior. This individual may be *S. nuttallii*, but further anatomical research needs to be completed before species designation.

UF379054

UF375861

170

CLUSTER 19
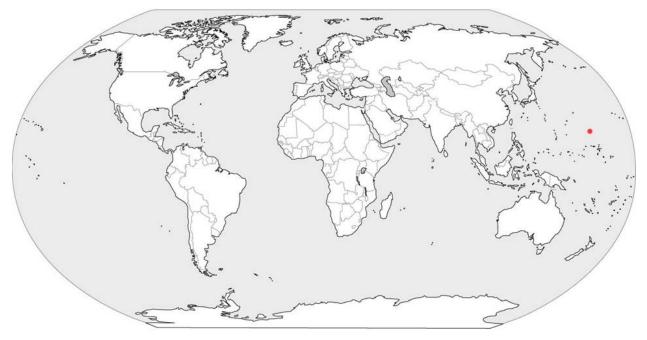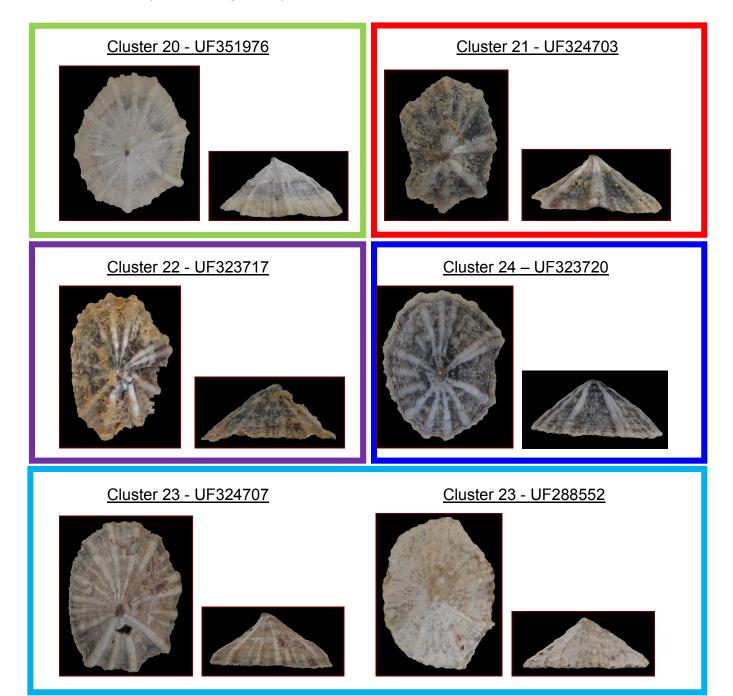
Clusters 20 - 26 – *Siphonaria laciniosa* (Linné, 1758) species complex (Siphonaria)

The robust shell of this species is small to medium in size, medium to high in height, oval in shape, and the anterior end may or may not be narrower than the posterior end of the shell. In general, the shell is bilaterally symmetrical, but at the location of the siphon, the shell can have a slight projection that includes two distinct ridges or the shell can continue to project posteriorly from the two distinct ridges to the next distinct ridge. There are approximately 12 to 14 distinct ridges that can have anywhere from one to nine fine ridges in between two distinct ridges. This ridging causes the edge of the shell to be scalloped. Typically, the shell has three distinct ridges that are closely spaced together extending from the apex to the anterior end of the shell. The apex is central to slightly posterior (0 to -0.5) in the anterior-posterior axis, central (0) in the left-right axis, not hooked, and points towards the posterior of the shell. Coloration of the inner side of the shell varies. The apices can be white, brown, or brown mottled with a small amount of white. The margins range from brown with white rays, white with sparse fine brown rays, or entirely white. If rays are present, they extend beyond the brown or light brown muscle scar. The species range for *S. laciniosa* includes Okinawa, Taiwan, Philippines,

Singapore, Indonesia, northern shores of Australia, New Caledonia, Solomon Islands, and Loyalty Islands. Since none of the clusters contain a specimen from the type locality, none of the specimens can be designated as *S. laciniosa*. Possible names for individuals in Clusters 20-26 are: *acuta*, *alba*, *albicante*, *commixtus*, *cornuta*, *corrugata*, *densatus*, *depressa*, *elegans*, *optivus*, *rucuana*, or *viridis*.

Cluster 20 - UF351976

Cluster 21 - UF324703

Cluster 22 - UF323717

Cluster 24 – UF323720

Cluster 23 - UF324707

Cluster 23 - UF288552

Cluster 25 - Extr. #668-2

Cluster 25 - UF368385

Cluster 25 - UF351778

Cluster 25 - UF310711

Cluster 25 - UF292259

Cluster 25 - UF324725

Cluster 25 - UF324728

Cluster 25 - UF367180

Cluster 25 - UF368378

Cluster 25 - UF368380

Cluster 25 - UF368381

Cluster 25 - UF375653

Cluster 25 - UF368377

Cluster 26 - UF296570

Cluster 26 - UF299501

Cluster 26 - UF367624
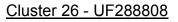
Cluster 26 – UF368762

Cluster 26 – UF310183

Cluster 26 - UF288808

Cluster 26 – UF292268

Cluster 26 - BMNH20080195

Cluster 26 - BMNH20080197

Cluster 26 - BMNH20040811

Cluster 26 - BMNH20040741

Cluster 26 - UF295378

Cluster 26 - UF322540

Cluster 26 - UF327900

Cluster 26 - UF366438
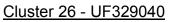
Cluster 26 - UF310785

Cluster 26 - UF329040

Cluster 26 - UF329052

Cluster 26 - UF330847
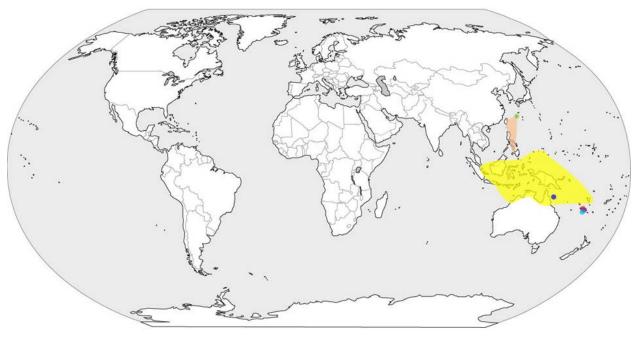
Cluster 26 - AM C.459332

CLUSTERS 20 - 26

Cluster 27 – *Siphonaria belcheri* Hanley, 1858 (Patellopsis)

This species inhabits the Persian Gulf and the eastern coast of Oman, including Masirah Island. The robust shell is small to medium in size and low in height. In general, the shell is oval, bilaterally symmetrical with the anterior end is narrower than the posterior end; however, the two distinct ridges at the siphon noticeably extend past the margin of the shell. These siphonal ridges may be fused together. The ridge pattern consists of about 11 to 12 distinct ridges with one to five fine ridges interspersed in between each pair of distinct ridges. Between the siphonal ridges and the next distinct
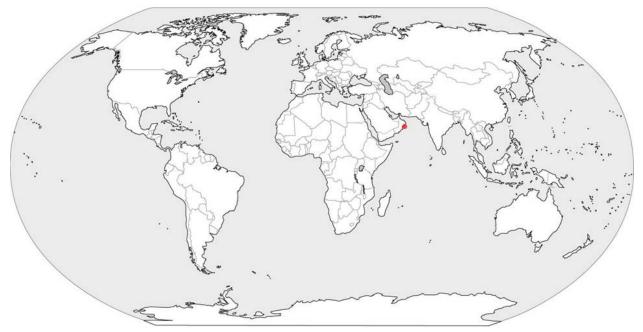
ridge, both anteriorly and posteriorly, are the largest number of adjacent fine ridges. The edge of the shell is scalloped. The apex is not hooked, slightly posterior (-0.5) in the anterior-posterior axis, and slightly left (-0.5) in the left-right axis. Due to the erosion of the apices of the available specimens, the orientation of the apical shell tip is unknown although the apex of one small specimen pointed to the posterior of the shell. The inner side coloration of the shell at the apex is brown and white and the margin is brown with white rays. The white rays extend beyond the colorless, slighter lighter muscle and the ray associated with the siphon extends to the apex.

UF296586

UF295359
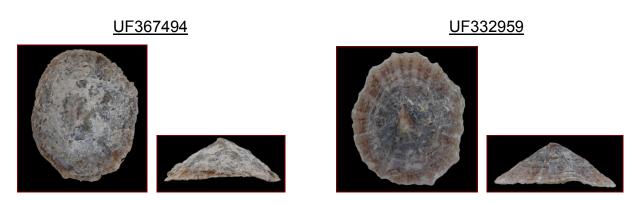
CLUSTER 27
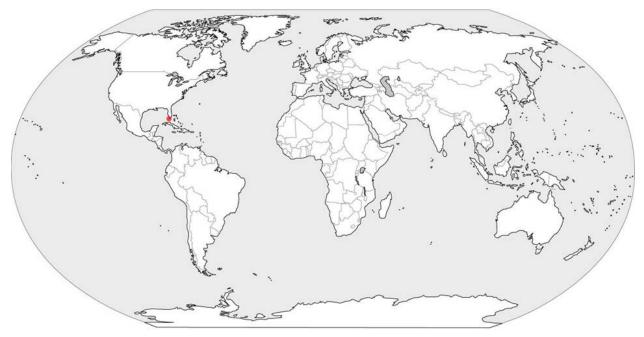
Cluster 28 – *Siphonaria alternata* (Say, 1827) (Siphonaria)

Located in the Gulf of Mexico, the Caribbean, south and east Florida, and Bermuda, the robust shell of this species is small in size and medium in height. The anterior end of the shell is narrower than the posterior end and the shell is oval in shape. There is a slight projection of the shell at the siphon, but the shell is bilaterally symmetrical with a scalloped edge. Two distinct ridges mark the location of the siphon. Approximately 14 to 16 distinct ridges are each separated by one to five fine ridges. The apex is central (0, 0) in both the anterior-posterior and left-right axes, not hooked, and points posteriorly. Coloration of the inner side is white at the apex and the margin is also white with fine light brown rays. These rays extend beyond the slightly darker, colorless muscle scar.

UF367494   UF332959

CLUSTER 28

Cluster 29 – *Siphonaria savignyi* Philippi in Krauss, 1848 (Siphonaria)

The fragile shell of this species is small in size, low to medium in height, and has an edge that is scalloped. Excluding the projection that extends from the siphon to the posterior end of the shell, the shell is generally bilaterally symmetrical, oval in shape, and the anterior end is narrower than the posterior end. There are approximately 15 distinct ridges on the shell with one to five fine ridges in between each pair of distinct ridges. Two closely spaced distinct ridges mark the location of the siphon. The apex is centrally (0, 0) located in both the anterior-posterior and left-right axes, not hooked, and uniquely points to the left posterior of the shell. Also distinctive to this species is the coloration; the inner side is entirely white with fine brown rays. Some of these brown rays extend beyond the white muscle scar. The internal coloration is reflected in the external coloration and the light brown rays may even be linear brown dots. This species inhabits the Gulf of Suez, Red Sea, and Oman.

UF367757   UF367756
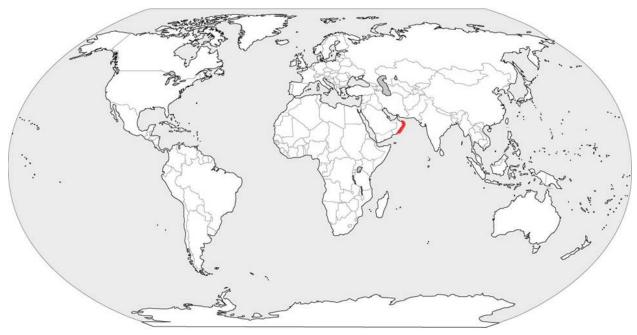
CLUSTER 29

Cluster 30 – *Siphonaria* sp.
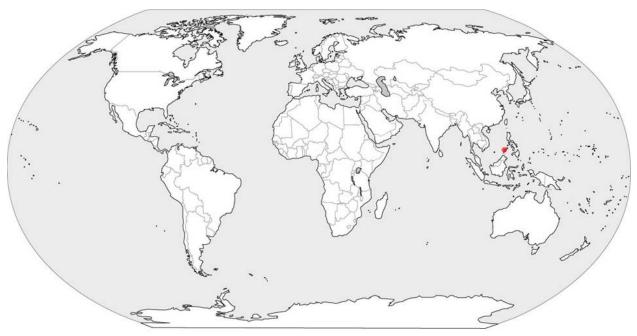
Individuals of this species were collected on Palawan Island in the Philippines and are unique in that their robust shells have greatly raised distinct ridges. The shell is both medium in size and height and has a scalloped edge. Typically, the anterior end of the shell is narrower than the posterior end which causes the shell to appear oval in shape; however, some shells may be more circular than oval. Regardless of the overall shape of the shell, it is bilaterally symmetrical. Two closely spaced, distinct ridges mark the location of the siphon. There are approximately 12 distinct ridges with one to five fine ridges in between. Fine ridges are more numerous between the distinct siphonal ridges and the next anterior and posterior distinct ridges. The apex is centrally (0, 0) located in

both the anterior-posterior and left-right axes, not hooked, and points towards the posterior end of the shell. Coloration of the apex on the inner side is brown or brown mixed with milky white and the margin is brown with white rays that extend beyond the muscle scar. The muscle scar may have no distinct color, may be lighter, or dark brown.

UF117293

CLUSTER 30
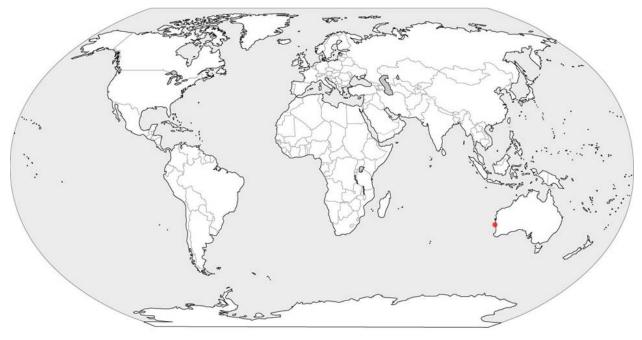
Cluster 31 – *Siphonaria denticulata* Quoy and Gaimard, 1833

The robust shell of species was collected from the east coast of Western Australia is small to medium in size and medium in height, oval in shape with the anterior end narrower than the posterior end, and bilaterally symmetrical. There is a slight protrusion of two distinct rays at the siphon and the shell edge is scalloped. Due to the calcification and erosion of the specimens, the exact number of distinct and fine ridges is difficult to determine (approximately 11 distinct ridges with one to two fine ridges in between each pair of distinct ridges). The apex is located centrally (0, 0) in both the anterior-posterior and left-right axes and is not hooked. Orientation of the apex is unclear due to the condition of the specimens. The inner side of the shell is entirely white with scattered brown rays at the margin. These brown rays do not extend past the light brown muscle scar.

CLUSTER 31

Cluster 32 – *Siphonaria acmaeoides* Pilsbry, 1894 (Patellopsis)

The general range of this species extends from Japan (Honshu) southeastward to New South Wales, Australia (Bateau Bay) and southwestward to Western Australia (Cape Leeuwin). The shell of this species is robust, small to medium in size, and medium in height. In general, the shell is oval and bilaterally symmetrical although the right side of the shell may extend further outwards than the left side. The anterior end of the shell may or may not be narrower than the posterior end, the edges are scalloped, and the siphonal projection is slight or absent. If the shell protrudes at the siphon, the projection begins at one distinct ridge and ends at the next posterior distinct ridge and has three to

four fine ridges in between these two distinct ridges. There are approximately 17 to 18 distinct ridges that are not greatly raised upon the shell's surface and in between each pair of distinct ridges are always two to three fine ridges. This consistent ridge pattern is a distinctive characteristic of this species. The apex is central to slightly posterior (0, -0.5) in the anterior-posterior axis, slightly left (-0.5) in the left-right axis, not hooked, and points towards the posterior end of the shell. Internal coloration of the apex is white, brown, or white with brown specks. The inner side margin is white with brown rays that extend beyond the light brown muscle scar.

Extr. #667-1

BMNH20080196

BMNH20080197
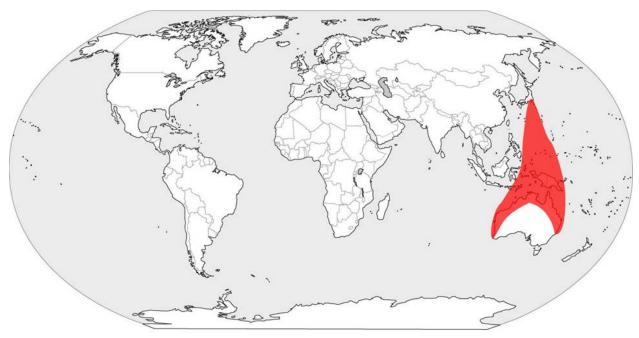
Extr. #892-2

Cluster 33 – *Siphonaria sirius* Pilsbry, 1894 (Siphonaria)

This easily identifiable species inhabits Japan from Honshu to Kyushu and can be found further south in Tonga (Tongatapu). The robust shell is small to medium in size, low in height, and has a scalloped edge. In general, the shell is bilaterally symmetrical, oval in shape, and the anterior end is narrower than the posterior end. However, the anterior end of the shell can be angular, or more pointed than round, which can cause asymmetry. There are approximately six to ten distinct ridges (typically seven) with one to seven fine ridges in between each pair of distinct ridges. The distinct ridge that points towards the shell's anterior end and the next distinct ridge on the right side of the shell are almost at a right angle to one another; if the two distinct ridges were hands on a clock, the time would appear to be two or three o'clock. Another morphological feature unique to the shell of *S. sirius* is the single protruding distinct ray that marks the location of the siphon. The apex is slightly anterior (0.5) in the anterior-posterior axis, central (0) in the left-right axis, and is not hooked. Due to erosion of the apex, the orientation of the tip is unclear. The inner side of the shell at the apex is white and the margin is dark brown with white rays. These marginal rays extend beyond the brown muscle scar.

UF348581

Extr. #889-1
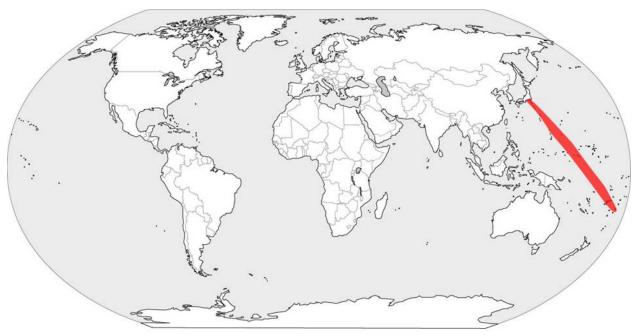
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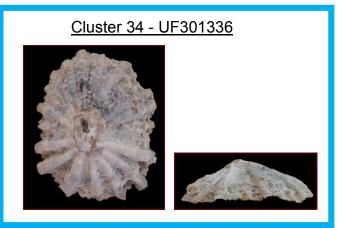
CLUSTER 33
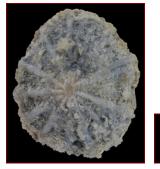
<u>Clusters 34 and 35</u> – *Siphonaria* sp.

Shells of individuals in this species complex are robust, small to medium in size, and medium in height. The overall shell shape is bilaterally symmetrical and oval with the anterior end being narrower than the posterior end (although some individuals in Cluster 35 may have a more rounded appearance). There is a protrusion of the shell at the siphon that is either two distinct ridges (Cluster 34) or the margin of the shell (Cluster 35). Two distinct ridges indicate the siphon's location and the shell edge is scalloped. There are approximately 11 to 13 distinct ridges with one to three fine ridges in between each pair of distinct ridges. Some distinct ridges may be adjacent to one another. A large space with four to five fine ridges occurs between the distinct siphonal ridges and the next posterior distinct ridge. Distinct ridges that are larger are concentrated on the posterior half of the shell. The apex is slightly posterior (-0.5) in the anterior-posterior axis, central (0) in the left-right axis, not hooked, and points to the posterior end of the shell. Coloration of the interior side of the shell at the apex is brown and the margins are either mostly white with some fine brown rays (Cluster 34) or brown with white rays (Cluster 35). The inner side marginal rays typically do not extend beyond the muscle

scar, but can in some individuals (Cluster 35). The muscle scar is either brown (Cluster 34) or without a distinct color and slightly darker (Cluster 35). Cluster 34 is comprised of a single individual from Tutuila Island, American Samoa and Cluster 35 contains specimens from Reunion Island, Mascarene Islands and Christmas Island, Australia.

Cluster 34 - UF301336

Cluster 35 - UF332091

Cluster 35 - UF332090

Cluster 35 - UF301579
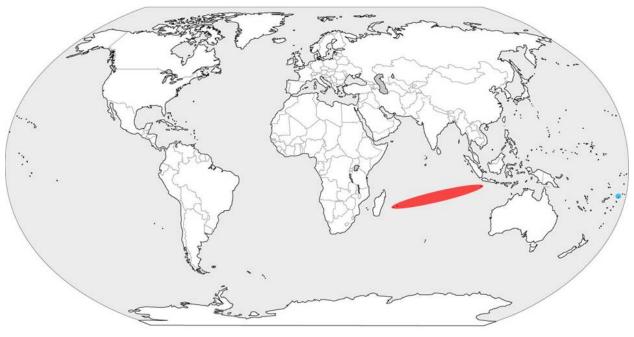
Cluster 35 - UF304119

CLUSTERS 34 & 35
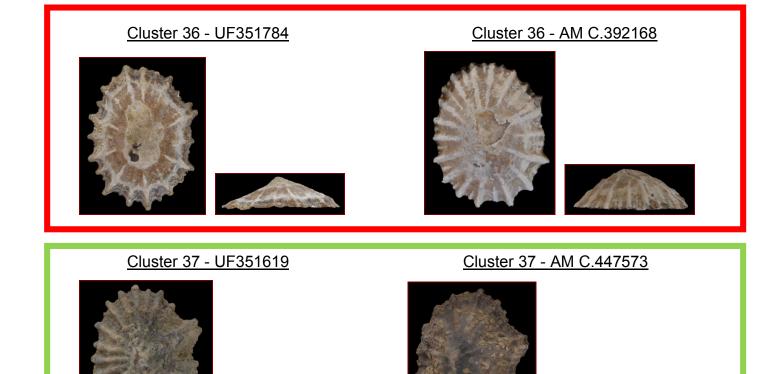
Clusters 36 - 38 – *Siphonaria atra* Quoy and Gaimard, 1833 (Siphonaria)

This species has a broad distribution that extends eastward from Mozambique and Tanzania to New Caledonia and Fiji, northward to include Pakistan, Cambodia, Hong Kong, and Japan, and southward to Australia. Hedley (1917) reported that *S. atra* does not occur in New South Wales, but his conclusion was erroneous. The robust shell of this species is small to medium in size, low to medium in height, and has a scalloped edge. Symmetry is bilateral with the exception of the siphonal projection in some specimens and the anterior end is narrower than the posterior end thus making the shell

appear oval in shape. The siphonal projection consists of two adjacent distinct ridges and may also include portions of the shell anterior and posterior to these distinct ridges. Also, the shape of the shell can be concave both anterior and posterior from the siphonal distinct ridges to the next distinct ridge. In some cases, the shell may extend further outwards from the siphonal distinct ridges to the next posterior distinct ridge than towards the anterior end of the shell. There are approximately 11 to 15 distinct ridges with zero to four fine ridges in between each pair of distinct ridges and there is a higher number of fine ridges anterior and posterior to the siphonal distinct ridges – about three to five fine ridges anterior and five to eight posterior. Several specimens have one fine ridge alternating with one distinct ridge. The apex is central (0) in the anterior-posterior axis, central to slightly left (0 to -0.5) in the left-right axis, not hooked, and points towards the posterior end of the shell. Coloration of the inner side at the apex is brown, brown with white mottling, or white. The margin of the inner side is brown with white rays that may or may not extend beyond the colorless, slightly darkened muscle scar.

Cluster 36 - Extr. #663-1

Cluster 36 - Extr. #667-2

Cluster 36 - AM C.392698

Cluster 36 - UF351589

Cluster 36 - UF351784

Cluster 36 - AM C.392168

Cluster 37 - UF351619

Cluster 37 - AM C.447573

Cluster 38 - UF332091

Cluster 38 - BMNH20080192

Cluster 38 - BMNH20060243
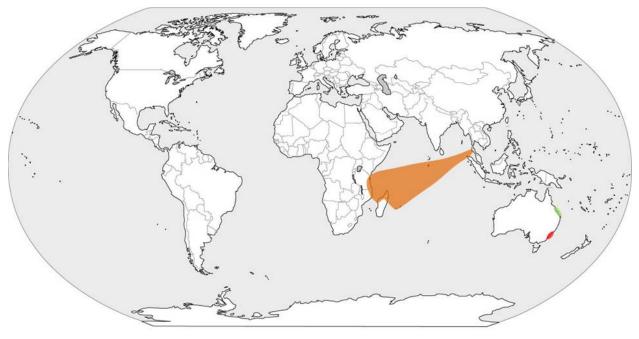
Cluster 38 - BMNH20060463

Cluster 38 - UF366011

CLUSTERS 36 - 38
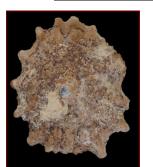
Clusters 39 - 44 – *Siphonaria subatra* Pilsbry, 1904 species complex

The robust shell of this species is small to large in size and consistently low in height. While generally oval in shape and bilaterally symmetrical, the projections of the distinct ridges (especially the distinct siphonal ridges) cause the shell to be asymmetrical. The anterior end of the shell may or may not be narrower than the posterior end and the edge of the shell is scalloped. Two distinct ridges mark the location of the siphon and fine ridges may be present between these two distinct ridges (typically only one fine ridge). The siphonal projection may also include portions of the shell both anterior and

posterior of the two distinct ridges. There are about 10 to 15 distinct ridges with one to eight fine ridges in between each pair of distinct ridges, and like *S. atra*, there are a higher number of fine ridges both anterior and posterior of the distinct siphonal ridges (more fine ridges posterior than anterior). A unique character of the distinct ridges is the light-colored crest which gives the appearance of two fine dark stripes running down the sides of each ridge. The apex is central (0) in the anterior-posterior axis, central to slightly left (0 to -0.5) in the left-right axis, and not hooked. Due to the worn nature of the apex, the orientation (upwards or posterior) is undetermined. Coloration of the inner side apex is typically brown, but may be white. The margin coloration can be dark brown with white rays, white with fine brown rays, or white. Another unique characteristic of the inner side of the shell is the iridescent, almost pearl-like margin. If marginal rays are present, they may or may not extend beyond the muscle scar. The muscle scar is typically slightly darker to light brown although the muscle scar in the individual from Hawaii is colorless. This species is also found in Japan, Korea, Taiwan, Philippines, Palau, Sulawesi, Bali, Papua New Guinea, New Caledonia, Queensland, American Samoa, and Fiji.

Cluster 39 - UF303696

Cluster 40 - UF351975

Cluster 40 - UF313434

Cluster 40 - UF313422

Cluster 40 - UF351755

Cluster 41 - UF323716

Cluster 41 - UF301157
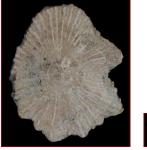
Cluster 41 - UF301147
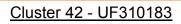
Cluster 42 - Extr. #673-1

Cluster 42 - UF310183

Cluster 42 - UF368376

Cluster 42 - UF368384

Cluster 42 - UF368379

Cluster 42 - UF351673

Cluster 43 - UF288552
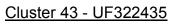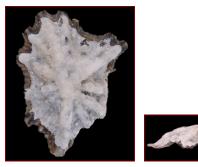
Cluster 43 - AM C.447275

Cluster 43 - UF322435

Cluster 44 - UF324703

Cluster 44 - UF327917

Cluster 44 - BMNH20080198

Cluster 44 - UF295378

Cluster 44 - UF332973
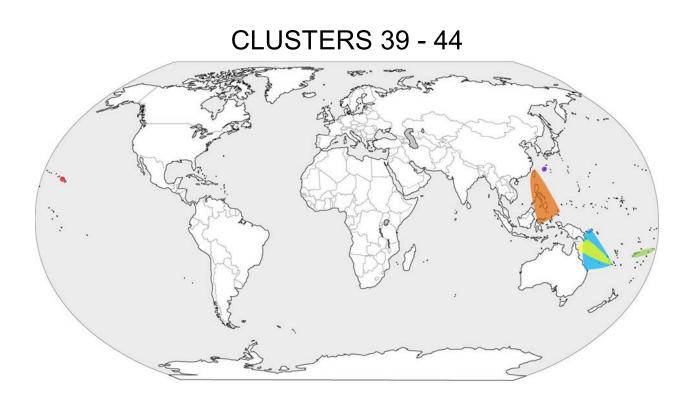
Cluster 44 - UF324987

CLUSTERS 39 - 44

Discussion

Hubendick (1946, 1955) commented that species of *Siphonaria* inhabiting the Indo-West Pacific demonstrate a high degree of variation in shell morphology and many specimens appear to be transitional forms linking together multiple species. Molecular sequence data corresponded to species delineations based on shell morphology with few exceptions and also revealed the presence of species complexes, possibly cryptic species, in the Indo-West Pacific.

The most unusual pattern revealed by the phylogenetic tree pertains to the clade containing *S. lateralis* (Cluster 12), *S. funiculata* (Clusters 13 and 14), and *S. lessonii* (Cluster 15). Shell morphology indicates that specimens of Clusters 13 and 14 are the same species, but the phylogenetic tree depicts a different story. Individuals from these two clusters inhabit the southeastern coast of Australia: Victoria (Cluster 13), New South Wales and Tasmania (Cluster 14). Even though they are in close proximity to one

another, the *S. funiculata* cluster from New South Wales and Tasmania is more closely related to *S. lessonii*. The amount of sequence divergence between *S. funiculata* (Cluster 14) and *S. lessonii* is 2.2% whereas the sequence divergence between the two clusters of *S. funiculata* is 5.1%, which is still a fairly low percentage. Perhaps the historical range of *S. funiculata* was a continuous distribution along the southeastern coast of Australia, including Tasmania, and due to a change in currents this species is now undergoing allopatric speciation. A portion of the West Wind Drift is diverted north at Victoria, moves west along the southern coast of Australia, and then joins the West Australian Current which flows into the South Equatorial Current. The East Australian Current sweeps southward along New South Wales and the east coast of Tasmania and then eastward to the southern tip of South America. The type of larval development of *S. funiculata* is not recorded in the literature, but the likelihood of planktotrophic development is high since the currents appear to be mechanism behind the limited gene flow between individuals of these two clusters. Also, planktotrophic larvae could explain the low sequence divergence between Cluster 14 and *S. lessonii* in that some larvae may be traveling back and forth across the southern Atlantic and continuing gene flow between these species since *S. lessonii* has been reported as having planktotrophic larvae (see Chambers and McQuaid 1994).

Another interesting aspect of siphonarian species diversification revealed by the phylogenetic tree is that Oman, which is a speciose location, served as the source for species inhabiting the Mediterranean, east coast of North America, Gulf of Mexico, and Caribbean. *Siphonaria ashgar* and *S. pectinata* are sister species and *S. savignyi* and *S. alternata* are sister taxa, as well. The westward current through the Tethys Sea likely assisted the planktotrophic larva from species in Oman to spread to the west coast of Africa and southeastern North America. The mode of larval development for the Oman siphonarians is unpublished, but *S. pectinata* is planktotrophic and *S. alternata* is swimming/crawling (see Chambers and McQuaid 1994). This latter manner of development is likely the explanation as to why the range of *S. alternata* is greatly reduced in comparison to that of *S. pectinata*.

With regards to the ancestral mode of larval development, the first siphonarians were planktotrophic based on the findings in this paper which supports the conclusion made

by Chambers et al. in 1996. *Siphonaria gigas* is located in a basal position of one of the two large clades of the phylogenetic tree and the larvae of this species are planktotrophic (Levings and Garrity 1986). This would also point to a marine ancestry of siphonarians; mitochondrial genome sequence data of *S. gigas* and *S. pectinata* placed them within the opisthobranch clade (White et al. in prep.). *Siphonaria maura* is at the base of the second large clade of the tree and while there is no information published specifically describing this species' larval development, several articles mentioning larval settlement include *S. maura* (e.g. Reimer 1976, Sibaja-Cordero and Cortés 2008); therefore, the larvae of *S. maura* are probably planktotrophic. Another aspect of *S. gigas* and *S. maura* occupying basal positions of the two main clades is that both species inhabit the west coast of the Americas. Thus, the ancestor of siphonarians occurred in what is currently the tropical east Pacific. The first fossil record of *Siphonaria* is the Upper Cretaceous (Zilch 1959), a time when the Tethys Sea was open between Laurasia and Gondwana and water flowed westward between these two supercontinents. The planktotrophic larvae of the ancestral species would have travelled to the west and begun inhabiting what is today east Asia, India, Africa, the Medtierranean, etc. and continuing on further west.

As mentioned in the previous paragraph, there are two large clades in the phylogenetic tree. The sectia of each species (if known) was mapped onto the tree (Figure 2) and despite the incompleteness, the species of each sectia appeared to be at least in close proximity to one another. Heterosiphonaria and Patellopsis occurred in both clades and if a subgeneric label could be tentatively placed on each of the two clades, the *S. gigas* clade would be *Liriola* and the *S. maura* clade, *Siphonaria*.

The three species complexes (*laciniosa*, *normalis*, and *subatra*) have the potential of including cryptic species, but some clusters within each complex consist of only one or two specimens which is problematic since sampling is not rigorous. Therefore, until further sampling and morphological studies can be performed, new species names and descriptions will not be provided. The *S. laciniosa* complex consists of Clusters 20-26 with the lowest sequence divergence between Clusters 25 and 26 an 8.5%, indicating each of the seven clusters is likely a separate species. Clusters 21 and 22 were collected at the same locality in New Caledonia (Poindimie) and the sequence

divergence is 15.0%. The *S. normalis* complex is comprised of Clusters 7-11. Clusters 10 and 11 only have a 3.0% sequence divergence and should be regarded as conspecific and as specimens of *S. normalis* since the clade includes a specimen from the type locality of Hawaii. The lowest amount of sequence divergence between the remaining clusters (7-9) is 7.5% (Clusters 7 and 8). Individuals from Clusters 7 and 9 occur in the east Indian Ocean and could be located too far west to receive larval recruits from the east, but Cluster 8 is clearly within the range of *S. normalis*. The *S. subatra* complex (Clusters 39-44) consists of Cluster 39 and the remaining clusters which are *S. subatra*. The morphology of the specimen from Hawaii is *S. subatra*, but the sequence divergence between Cluster 39 and *S. subatra* averages 19.7%, which is well above the intraspecific range. A possible explanation may be that the long distance between the Hawaiian individual and the other specimens provides a reproductive barrier, but in years of El Nino, the larvae from the Indo-West Pacific populations move eastward and can reach the population in Hawaii (see Palumbi 1994).

Technically, the population of individuals in Hawaii resembling *S. subatra* should be described as a new species, but a larger sample size of specimens should be collected and studied before describing a new species. There are also six other clusters (17, 18, 19, 30, 34, and 35) in the phylogenetic tree that were not specifically identified and may be new species, but again, most of these clusters consist of one specimen and further studies are needed. Clusters 17-19 are each a single small specimen and resemble *S. normalis*. Even though these three clusters are not in close proximity of *S. normalis* in the phylogenetic tree, geographically they are; they were collected from locations at the periphery of the range of *S. normalis*. Cluster 30 is closely related to and occurs in the same region as *S. acmaeoides*. Perhaps the evolution of different modes of larval development in each of these clusters caused the diversification in this clade. Clusters 34 and 35 only have a genetic divergence 5.5% which approaches the limit of intraspecific variation. At first glance, the ranges of these clusters appear disparate with Cluster 34 located in the west Pacific and Cluster 35 spanning the Indian Ocean. Nevertheless, gene flow from Cluster 34 to Cluster 35 is plausible given the westward flowing New Guinea Coastal Current and South Equatorial Current. Also of particular interest is the siphonarian from Oman (Cluster 6) that resembles *S. compressa* in South Africa. Molecular sequence data should be obtained from the two South African

populations of *S. compressa* and analyzed to see if the individuals from Oman are a new species or even possibly a remnant population from a once larger range of *S. compressa*. Again, this reiterates the need for a comprehensive sampling of siphonarians for both molecular and morphological studies, as well as knowledge of their larval development strategies so a complete body of knowledge is assembled before inferences are made about patterns of speciation.

Conclusion

The use of molecular data has provided an effective tool in delineating species of siphonarians and has reaffirmed the high species diversity in the Indo-West Pacific. (see Hubendick 1946, 1955; White and Dayrat submitted). Interestingly, some clusters of the siphonarians were easily identified upon visual inspection of the aligned sequences of COI, 12S, and 16S, but then again so were some species based on the inspection of shell morphology. Undoubtedly, DNA barcoding could be utilized to delineate siphonarian species and is a useful tool for a quick assessment of genetic diversity, especially in the face of habitat destruction and extinction of undescribed species, but the method isn't exactly fool proof (Will and Rubinoff 2004, Dasmahapatra et al. 2010). Therefore, molecular data should not be the sole data set used to identify species but rather as an addition to data collected from morphology, biogeography, behavior, etc. (Will and Rubinoff 2004, Smith et al. 2005, Bickford et al. 2006). Another aspect to consider in the case of siphonarians is the fact that many unidentified or misidentified museum specimens consist of the shell only and any tissue available for molecular research is either missing, dried out, or preserved in formaldehyde. On the other hand, Bickford et al. (2006) discusses that species living in harsh environments may have environmental stressors that select for similar morphologies and characters that delineate species may be on a biochemical level that are not easily detected. Siphonarians inhabit one of the most severe habitats, the intertidal zone, so perhaps more research should be directed at the biochemical between species (i.e. polypropionates, reproductive cues, etc.) and then possibly the genes that code for these products. Until that time and when possible, molecular data should be incorporated with morphological characters to define siphonarian species and determine their evolutionary relationships.

Also helpful in the demarcation of siphonarian species is the use of sequence divergence percentages and a threshold percentage. The threshold percentage for siphonarians appears to be approximately 5% based on my data set. This number may change in the future or it may not; the threshold percentage is a somewhat arbitrary number that differs for each type of organism (Meyer and Paulay 2005). For example, Meyer and Paulay (2005) found that the optimum threshold for cowries is 2.6%, turbinids is 1.2%, and true limpets (in the genus *Patelloida*) is 1.7%; Hebert et al. (2004) determined a 2.7% threshold for North American birds; and Dasmahapatra et al. (2010) applied a threshold of 1.5% for ithomiine butterflies. Hebert et al. (2004) provides a formula to calculate a standard threshold value for any data set – determine the average intraspecific variation and then multiply it by 10. I calculated this value for clusters with two or more individuals and the threshold for my data set is 5.9%, which is close to my best guess value of 5%. Forty-four clusters are identified on the siphonarian phylogenetic tree and 35 evolutionary significant units (ESUs) are recognized (Figure 2) based on the sequence divergence threshold value for the siphonarians, with the exception of *S. lessonii* (see above discussion).

To better understand the pattern of species diversification, an increase in sampling size of the siphonarians is needed, which includes both the number of individuals collected from a locality and the number of collection localities. Persons familiar with the local intertidal fauna should be consulted so the region's siphonarian diversity can be thoroughly sampled. White and Dayrat (submitted) compiled all of the primary literature on siphonarians which included type localities; this would be a good starting point for sampling, as well as a good reference of available names for future new species descriptions.

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Table 1

Specimen data table. Includes DNA extraction number (personal lab use); cluster number; museum lot number of specimen; species name; general location where specimen was collected; and shell measurements. (UF: Florida Museum of Natural History; BMNH: British Museum of Natural History; MLP: Museo de La Plata; AM C.: Australian Museum)

Extraction #	Cluster #	Museum Lot ID	Species	Location	l x w x h (mm)
686-1	1	UF359682	S. gigas	Panama	41 x 34 x 15
808-1	1	UF359645	S. gigas	Panama	48 x 39 x 27
682-1	2	UF359679	S. maura	Panama	21 x 16 x 5
848-1	2	UF141401	S. maura	Ecuador	25 x 20 x 5
854-1	2	UF351511	S. maura	Panama	18 x 16 x 4
855-1	2	UF359623	S. maura	Panama	18 x 15 x 7
856-1	2	UF359681	S. maura	Panama	17 x 15 x 5
857-1	2	UF371626	S. maura	Panama	23 x 17 x 5
858-1	2	UF371937	S. maura	Panama	22 x 17 x 5
859-1	2	UF371950	S. maura	Panama	18 x 13 x 4
860-1	2	UF371957	S. maura	Panama	20 x 15 x 5
691-1	3	UF368014	S. ashgar	Oman	9 x 8 x 3
694-1	3	UF296019	S. ashgar	Oman	12 x 9 x 4
749-1	4	UF382817	S. pectinata	Trinidad Island	23 x 17 x 9
801-1	4	UF54117	S. pectinata	Florida	14 x 11 x 5
802-1	4	UF79313	S. pectinata	Florida	13 x 9 x 5
803-1	4	UF254828	S. pectinata	Florida	12 x 9 x 5
804-1	4	BMNH20080071	S. pectinata	Ghana	15 x 10 x 6
739-1	5	UF350544	S. japonica	Japan	15 x 12 x 5
740-1	5	UF350553	S. japonica	Japan	17 x 13 x 5
743-1	5	UF310519	S. japonica	Taiwan	12 x 9 x 4
746-1	5	UF368383	S. japonica	Taiwan	17 x 12 x 5
892-1	5	to be deposited	S. japonica	Honshu, Japan	14 x 11 x 4
693-1	6	UF367730	S. cf compressa	Oman	6 x 4 x 2
873-1	7	UF296423	S. normalis complex	Cocos-Keeling Island, Australia	8 x 6 x 3
599-1	8	UF310368	S. normalis complex	Caroline Islands	4 x 3 x 2
824-1	9	BMNH20080191	S. normalis complex	Thailand	10 x 7 x 3
827-1	9	BMNH20080194	S. normalis complex	Thailand	14 x 11 x 5

751-1	10	UF292269	S. normalis	Singapore	12 x 9 x 5
753-1	10	UF341298	S. normalis	Singapore	13 x 10 x 5
586-2	11	UF324705	S. normalis	Fiji	15 x 12 x 6
603-1	11	UF294623	S. normalis	Society Islands	11 x 9 x 5
604-1	11	UF292011	S. normalis	Society Islands	9 x 7 x 4
610-1	11	UF324719	S. normalis	Samoa Islands	9 x 7 x 4
611-1	11	UF301195	S. normalis	Samoa Islands	11 x 8 x 3
617-1	11	UF303670	S. normalis	Hawaii	9 x 7 x 4
624-1	11	UF348566	S. normalis	Nauru	8 x 6 x 3
625-1	11	UF348025	S. normalis	Nauru	12 x 9 x 4
674-1	11	UF400391	S. normalis	Mariana Islands, Guam	6 x 4 x 2
677-1	11	UF392234	S. normalis	Gambier Islands	11 x 8 x 3
835-1	11	BMNH20080069	S. normalis	Marquesas Island	10 x 8 x 4
807-3	12	MLP13170	S. lateralis	Argentina	10 x 7 x 4
669-1	12	MLP13163	S. lateralis	Argentina	13 x 9 x 5
806-1	12	BMNH1994092	S. lateralis	South Georgia	14 x 10 x 6
665-1	13	to be deposited	S. funiculata	Victoria	10 x 8 x 4
666-1	13	to be deposited	S. funiculata	Victoria	13 x 10 x 4
810-1	14	AM C.395918	S. funiculata	New South Wales	12 x 8 x 5
838-1	14	BMNH20080193	S. funiculata	Tasmania	22 x 18 x 10
879-1	14	UF351617	S. funiculata	New South Wales	14 x 11 x 5
882-1	14	UF351837	S. funiculata	New South Wales	10 x 7 x 3
670-2	15	MLP13164	S. lessonii	Argentina	15 x 11 x 8
671-3	15	MLP13165	S. lessonii	Argentina	10 x 8 x 5
672-1	15	MLP13166	S. lessonii	Argentina	14 x 10 x 8
861-1	15	MLP13168	S. lessonii	Argentina	18 x 13 x 9
862-2	15	MLP13169	S. lessonii	Argentina	15 x 10 x 8
863-2	15	MLP13167	S. lessonii	Argentina	17 x 15 x 11
850-1	16	UF303783	S.pascua	Chile	8 x 7 x 3
675-1	17	UF400392	S. sp. ?	Mariana Islands, Saipan	6 x 5 x 2
587-1	18	UF291950	S. sp. ?	Cook Islands	5 x 4 x 2
607-1	19	UF379054	S. sp. ?	Wake Island	7 x 5 x 2
608-1	19	UF375861	S. sp. ?	Wake Island	7 x 5 x 2
680-1	20	UF351976	S. laciniosa complex	Japan	22 x 18 x 11
621-2	21	UF324703	S. laciniosa complex	New Caledonia	12 x 8 x 5

620-1	22	UF323717	S. laciniosa complex	New Caledonia	16 x 12 x 7
619-1	23	UF324707	S. laciniosa complex	New Caledonia	15 x 11 x 7
622-2	23	UF288552	S. laciniosa complex	New Caledonia	20 x 15 x 8
876-1	24	UF323720	S. laciniosa complex	Queensland	17 x 14 x 8
668-2	25	to be deposited	S. laciniosa complex	Japan	17 x 13 x 7
687-1	25	UF368385	S. laciniosa complex	Philippines	27 x 22 x 16
742-2	25	UF351778	S. laciniosa complex	Japan	12 x 9 x 6
745-1	25	UF310711	S. laciniosa complex	Taiwan	11 x 9 x 5
815-1	25	UF292259	S. laciniosa complex	Philippines	15 x 13 x 8
816-1	25	UF324725	S. laciniosa complex	Philippines	10 x 9 x 4
817-1	25	UF324728	S. laciniosa complex	Philippines	14 x 11 x 5
818-1	25	UF367180	S. laciniosa complex	Philippines	16 x 11 x 6
819-1	25	UF368378	S. laciniosa complex	Philippines	20 x 17 x 12
820-1	25	UF368380	S. laciniosa complex	Philippines	19 x 16 x 8
821-1	25	UF368381	S. laciniosa complex	Philippines	13 x 10 x 5
823-1	25	UF375653	S. laciniosa complex	Philippines	11 x 9 x 5
840-1	25	UF368377	S. laciniosa complex	Philippines	17 x 14 x 7
600-1	26	UF296570	S. laciniosa complex	Caroline Islands	13 x 11 x 6
602-1	26	UF299501	S. laciniosa complex	Caroline Islands	13 x 10 x 6
605-2	26	UF367624	S. laciniosa complex	Vanuatu	18 x 15 x 5
606-1	26	UF368762	S. laciniosa complex	Vanuatu	8 x 7 x 3
678-2	26	UF310183	S. laciniosa complex	Palau	10 x 9 x 4
685-1	26	UF288808	S. laciniosa complex	Palau	16 x 13 x 7
750-1	26	UF292268	S. laciniosa complex	Singapore	14 x 11 x 7
826-1	26	BMNH20080195	S. laciniosa complex	Queensland	14 x 11 x 5
831-1	26	BMNH20080197	S. laciniosa complex	Western Australia	13 x 11 x 5
834-1	26	BMNH20040811	S. laciniosa complex	East Timor	7 x 5 x 3
837-1	26	BMNH20040741	S. laciniosa complex	East Timor	22 x 18 x 10
866-2	26	UF295378	S. laciniosa complex	Papua New Guinea	14 x 11 x 6
868-1	26	UF322540	S. laciniosa complex	Papua New Guinea	18 x 16 x 9
869-1	26	UF327900	S. laciniosa complex	Papua New Guinea	16 x 12 x 8
871-1	26	UF366438	S. laciniosa complex	Papua New Guinea	18 x 14 x 8
883-1	26	UF310785	S. laciniosa complex	Indonesia, Bali	9 x 8 x 3
885-1	26	UF329040	S. laciniosa complex	Indonesia, Sulawesi	15 x 12 x 5
886-1	26	UF329052	S. laciniosa complex	Indonesia, Sulawesi	11 x 9 x 5

887-1	26	UF330847	S. laciniosa complex	Indonesia, Bali	12 x 10 x 6
895-1	26	AM C.459332	S. laciniosa complex	Queensland	15 x 11 x 6
690-1	27	UF296586	S. belcheri	Oman	14 x 10 x 3
692-1	27	UF295359	S. belcheri	Oman	10 x 7 x 3
849-1	28	UF367494	S. alternata	Florida	14 x 12 x 5
853-1	28	UF332959	S. alternata	Florida	12 x 10 x 4
689-1	29	UF367757	S. savignyi	Oman	9 x 6 x 3
695-1	29	UF367756	S. savignyi	Oman	13 x 9 x 4
814-1	30	UF117293	S. sp. ?	Philippines	16 x 14 x 6
832-1	31	BMNH20080199	S. denticulata	Western Australia	15 x 12 x 5
667-1	32	to be deposited	S. acmaeoides	New South Wales	12 x 9 x 3
830-1	32	BMNH20080196	S. acmaeoides	Western Australia	15 x 13 x 4
831-2	32	BMNH20080197	S. acmaeoides	Western Australia	13 x 10 x 4
892-2	32	to be deposited	S. acmaeoides	Honshu, Japan	12 x 10 x 5
623-1	33	UF348581	S. sirius	Tonga	13 x 11 x 3
889-1	33	to be deposited	S. sirius	Honshu, Japan	21 x 17 x 5
890-1	33	to be deposited	S. sirius	Honshu, Japan	23 x 17 x 6
612-1	34	UF301336	S. sp. ?	Samoa Islands	12 x 10 x 4
679-1	35	UF332091	S. sp. ?	Mascarene Islands	15 x 13 x 5
852-1	35	UF332090	S. sp. ?	Mascarene Islands	16 x 13 x 5
874-1	35	UF301579	S. sp. ?	Christmas Island, Australia	6 x 4 x 2
875-1	35	UF304119	S. sp. ?	Christmas Island, Australia	11 x 9 x 4
877-1	35	UF329990	S. sp. ?	Christmas Island, Australia	12 x 9 x 4
663-1	36	to be deposited	S. atra	New South Wales	21 x 15 x 6
667-2	36	to be deposited	S. atra	New South Wales	16 x 12 x 4
809-1	36	AM C.392698	S. atra	New South Wales	17 x 13 x 5
878-1	36	UF351589	S. atra	New South Wales	20 x 18 x 6
881-1	36	UF351784	S. atra	New South Wales	21 x 16 x 6
897-1	36	AM C.392168	S. atra	New South Wales	21 x 15 x 7
880-1	37	UF351619	S. atra	Queensland	21 x 16 x 5
896-1	37	AM C.447573	S. atra	Queensland	22 x 17 x 7
679-2	38	UF332091	S. atra	Mascarene Islands	24 x 18 x 8
828-1	38	BMNH20080192	S. atra	Thailand	12 x 9 x 3
833-1	38	BMNH20060243	S. atra	Tanzania	11 x 9 x 4
836-1	38	BMNH20060463	S. atra	Mozambique	13 x 11 x 3
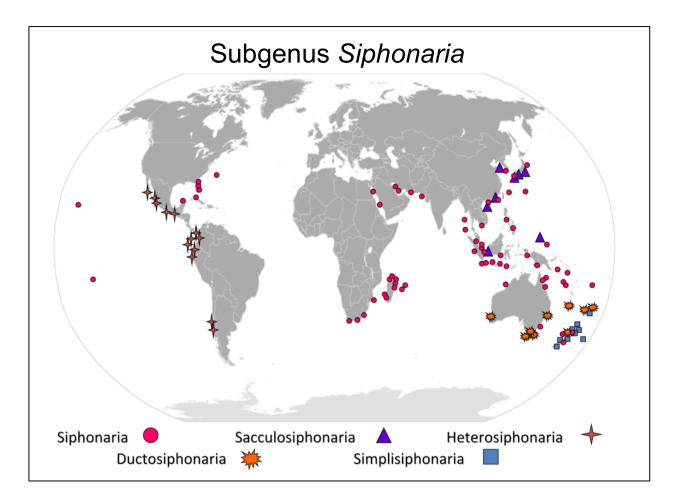
847-1	38	UF366011	S. atra	Mauritius	19 x 16 x 6
618-1	39	UF303696	S. subatra complex	Hawaii	11 x 9 x 2
684-1	40	UF351975	S. subatra	Japan	24 x 19 x 6
737-1	40	UF313434	S. subatra	Japan	18 x 13 x 5
738-1	40	UF313422	S. subatra	Japan	22 x 18 x 5
741-1	40	UF351755	S. subatra	Japan	21 x 15 x 4
585-2	41	UF323716	S. subatra	Fiji	17 x 13 x 4
613-1	41	UF301157	S. subatra	Samoa Islands	29 x 18 x 4
614-1	41	UF301147	S. subatra	Samoa Islands	25 x 21 x 5
673-1	42	to be deposited	S. subatra	Taiwan	30 x 23 x 7
678-1	42	UF310183	S. subatra	Palau	15 x 12 x 4
688-1	42	UF368376	S. subatra	Taiwan	28 x 21 x 8
822-1	42	UF368384	S. subatra	Philippines	21 x 16 x 6
841-1	42	UF368379	S. subatra	Philippines	24 x 18 x 5
888-1	42	UF351673	S. subatra	Indonesia, Sulawesi	17 x 13 x 3
622-1	43	UF288552	S. subatra	New Caledonia	26 x 21 x 6
811-1	43	AM C.447275	S. subatra	Queensland	18 x 14 x 4
867-1	43	UF322435	S. subatra	Papua New Guinea	15 x 11 x 4
621-1	44	UF324703	S. subatra	New Caledonia	19 x 14 x 4
681-1	44	UF327917	S. subatra	Papua New Guinea	18 x 13 x 3
825-1	44	BMNH20080198	S. subatra	New Caledonia	15 x 12 x 4
866-1	44	UF295378	S. subatra	Papua New Guinea	16 x 12 x 4
870-1	44	UF332973	S. subatra	Papua New Guinea	11 x 8 x 4
884-1	44	UF324987	S. subatra	Queensland	33 x 27 x 9

Table 2

Pairwise sequence divergences.

Subgenus Liriola

Figure 2

Tree produced by the ML and BI analyses. The dotted line at Clusters 12 and 13 show where the topography of the BI tree differs from the ML tree. The ML bootstrap values are the top number and BI posterior probabilities are the bottom number.

UF303783 Chile **16** *S. pascua*

UF400392 Saipan **17** *S. sp.?*

UF291950 Cook Islands **18** *S. sp.?*

UF379054 Wake Island
UF375861 Wake Island **19** *S. sp.?*

UF324703 New Caledonia **21**
UF351976 Japan **20**
UF323717 New Caledonia **22**
UF324707 New Caledonia
UF288552 New Caledonia **23**
UF323720 Queensland Australia **24**

UF310711 Taiwan
JAP10_31_07 Japan
UF351778 Japan
UF324725 Philippines
UF375653 Philippines
UF292259 Philippines
UF368381 Philippines **25**
UF368385 Philippines
UF368378 Philippines
UF367180 Philippines
UF368380 Philippines
UF324728 Philippines
UF368377 Philippines

UF310785 Bali
UF295378 Papua New Guinea
UF329040 Sulawesi
BMNH20040741 East Timor
UF330847 Bali
UF329052 Sulawesi
BMNH20040811 East Timor
UF292268 Singapore
UF310183 Palau
UF288808 Palau **26**
BMNH20080197 Western Australia
UF299501 Caroline Islands
UF296570 Caroline Islands
AM C.459332 Queensland Australia
BMNH20080195 Queensland Australia
UF322540 Papua New Guinea
UF366438 Papua New Guinea
UF327900 Papua New Guinea
UF368762 Vanuatu
UF367624 Vanuatu

S. laciniosa complex

UF117293 Philippines **30** *S. sp.?*
BMNH20080199 Western Australia **31** *S. denticulata* (Ductosiphonaria)
JAP#4SJAPONICA Japan
BMNH20080197 Western Australia **32** *S. acmaeoides* (Patellopsis)
BMNH20080196 Western Australia
AUS10_35_7 New South Wales Australia

UF296586 Oman **27** *S. belcheri* (Patellopsis)
UF295359 Oman
UF367757 Oman **29** *S. savignyi* (Siphonaria)
UF367756 Oman
UF367494 Florida **28** *S. alternata* (Siphonaria)
UF332959 Florida

UF348581 Tonga
JAP#1SSIRIUS Japan **33** *S. sirius* (Siphonaria)
JAP#2SSIRIUS Japan
UF301336 Samoa Islands **34**
UF329990 Christmas Island
UF332090 Mascarene Islands
UF332091 Mascarene Islands **35** *S. sp.?*
UF304119 Christmas Island
UF301579 Christmas Island

UF351589 New South Wales Australia
AM C.392168 New South Wales Australia
UF351784 New South Wales Australia
AM C.392698 New South Wales Australia **36**
AUS7_25_6 New South Wales Australia
AUS10_35_7 New South Wales Australia
UF351619 Queensland Australia **37**
AM C.447573 Queensland Australia
BMNH20060243 Tanzania
BMNH20060463 Mozambique
BMNH20080192 Thailand **38**
UF366011 Mauritius
UF332091 Mascarene Islands

S. atra (Siphonaria)

UF303696 Hawaii **39**
UF301147 Samoa Islands **41**
UF301157 Samoa Islands
UF323716 Fiji
UF313434 Japan
UF351755 Japan **40**
UF313422 Japan
UF351975 Japan

UF368384 Philippines
UF310183 Palau
UF351673 Sulawesi
TAI5_7_2001 Taiwan **42**
UF368376 Taiwan
UF368379 Philippines

UF322435 Papua New Guinea **43**
UF288552 New Caledonia
AM C.447275 Queensland Australia
UF332973 Papua New Guinea
UF324703 Papua New Guinea
BMNH20080198 New Caledonia
UF324987 Queensland Australia **44**
UF327917 Papua New Guinea
UF295378 Papua New Guinea

S. subatra complex

S. subatra (Siphonaria)

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CONCLUSION

All three components of my research are significant contributions to the field of gastropod systematics, as well as molecular biology and taxonomy: the complete sequences of 10 pulmonate mitochondrial genomes, a comprehensive and thorough review of siphonarian nomenclature, and molecular sequence data from portions of three mitochondrial genes (COI, 16S, and 12S) of 159 individuals of *Siphonaria*. While all three of these contributions are tremendous in their own right, the data from my research will play an even larger role in future scientific studies.

In order to provide a more complete understanding of the relationships of pulmonates and opisthobranchs, we targeted species from underrepresented pulmonate groups for the mitochondrial genome sequencing. While dramatically increasing the number of available mitochondrial genomes, our contributions still do not cover the breadth of diversity. This is the sacrifice of genomic sequencing – more data, but decreased taxon sampling. Hopefully this problem can be alleviated with the assistance of my detailed methods sections and new sequencing techniques, such as pyrosequencing. Another challenging aspect of genomic data is the method(s) used to analyze the large amount of sequence data. In phylogenetic analyses, authors will use amino acid sequences; nucleotide sequences that consist of protein-coding, ribosomal, tRNA, or any combination of those three types of genes; and when utilizing the protein-coding genes, the codon position of each nucleotide must be considered: first, second, or third. Additionally, one must determine the evolutionary rates of each gene and incorporate those parameters into the phylogenetic analyses. Initially, I analyzed two data sets: amino acids of all protein-coding genes and nucleotides of ribosomal and protein-coding genes (1st and 2nd codon positions only). Three of the four trees produced by the Bayesian Inference and Maximum Likelihood analyses were identical; the Bayesian Inference tree of the nucleotide data had a different topology. I then removed the outgroup and re-ran all four analyses which resulted in unrooted trees with the same topology. Ultimately, I only submitted the amino acid trees for publication, but given my experience with analyzing mitochondrial genome sequence data, the decisions about which data to use and how to analyze it are copious and the likelihood for inaccurate results due to compounding errors is great.

Surprising in its simplicity, the gene order provided direct visual confirmation that siphonarians are opisthobranchs. While the sequential arrangement of mitochondrial genes is a useful phylogenetic character, caution should be practiced when inferring the evolutionary relationships of higher gastropod taxa due to the mechanisms of mitochondrial replication. There are areas in the genome that are constrained from rearrangements and there are areas that are more susceptible to rearrangements (hotspots). Constraints may include the need of gene regulatory regions also being included as part of the rearrangement or the necessary spatial arrangement of two genes in relation to one another. Hotspots typically occur around the origin(s) of mitochondrial replication where slipped-strand mispairing is more likely to occur or errors in replication termination result in multiple copies of genes or deletions.

Mitochondrial gene sequences and arrangements are useful tools for inferring phylogenies, but more taxa need to be added to the current data set so a clear and accurate picture of euthyneuran evolution can be depicted. As the amount of sequenced mitochondrial genomes increases, pinpointing which morphological characters are the most phylogenetically informative will be further elucidated, and a better understanding of the relationships of pulmonates to other gastropod taxa will be attained which will provide needed clues to the evolutionary transitions of pulmonates (marine vs. terrestrial vs. freshwater).

My taxonomic paper is a review, not a revision of species in the genus *Siphonaria*. A revision would consist primarily of resolving issues dealing with synonymies and due to the completeness of my review, the individual who will undertake this task will not have to track down the primary literature that contains new species descriptions. My review also provides information on the opinions of authors studying siphonarians (secondary literature) regarding the synonyms. Overall, the literary information pertaining to the taxonomy of siphonarians is complete and now the type specimens of species with nomenclatural problems need to be located and studied. If type specimens do not exist, lectotypes will need to be designated so that future researchers have a physical representative of the species available for study.

One aspect not covered in my taxonomic review is the fossil species of *Siphonaria*. Hubendick listed several in his monograph, but I am aware that he has overlooked at least one fossil species. There is also debate over when siphonarians first appeared in the fossil record. This information will impact molecular clock calibrations for evolutionary analyses and needs to be determined.

My phylogenetic analyses of the 159 individuals produced a tree with 44 clusters, of which 35 were recognized as species-groups. I would have acknowledged only 25 species-groups based on shell morphology alone; molecular sequence data is a tremendous tool needed to detect species diversity in siphonarians. Shell morphology is the primary characteristic utilized to distinguish species of *Siphonaria*. The morphology of the radula and reproductive system are also important characters, but studying these features can be difficult, especially when the soft tissue is missing (as is the case in many museum collections). Not only does the paucity of morphological characters make inferring phylogenies difficult, these characteristics are also heavily impacted by the environment. Molecular sequence data is necessary to demarcate species and provide an initial road map of species-groups. Species with the same shell morphology can then be more closely studied to see if there are distinguishing radular or reproductive characters. Ideally, species identification should be based on the shell alone since that is what is encountered in the field; since general shell morphology may not always be a good indicator of species, perhaps shell morphometrics would be a facet of the shell morphology that would provide more specific measurements for delineating cryptic species.

Based on visual inspections of the COI sequence data, species-groups could be visually identified; therefore, DNA barcoding to detect species diversity in siphonarians is plausible. On the other side of the coin, DNA barcoding can also reveal that species with different shell morphology are the same species, which appears to be the case with several species of South African siphonarians. DNA barcoding may also be a quick way to obtain a great deal of sequence data to add on to my large data set. Many of my clusters consisted of single, small specimens so increased sampling of siphonarians for DNA barcoding would help improve identification of these individuals, as well as provide a more accurate glimpse of the phylogeography of *Siphonaria*.

In conclusion, siphonarians are not basal pulmonates, but are opisthobranchs. Of the 269 species-group names included in the primary literature, 204 are available and not permanently invalid. All other names are either not available (e.g. incorrect subsequent spellings) or available but permanently invalid (e.g. primary homonymy). Phylogenetic analyses of portions of the COI, 12S, and 16S mitochondrial genes sequenced for 159 specimens of *Siphonaria* resulted in 44 distinct clusters, of which 35 evolutionary significant units (species) were recognized. The threshold percentage of sequence divergence used in demarcating species of siphonarians is approximately 5.9%.