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Taxonomic reassessment of the Indo-Pacific Scytosiphonaceae (Phaeophyceae): Hydroclathrus rapanuii sp. nov. and Chnoospora minima from Easter Island, with proposal of Dactylosiphon gen. nov. and Pseudochnoospora gen. nov.

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Abstract: A new and putatively endemic species of Hydroclathrus, Hydroclathrus rapanuii, is described from the geographically isolated Easter Island in the southeastern Pacific based on morphological and molecular phylogenetic data. It is distinguished from other Hydroclathrus by thalli of unevenly furrowed thin membranes, and angular, block-like plurangial sori. Our phylogenetic analyses indicated that H. rapanuii is closely related to the generitype Hydroclathrus clathratus. We also report on the morphology and phylogeny of Chnoospora minima from Easter I. and elsewhere in the Indo-Pacific Ocean, noting the previously unreported presence of hollow portions in its medulla. Although not collected from Easter I., we herein propose the recognition of two new genera, Dactylosiphon gen. nov. and Pseudochnoospora gen. nov., based on our three-gene phylogeny and their known morphologies and anatomies. Dactylosiphon is based on the three species currently assigned to Colpomenia (C. bullosa, C. durvillei, and C. wynnei) that are genetically and morphologically (i.e. thalli with erect and finger-like tubes arising from a common saccate base) distinct from other members of Colpomenia. The monotypic genus Pseudochnoospora is represented by the decumbent, branching, and inter-adhesive species currently known as Chnoospora implexa. With the above proposals, we further increase the genus-level diversity of Scytosiphonaceae in the Indo-Pacific Ocean.

Keywords: Dactylosiphon gen. nov.; Easter Island; Indo-Pacific Ocean; Pseudochnoospora gen. nov.; Scytosiphonaceae.

Introduction

Easter Island, locally known by its Polynesian name as “Rapa Nui”, is a geographically isolated volcanic island located in the South Pacific Ocean. Owing largely to its remoteness, its macroalgal flora has been subjected to several floristic and biogeographical studies (e.g. Børgesen 1924, Santelices and Abbott 1987, Ramírez and Müller 1991, Santelices and Meneses 2000), which has resulted in a present total of 143 recorded species (Fernández et al. 2014). Some 14% of the species appear to be endemic to the island and, collectively, its flora has an Indo-Pacific affinity (Santelices and Abbott 1987, Ramírez and Müller 1991, Santelices and Meneses 2000). Somewhat unexpectedly, the flora seems to share more common elements with Nha Trang, Vietnam (ca. 16,000 km) than with the relatively near Juan Fernández Archipelago (ca. 3200 km away) (Santelices and Abbott 1987). The stark differences between the flora of Easter Island and Juan Fernández Archipelago have been attributed to the isolating effects of ocean currents and temperatures that intervene between these localities, especially the cold Humboldt Current (Santelices and Abbott 1987, Santelices and Meneses 2000).

Recent assessment of the diversity of the brown algal genus Hydroclathrus Bory de Saint-Vincent suggested that species diversity is high within the Indo-Pacific Ocean (Santiañez et al. 2018), with four out of the five currently known species originally described from...
the area. These include *Hydroclathrus tenuis* Tseng et Lu from Paracel Islands in the South China Sea (Tseng and Lu 1983), *Hydroclathrus stephanosorus* Kraft from Lord Howe I., Australia, *Hydroclathrus tumulis* Kraft et Abbott from Necker I. in the Northwestern Hawaiian Islands, USA (Kraft and Abbott 2003), and the most recently described *Hydroclathrus minutus* Santiañez et Kogame from Okinawa, Japan (Santiañez et al. 2018). As previous taxonomic studies on *Hydroclathrus* focused on the northern hemisphere and as pseudo-cryptic species were present in the genus (Santiañez et al. 2018), we extended our work into the southern Pacific, particularly at Easter I., Chile.

With respect to scytosiphonacean algae, Easter I. is geographically important as it represents the southeastern Pacific distribution limit of *Chnoospora minima* (K. Hering) Papenfuss and is second only to Juan Fernández Archipelago (Etcheverry 1986) as the easternmost distribution limit of the widely distributed *Hydroclathrus clathratus* (C. Agardh) Howe. As *H. clathratus* is the default species-designation for perforate sac-like Scytosiphonaceae, and as there is a tendency for new *Hydroclathrus* species to be discovered at isolated volcanic islands (Kraft and Abbott 2003, Santiañez et al. 2018), we assessed the identity of the purported “*H. clathratus*” at the remote volcanic Easter Island. We herein describe a new and putatively endemic species of *Hydroclathrus* based on specimens from Vaihu, Easter I. Additionally, we report on the morphology/anatomy and phylogeny of the widely distributed *Ch. minima* collected from the island.

The genus-level taxonomy in the family Scytosiphonaceae has been problematical due to the unresolved relationships of the different taxa as highlighted in phylogenies based on single and multiple genes (e.g. Kogame et al. 1999, Cho et al. 2006, Kogame et al. 2011, West et al. 2015, McDevit and Saunders 2017, Santiañez et al. 2018). These difficulties have been attributed to the frequently broad taxonomic circumscriptions of the genera, resulting in the assignment of species to genera such as *Chnoospora* J. Agardh, *Colpomenia* (Endlicher) Derbès et Solier in Castagne, *Hydroclathrus* Bory de Saint-Vincent, *Petalonia* Derbès et Solier, and *Scytosiphon* C. Agardh despite distinct morpho-anatomical and life history differences from the type species of these genera (Santiañez et al. 2018). Recently, McDevit and Saunders (2017) proposed the recognition of the genus *Planosiphon* McDevit et Saunders to accommodate species previously assigned to *Scytosiphon* [S. complanatus (Rosenvingea) Doty, S. gracilis Kogame] and *Petalonia* [P. zosterifolia (Reinke) Kuntze], which possess flattened, non-constricted blades that are hollow or partially hollow, lack paraphyses among aggregates of uniseriate plurangia, and whose prostrate sporophyte thalli are *Compsoneema*-like and bear only unangia (Santiañez and Kogame 2017). Santiañez et al. (2018) also suggested the possibility of segregating *Chnoospora implexa* J. Agardh from the genus *Chnoospora* based on significant morphological and genetic differences. In the light of these recent developments, we have now reviewed the generic circumscriptions within the family and propose several taxonomic revisions. Based on morpho-anatomical, genetic, and life history differences, we propose the removal of the elongate species of *Colpomenia* [C. bullosa (D.A. Saunders) Yamada, C. durvillei (Bory de Saint-Vincent) M.E. Ramírez, and C. wynnei K.M. Lee, R. Riosmena-Rodríguez, Kogame et S.M. Boo] to the new genus *Dactylosiphon* gen. nov. as well as that of *Ch. implexa* to *Pseudochnoospora* gen. nov.

### Materials and methods

Samples of *Hydroclathrus* and *Scytospora* were collected by snorkeling in Vaihu and Tahai, Easter I. in March and November 2016 (Table S1). A portion of each sample was dried in silica-gel prior to air-drying as herbarium specimens. Voucher specimens are deposited in the Herbarium, Botany Section, Museo Nacional de Historia Natural, Santiago, Chile (SGO) and the Herbarium of the Faculty of Science, Hokkaido University, Sapporo, Japan (SAP).

For morpho-anatomical analyses, sections were made by hand, stained with 0.5% aniline blue with phenol, and mounted in 50% glycerol or 30% Karo in distilled water on glass slides. A Nikon Digital Sight DS-L1 camera (Tokyo, Japan) mounted on a Nikon Optiphot-2 microscope was used for taking photomicrographs.

For molecular analyses, DNA extraction, PCR, and sequencing of the mitochondrial *cox3* as well as the plastid *rbcL* and *psaA* genes, including their respective sequencing primers, followed procedures outlined in Santiañez et al. (2018).

Phylogenetic analyses were conducted using individual genes (*cox3*: 660 bp, *psaA*: 1488 bp, and *rbcL*: 1467) and concatenated (*cox3*: 610 bp, *psaA*: 740 bp, and *rbcL*: 1383 bp = 2733 bp; partitioned by gene and codon) datasets. Newly generated sequence data were analyzed together with sequences of other scytosiphonacean algae downloaded from GenBank. All trees were rooted with *Ectocarpus siliculosus* (Dillwyn) Lyngbye, *Chordaria flagelliformis* (O.F. Müller) C. Agardh, and *Pylaiella littoralis* (Linnaeus) Kjellman (Table S1). ClustalW in MEGA 5 was used to align the sequences and distance matrix calculated using ClustalW. Phylogenetic analyses were conducted using the maximum likelihood approach implemented in MEGA 5 using the Tamura 3-parameter model and the percent sequence identity cut-off of 85% for the concatenated dataset, because the *cox3* gene has a different phylogenetic signal than the *psaA* and *rbcL* genes, which resulted in the exclusion of certain species.
v.6 (Tamura et al. 2013) was used to align sequences. All datasets were analyzed for Maximum Likelihood (ML) and Bayesian Inference (BI); in both cases, GTR + I + Γ model, as selected by Akaike Information Criterion (AIC) in MrModeltest 2.3 (Nylander 2004), was used. ML analyses with 1000 bootstrap pseudoreplicates were conducted using RAxML v.8 (Stamatakis 2014) in the CIPRES Phylogenetic Portal (Miller et al. 2010). BI was conducted in MrBayes v3.2.1 (Huelsenbeck and Ronquist 2001). Markov-chain Monte Carlo iterations were run for 25 million generations until the average standard deviations of split frequencies fell below 0.01, indicating convergence of the iterations. A burn-in of 25% was set before calculating the trees.

Results
Phylogenetic analyses
Nine samples of scytosiphonacean algae, representing 13 new sequences, were used in this study (Table S1).

Our phylogenetic analyses based on cox3 sequence data recovered all Hydroclathrus species, with the exception of Hydroclathrus minutus, in a highly-supported clade (Figure 1). The genetically identical Hydroclathrus specimens from Easter I. clustered with Hydroclathrus clathratus but were genetically distinct. We describe this species below as Hydroclathrus rapanuii Santíañez,
Macaya et Kogame sp. nov. Specimens of Chnoospora minima from Easter I. were also genetically identical and formed a highly-supported clade with Ch. minima from southern Japan (Figure 1). The Chnoospora clade, however, did not include Chnoospora implexa, which grouped with the recently described taxa Tronoella ryukyuana Santiañez et Kogame and H. minutus, albeit with low support.

Similar to the cox3 gene-based phylogeny, the concatenated (cox3/rbcL/psaA; Figure 2) and plastid gene (Figure S1) phylogenies of the family Scytosiphonaceae showed that H. rapanuii was nested within the main Hydroclathrus clade. Hydroclathrus rapanuii was more closely related with the robust species H. clathratus and Hydroclathrus stephanosorus than to either of the thinner and fibrous Hydroclathrus tenuis or H. minutus.

Based on our concatenated tree, two major clades were suggested in the Scytosiphonaceae (Figure 2). One highly supported clade (which we designate as the “Scytosiphon group”) consisted mainly of subtropical to temperate species from the genera Colpomenia, Petalonia, Planosiphon, Melanosiphon, Myelophycus and Scytosiphon. The other unresolved clade (the “Hydroclathrus group”) was composed of tropical to warm temperate species of the genera Colpomenia, Chnoospora, Hydroclathrus, Rosenvingea Bergesen, and Tronoella Santiañez et Kogame. The relationships of most genera that are closely related to Hydroclathrus, including Chnoospora, Colpomenia and Rosenvingea, were unresolved. A particularly pronounced polyphyly was observed among Chnoospora species, where Ch. minima was consistently recovered as one of the early-diverged taxa within the “Hydroclathrus group” while Chnoospora implexa appeared to have diverged later. With respect to the genus Colpomenia, three lineages were apparent in our concatenated tree (Figure 2): Lineage 1 is represented by Colpomenia sinuosa (Mertens ex Roth) Derbès et Solier but also possibly includes Colpomenia tuberculata D.A. Saunders and Colpomenia ramosa W.R. Taylor (Figures 1 and S1); Lineage 2, represented by Colpomenia peregrina Sauveageau, includes Colpomenia claytoniae S.M. Boo, K.M. Lee, G.Y. Cho et W. Nelson and Colpomenia expansa (D.A.Saunders) Y.-P. Lee (Figure S1); and Lineage 3, as represented by Colpomenia bullosa, also includes Colpomenia durvillei and Colpomenia wynnei (Figure S1). Lineages 1 and 2 are found within the “Hydroclathrus group” (Figure 2) and, although their
phylogenetic positions remain ambiguous, both lineages were more closely related to each other than to Lineage 3. The latter clustered with high support in the “Scytosiphon group” (Figure 2).

**Taxonomic observations**

*Hydroclathrus rapanuii* Santiañez, Macaya et Kogame sp. nov. (Figures 3–11)

**Description**
Thalli saccate, up to 10 cm in diameter; membranes thin, 60–350 μm thick, surfaces furrowed, perforated with numerous holes. Cortical cells 4.5–12.5 μm by 7–14 μm, narrowly to broadly oblong; medullary cells thin-walled, up to 190 μm wide. Hair primordia in tufts, distally extending into hyaline hairs. Plurangial sori angular, block-like, often confluent with adjacent sori. Plurangia erect, quadriseriate, cylindrical to slightly clavate, 15–23 μm long.

**Holotype**
SGO168251 (Figures 3–11), Vaihu, Easter I., 1.5–2 m depth, 20 March 2016, E.C. Macaya; deposited in SGO.

**Isotypes**
SGO168250, SGO168252, Vaihu, Easter I., 20 March 2016, E.C. Macaya; deposited in SGO.

**Type locality**
Vaihu, Easter Island, Chile (27° 9’ 57.22” S, 109° 21’ 48.20” W).

**Etymology**
Named in honor of the Rapanui people, the indigenous people of Easter Island.

**Distribution**
Currently only known from the type locality.

**Representative sequences**
Genbank accession numbers: **cox3** = MG450663, **psaA** = MG450664, **rbcL** = MG251837 (sequenced from SGO168251).

**Specimens examined**

**Observations**
Thalli yellowish to light brown in color (Figure 4), becoming dark brown when dried on herbarium sheets (Figure 3), initially saccate (when young), later convoluted, attached to the substrate by rhizoids. Membranes 60–350 μm thick, irregularly perforated by holes of various sizes (Figures 3 and 4) rimmed by slightly folded to revolute margins. Membrane surfaces dimpled, furrowed, with hair tufts developing in depressions and creases (Figures 5 and 6).

Membranes composed of a layer of small pigmented cortical cells and 3–6 (rarely 7) layers of clear medullary cells (Figure 7). Cortical cells square or rectilinear to polygonal in surface view, (4–) 5–9 by (5–) 6–12 (–14) μm (Figures 5 and 6); in cross-section, thin-walled, variable in shape but mostly narrowly to broadly oblong, 4.5–12.5 μm wide by 7–14 μm in height (Figure 8), apices smooth, sometimes domed to obtuse, those adjacent to hair primordia often becoming papillate. Medullary cells also thin-walled, progressively larger towards thallus interior, up to 190 μm wide (Figure 7).

Hair primordia slightly clavate, often basally constricted, each extending into long hyaline hairs (Figures 2, 6 and 9), and clustered in groups of 4–20.

Plurangial sori angular and block-like, surrounding or adjacent to hair pits, often merging with nearby sori (Figure 6). Plurangial primordia differentiating from surface cortical cells (Figure 10), forming dense palisades. Mature plurangia cylindrical to slightly clavate, densely aggregated, quadriseriate (biseriate in lateral view), 15–23 μm long, each tier divided into four locules (Figure 11).

**Ecology**
Usually few individuals found at low to mid-intertidal rocky pools down to shallow subtidal (2 m depth) of protected and semi-protected sites in the island, associated with other brown algae such as *Sargassum, Lobophora, Colpomenia* and *Stypodium*.

**Chnoospora minima** (K. Hering) Papenfuss

**Basionym**
*Fucus minimus* K. Hering 1841: 92.

**Synonyms**
*Chnoospora pacifica* J. Agardh *fide* Papenfuss 1956: 69.

Lectotype
HBG024509 collected by F. Krauss from Port Natal (Durban), South Africa: the lectotype was designated by Papenfuss (1956).

Distribution
Virtually cosmopolitan in tropical to subtropical Indo-Pacific (M.D. Guiry in Guiry and Guiry 2017).

Specimens examined

Additional specimens examined
Cook Islands: SAP115375, Ngatangiia, Rarotonga, 13 February 1993, A.D.R. N’Yeurt. Hawaiian Islands: SAP115377,

**Observations**

Living thalli yellow-brown (Figures 12–18); drying dark brown basally, lighter distally (Figure 13). Thalli erect, in dense clumps, arising from consolidated holdfasts.
smaller, squarish to rectangular locules 4–5 μm by mature plurangia up to 50 becoming transversely biseriate (Figures 15 and 16); Plurangial initials differentiating from cortical cells, with cuticles that are loosened as plurangia mature.

Hydroclathrus in subtropical to warm-temperate coasts of Japan indicated that H. clathratus can be sympatric with Hydroclathrus stephanosorus; the latter has been overlooked or misidentified, and was shown to be more widely distributed in Japan than the former (Santíañez et al. 2018).

With Hydroclathrus rapanuii, we add one more putatively endemic species to the seaweed flora of Easter I. Like H. stephanosorus from Lord Howe I., Australia (Kraft and Abbott 2003) and Hydroclathrus minutus from Okinawa I. (Santíañez et al. 2018), its type locality is a small Pacific volcanic island, and this is also true of the recently described scytosiphonacean species Petalonia tatewakii Kogame et A. Kurihara (Kogame et al. 2011), Petalonia tenuis K. Matsumoto et S. Shimada (Matsumoto et al. 2014), and Tronoella ryukyuana Santíañez et Kogame (Santíañez et al. 2018). Extensive taxon sampling of volcanic islands will likely result in new taxa discoveries right across the algal phyla.

Specimens of H. rapanuii were similar in habit to young H. clathratus but can be distinguished based on larger cortical cells, fewer medullary cell layers, and angular to block-like plurangial sori (Table 1). Hydroclathrus rapanuii resembles H. stephanosorus and Hydroclathrus tumulis in the breadth of the membrane surrounding the perforations. However, it can be differentiated from H. stephanosorus by its plurangial sori (angular and block-like as opposed to nearly circular oral outline), cortical cell shape (oblong to broadly oblong vs. broadly rounded), and thinner thallus membranes (Table 1). Although the angular and block-like sori of H. rapanuii were similar to those of H. tumulis, the latter has subapiculate cortical cells, laxly arranged and apparently stalked plurangia, and has an apparent restriction to deep waters (Kraft and Abbott 2003).

Discussion

Our current understanding of global algal biodiversity and the phylogenetic relationships of macroalgae has been reshaped by the advent of DNA phylogenies. Using molecular phylogenetic tools, reports of high levels of cryptic and/or pseudo-cryptic diversity are common, especially among widespread species, such as Actinotospore crinita (Carmichael) Sauvageau (Yaegashi et al. 2015), Centrocera clavatum C. Agardh (Schneider et al. 2015), Gibsmithia hawaiiensis Doty (Gabriel et al. 2016), Lobophora variegata (J.V. Lamouroux) Womersley ex E.C. Oliveira (Vieira et al. 2014, 2016, Schultz et al. 2015), and Portieria hornemanii (Lyngbye) P.C. Silva (Payo et al. 2013). Similarly, our molecular-assisted taxonomic studies of Hydroclathrus (Santíañez et al. 2018, this study) highlight the role of molecular tools in identifying and refining morpho-species boundaries among algae that have simple morphologies. Our studies also point to the importance of continuing to challenge the assumption that most, if not all, collections of Hydroclathrus made throughout the tropical to warm-temperate waters belong to a single, cosmopolitan, and highly polymorphic species, Hydroclathrus clathratus. For example, wide-scale sampling of Hydroclathrus in subtropical to warm-temperate coasts of Japan indicated that H. clathratus can be sympatric with Hydroclathrus stephanosorus; the latter has been overlooked or misidentified, and was shown to be more widely distributed in Japan than the former (Santíañez et al. 2018).
<table>
<thead>
<tr>
<th>Characters</th>
<th>Hydroclathrus rapanuii (Santíañez, Macaya et Kogame)</th>
<th>Hydroclathrus clathratus (C. Agardh) Howe</th>
<th>Hydroclathrus stephanosorus Kraft (C. Agardh) Howe</th>
<th>Hydroclathrus tumulis Kraft &amp; Abbott</th>
<th>Hydroclathrus tenuis Tseng &amp; Lu (Santíañez et al.)</th>
<th>Hydroclathrus minutus Santíañez &amp; Kogame</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thallus form</td>
<td>Saccate to convoluted; membranous, irregularly perforated</td>
<td>Strap-shaped to net-like, convoluted; membranous, irregularly perforated</td>
<td>Saccate to sheet-like; membranous, perforated by subcircular holes</td>
<td>Saccate to torn, sheet-like; membranous, irregularly perforated</td>
<td>Net-like, convoluted; perforated membranes thin to fibrous</td>
<td>Net-like, convoluted, sometimes inter-adhesive; membrane strands extremely thin and delicate &lt;130</td>
</tr>
<tr>
<td>Membrane thickness (μm)</td>
<td>60–350</td>
<td>100–650</td>
<td>60–520</td>
<td>120–280</td>
<td>40–590</td>
<td>&lt;130</td>
</tr>
<tr>
<td>Cortical cells</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of cell layers</td>
<td>1 (–2)</td>
<td>1–2 (3)</td>
<td>1–2</td>
<td>1–2</td>
<td>1–2</td>
<td>1–2</td>
</tr>
<tr>
<td>Shape (surface)</td>
<td>Square or rectilinear to polygonal</td>
<td>Oblong to rectilinear to pentagonal/hexagonal (3–) 4–9 (–11) × 5–11 (–16)</td>
<td>4–7 (–8) × (5–) 6–12</td>
<td>7–13 × 7–15</td>
<td>4–8 × 6–9 (–11)</td>
<td>3–6 × (4–) 5–8 (–9)</td>
</tr>
<tr>
<td>Size (surface; width × length, μm)</td>
<td>(6–) 5–9 × (5–) 6–12 (–14)</td>
<td>(4–) 5–11 (–12) × (5–) 6–14 (–16)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shape (cross section)</td>
<td>Oblong to broadly oblong, apices domed to obtuse</td>
<td>Oblong to broadly ovate to papillate</td>
<td>Broadly rounded to ovoid, apices sometimes domed to obtuse</td>
<td>Subacutely papillate</td>
<td>Ovate to broadly ovate, domed to papillate</td>
<td>Broadly obovate to ovate, apices protuberant</td>
</tr>
<tr>
<td>Size (cross section; width × length, μm)</td>
<td>4.5–12.5 × 7–14</td>
<td>(4–) 5–11 (–12) × (5–) 6–14 (–16)</td>
<td>(4–) 5–11 (–13) × (5–) 6–10 (–15)</td>
<td>8–10 × 10–13</td>
<td>5–9 (–10) × 7–11 (–12)</td>
<td>4–7 (–9) × 7–9 (–11.5)</td>
</tr>
<tr>
<td>Medullary cells</td>
<td>3–6 (–7) layers; thin-walled</td>
<td>5–9 layers; thin-walled</td>
<td>2–4 layers; thin-walled</td>
<td>Up to 220</td>
<td>Up to 250</td>
<td>1–5 layers; thick-walled</td>
</tr>
<tr>
<td>Size (width, μm)</td>
<td>Up to 190</td>
<td>Up to 260</td>
<td>(3–) 5–6 (–8) layers; thin-walled</td>
<td></td>
<td></td>
<td>Up to 200</td>
</tr>
<tr>
<td>Hair primordia</td>
<td>Occur in groups of up to 20 in depressions, pits, and channels; each usually extended into long hyaline hairs</td>
<td>Occur in groups of not more than 25 in depressions, pits, and channels; often extended into long hyaline hairs</td>
<td>Occur in groups of not less than five in shallow depressions, sometimes in pits; sometimes extended into long hyaline hairs</td>
<td>Occur singly or in groups of three to six</td>
<td>Occur in groups of not less than five; often with long hyaline hair extensions</td>
<td>Occur in groups of not more than eight, often with long hyaline hair extensions</td>
</tr>
<tr>
<td>Nature and arrangement</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plurangia</td>
<td>Sori associated with hair tufts, in angular and irregular blocks, often merged with adjacent sori</td>
<td>Sori often associated with hair tufts; diffused with angular margins, sometimes confluent</td>
<td>Sori surround hair tufts, discrete, nearly circular in outline; maintain circular margins when merged with adjacent sori</td>
<td>Sori angular to irregularly block-like, rarely confluent</td>
<td>Sori confluent, irregularly shaped with margins angular, may occur extensively across surface; may grow without hairs</td>
<td>Sori often surround hair tufts; generally discrete with subcircular margins, sometimes merged with adjacent sori</td>
</tr>
</tbody>
</table>
these variously sized hollowed areas in the medullas of thalli collected from within the central and western Pacific localities (i.e. southern Japan, Hawaiian Islands, and Cook Islands), as well as in the Indian Ocean (Anderson et al. 2016). The unattached Ch. minima reported from the deep waters of New Zealand were slightly longer than our Easter I. specimens and also appear to have hollow portions (Nelson and Duffy 1991, fig. 3), albeit they were not mentioned by the authors. Smaller and relatively thinner thalli of Hawaiian specimens showed inconspicuous medullary gaps, and it is likely that this character may have been overlooked or was thought to be taxonomically insignificant.

No fertile Ch. minima specimen was found among our Easter I. collections, but those from Cook and Hawaiian Is. possessed mature plurangia. Similar to those reported by J. Agardh (1848) and Barton (1898) in Chnoospora fastigiata J. Agardh (=Ch. minima), we also saw the presence of a cuticle on these uni- to biseriate plurangia. Plurangial cuticles in Ch. minima have not been mentioned in other reports (Fotos 1981, Trono 1997, Abbott and Huisman 2004, Kraft 2009, Anderson et al. 2016). Kraft (2009) suggested that the plurangia illustrated by Fotos (1981, figs. 4, 11) and Barton (1898, pl. 28, figs. 4, 5) were “anticlinal cortical filaments that are typical of vegetative cells lining the flat faces of the fronds”, as was illustrated in his fig. 38G, H. In contrast to his opinion, we confirm that those illustrated by Fotos and Barton were plurangia, similar to those found in our specimens and the South African specimen (Anderson et al. 2016). We do agree, however, that those illustrated by Kraft (2009, fig. 38I) were plurangial initials and were similar to those we observed (Figures 17 and 18).

When J. Agardh established the genus Chnoospora in 1847, he described two species: Chnoospora pacifica J. Agardh from Pacific Mexico and Chnoospora atlantica J. Agardh from Venezuela. A year later (Agardh 1848) synonymized these two species to Chnoospora fastigiata and described two additional species, Chnoospora implexa J. Agardh and Chnoospora pannosa J. Agardh. On both occasions, he failed to designate the generitype species. Papenfuss (1956: 69) proposed the conspecificity of Ch. fastigiata with Fucus minimus K. Hering and subsequently combined these names as Ch. minima based on Hering’s priority. In the same publication, Papenfuss also designated Hering’s specimen [HBG024509, collected by F. Krauss from Port Natal (Durban), South Africa; currently deposited at the Herbarium Hamburgense of the University of Hamburg, Germany], as the lectotype. He also noted the similarity of Hering’s specimen to the South African Ch. minima (as Ch. fastigiata) reported by Barton (1898). As mentioned earlier, the Ch. minima specimens we examined also agree well with Barton’s specimens, as well as those illustrated in...
Anderson et al. (2016) from South Africa. Taking all these observations into consideration, and because it has not been done yet (M.D. Guiry in Guiry and Guiry 2017), we herein designate *Ch. minima* as the generitype of the genus *Chnoospora*.

Similar to previous works on the Scytosiphonaceae (e.g. Cho et al. 2006, Lee et al. 2014a, McDevit and Saunders 2017), two major phyletic groups were apparent (i.e. the “*Scyotosiphon* group” and “*Hydroclathrus* group”) in our molecular trees. Species found in the “*Scyotosiphon* group” have upright, elongate and terete to flattened thalli that are hollow, partially hollow or solid in construction. Some members of this group produce only unilocular zoidangia in the prostrate sporophyte stage (Kogame et al. 1999, Kogame and Masuda 2001, Cho et al. 2006), and are distributed in subtropical to temperate waters (Kogame et al. 1999). The “*Hydroclathrus* group” includes species of varied morphologies ranging from upright to spreading, of either hollow or solid construction, and saccate to branched, some branches anastomosing to varying degrees. Species in this group are found in tropical to warm temperate waters and have prostrate sporophytes that produce both uni- and plurilocular zoidangia (Kogame et al. 1999, Kogame 2001, Cho et al. 2006).

Paraphyly and polyphyly of some genera have been a consistent theme among the Scytosiphonaceae since the pioneering molecular phylogenetic work by Kogame et al. (1999). Despite numerous follow-up studies, taxonomic revisions to achieve monophyly have been slow. Kogame et al. (1999) suggested that the morphology of prostrate sporophyte thalli (i.e. thallus structure and presence/absence of plurilocular zoidangia) are important taxonomic criteria at the generic level. However, as information on life histories and input of genetic data from other scytosiphonacean species have been scarce, no formal proposals have yet been made to settle the unresolved relationships in the family. Recently, members of the Scytosiphonaceae have received considerable attention, resulting in an increase of information on the life history, morphology and phylogeny of species of *Chnoospora* (Kogame 2001), *Colpomenia* (Kogame and Masuda 2001, Boo et al. 2011, Lee et al. 2012, Lee et al. 2014a), *Hydroclathrus* (Kraft and Abbott 2003, Santiañez et al. 2018), *Melanosiphon* (Lee et al. 2014b), *Myelophyclus* (Cho et al. 2006), *Rosenvingea* (West et al. 2010, Lee et al. 2014b) and *Petalonia* (Kogame et al. 2011, Matsumoto et al. 2014). Collectively, these works have provided insights into the taxonomic complexities but have also paved the way to clarifying specific and generic boundaries in the Scytosiphonaceae. In an attempt to partially resolve the non-monophyly in *Petalonia* and *Scyotosiphon*, McDevit and Saunders (2017) recently proposed the recognition of *Planosiphon*. Similar to previously mentioned reports, relationships among species of *Colpomenia*, *Chnoospora*, *Hydroclathrus*, *Rosenvingea* and *Scyotosiphon* still remain unresolved.

In the current work, *Colpomenia* did not resolve as monophyletic and was segregated into at least three distinct lineages: two of these (Lineages 1 and 2) were found within the “*Hydroclathrus* group” whereas one (Lineage 3) was within the “*Scyotosiphon* group”. The relationships of the *Colpomenia* lineages within the “*Hydroclathrus* group” were not resolved, but these are represented by species with globular/saccate to amorphously contoured, hollow thalli. Meanwhile, *Colpomenia* “Lineage 3”, whose species have upright, elongate (finger-like), hollow thalli, was sister to all other taxa within the “*Scyotosiphon* group”. In addition, compared to species of Lineage 1 (e.g. *C. sinuosa*), which has a prostrate sporophyte that produces both uni- and plurilocular zoidangia, *C. bullosa* of “Lineage 3” produces only unilocular zoidangia in its prostrate sporophyte thallus (Kogame et al. 1999). Considering these distinct differences, we believe it is best to remove the three former *Colpomenia* species nested within the “*Scyotosiphon* group” to a new genus *Dactylosiphon*.

We have previously suggested the possibility of segregating *Ch. implexa* from the genus *Chnoospora* based on genetic and morphological differences (Santiañez et al. 2018). In our current and in previous studies on the Scytosiphonaceae, the generitype *Ch. minima* was always segregated from *Ch. implexa* by at least representatives of *Rosenvingea* and *Colpomenia*, with moderate to high levels of support. This observed phylogenetic segregation is reflected in the distinct morpho-anatomical and ecological differences among these taxa outlined in Table 2.

Based on morphological and molecular phylogenetic criteria, we herein formally segregate *Ch. implexa* and species in “Lineage 3” of *Colpomenia* from their current generic affiliation and propose that *Pseudochnoospora gen. nov.* and *Dactylosiphon gen. nov.*, respectively, be recognized to accommodate them.

**Taxonomic proposals**

*Pseudochnoospora* Santiañez, G.Y. Cho et Kogame **gen. nov.**

**Description**

Thalli decumbent, branched, with branches attached to the substrata and to other branches at various points; axes solid, terete to compressed. Cortex up to two layers of small, pigmented cells. Medullary cells clear, thin-walled,
Table 2: Comparison among some genera in the family Scytosiphonaceae.

<table>
<thead>
<tr>
<th>Characters</th>
<th>Chnoospora</th>
<th>Pseudochnoospora gen. nov.</th>
<th>Colpomenia</th>
<th>Dactylosiphon gen. nov.</th>
<th>Tronoella</th>
<th>Hydroclathrus</th>
<th>Rosenvingea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thallus form</td>
<td>Erect; solid to partially hollow, compressed to flattened; branched</td>
<td>Decumbent; solid, terete to compressed; branched, entangled and mat-forming</td>
<td>Saccate and hollow, thallus walls thick; globular to cushion-like, surface sometimes perforated or with protrusions</td>
<td>Erect; finger-like and tubular, thallus walls thin; each tube arising from a common saccate base</td>
<td>Spreading; perforated hollow membranes initially arise as siphonous protrusions</td>
<td>Spreading; membranes perforated, hollow; margins of perforations folded to revolute</td>
<td>Erect to decumbent to mat-forming; hollow, branched, terete to compressed</td>
</tr>
<tr>
<td>Holdfast</td>
<td>Discoid, single</td>
<td>Rhizoidal, attached at various points on the surface</td>
<td>Rhizoidal</td>
<td>Rhizoidal</td>
<td>Rhizoidal</td>
<td>Rhizoidal</td>
<td>Discoid, rhizoidal</td>
</tr>
<tr>
<td>Cortex</td>
<td>2–5 cell layers; cells thick-walled, pigmented</td>
<td>1–2 cell layers; cells thin-walled, pigmented</td>
<td>1–2 (±3) cell layers, pigmented</td>
<td>1–3 cell layers, pigmented</td>
<td>1–2 cell layers, pigmented</td>
<td>1–3 cell layers, pigmented</td>
<td>1 cell layer, pigmented</td>
</tr>
<tr>
<td>Medulla</td>
<td>Clear cells thick-walled with lamellate regions; large and small cells intermixed; with hollow regions</td>
<td>Cells clear and thin-walled, often becoming larger towards the center</td>
<td>3–6 cell layers; clear, thin- to thick-walled</td>
<td>2–5 cell layers; clear, thick-walled to lamellate</td>
<td>1–4 cell layers; clear, thin-walled</td>
<td>1–9 cell layers; clear, generally thin-walled</td>
<td>1–5 cell layers; clear, thin-walled</td>
</tr>
<tr>
<td>Phaeophycean hairs</td>
<td>Occur as tufts in deep depressions, extended into hyaline hairs</td>
<td>Occur in pits</td>
<td>Occur in pits, extended into hyaline hairs</td>
<td>Occur in pits, extended into hyaline hairs</td>
<td>Occur in shallow pits, not extended into hyaline hairs</td>
<td>Occur in pits or depressions, generally extended into hyaline hairs</td>
<td>Occur in pits, generally extended into hyaline hairs, absent in some</td>
</tr>
<tr>
<td>Plurangial sori</td>
<td>Linear; associated with hairs; covered with cuticle</td>
<td>Irregularly shaped, generally not associated with hairs; may be covered with cuticle</td>
<td>Discrete to confluent; may be associated with hairs or covered with cuticle</td>
<td>Extensive and/or confluent; cuticle absent</td>
<td>Discrete, irregularly shaped, associated with hairs</td>
<td>Discrete to confluent, circular to irregular, angular to block-like, often associated with hairs</td>
<td>Discrete to confluent, shape linear to irregular, may be associated with hairs</td>
</tr>
<tr>
<td>Paraphyses</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Plurangia</td>
<td>Coherent, cylindrical to clavate, uni- to biseriate (lateral view)</td>
<td>Coherent, cylindrical to clavate, uni- to partially or completely biseriate (lateral view)</td>
<td>Cylindrical to clavate, uni- to biseriate (lateral view)</td>
<td>Cylindrical to clavate, uni- to biseriate (lateral view)</td>
<td>Cylindrical to subclavate, mostly uniseriate, some partially or completely biseriate; (lateral view)</td>
<td>Firmly coherent and massive</td>
<td>Loosely arranged, cylindrical to clavate, biseriate (lateral view)</td>
</tr>
<tr>
<td>Characters</td>
<td>Chnoospora</td>
<td>Pseudochnoospora gen. nov.</td>
<td>Colpomenia</td>
<td>Dactylosiphon gen. nov.</td>
<td>Tronoella</td>
<td>Hydroclathrus</td>
<td>Rosenvingea</td>
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<tr>
<td>Habitat</td>
<td>Wave-swept, rocky upper to mid-intertidal, epilithic</td>
<td></td>
<td>subtidal, epilithic, rarely epiphytic</td>
<td>subtidal, epilithic, sometimes epiphytic</td>
<td>Intertidal, often subtidal</td>
<td>Intertidal, often subtidal</td>
<td>Low to mid-intertidal; epiphytic or epilithic</td>
</tr>
<tr>
<td>Geographical distribution</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Prostrate thallus morphology</td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Prostrate sporophyte</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Type species</td>
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</tbody>
</table>

**Pseudochnoospora implexa** (J. Agardh) Santíañez, G.Y. Cho et Kogame comb. nov.

**Etymology**

*Pseudochnoospora*, or the “false *Chnoospora*”, is in reference to the previous erroneous assignment of the taxon to the genus *Chnoospora*.

**Basionym**


**Synonyms**


**Holotype**

BM000569565, Tor, Sinai Peninsula, W. Schimper; deposited in BM.

**Distribution**

Tropical to subtropical waters (M.D. Guiry in Guiry and Guiry 2017).

**Remarks**

When J. Agardh (1848) formally described *Sphaerococcus implexus* Hering *nom. nud.* as a new species, he placed it in *Chnoospora* under the heading “Species inquirenda”. Its original disposition has since been followed despite the absence of studies to confirm its generic assignment. Descriptions of “Ch. implexa” from various localities has been consistent, with Kraft (2009) providing detailed morphological work on the species based on Australian and Hawaiian samples. Morpho-anatomical observations becoming larger centrally. Plurangia covered with cuticle, coherent, cylindrical to clavate, uniseriate to partially to completely biseriate, paraphyses absent. Prostrate sporophyte produces both uni- and plurilocular zoidangia.

**Type species**

*Pseudochnoospora implexa* (J. Agardh) Santíañez, G.Y. Cho et Kogame comb. nov.
on “Ch. implexa” clearly indicate that it is different from the generitype Ch. minima (Table 2). That is, “Ch. implexa” can be differentiated from Ch. minima in possessing solid, decumbent and inter-adhesive thalli that are attached to various points on the substratum (vs. erect, freely branching, and partially hollow thalli that were densely growing from a consolidated holdfast) and in having thin-walled cortical and medullary cells (vs. thick-walled cells; Table 2). In addition, previous molecular phylogenetic studies (e.g. Cho et al. 2006, Santiañez et al. 2018) pointed to the polyphyly of the genus Chnoospora. Pseudochnospora implexa (as Ch. implexa) in culture was shown to have a prostrate sporophyte that produces both uni- and plurilocular zoidangia (Kogame 2001).

**Dactylosiphon Santiañez, K.M. Lee, S.M. Boo et Kogame gen. nov.**

**Description**

Thalli composed of hollow, elongate (finger-like) tubes, each tapering to an attenuate to cuneate basal portion and arising from a saccate base. Interiors hollow, bounded by several layers of large, clear, thick-walled medullary cells; outer layer composed of small pigmented cortical cells. Plurangia occurring extensively throughout the surface, always associated with short to slightly longer paraphyses, the plurangia mostly uniseriate, some partially to completely biseriate.

**Type species**

*Dactylosiphon bullosus* (D.A. Saunders) Santiañez, K.M. Lee, S.M. Boo et Kogame **comb. nov.**

**Etymology**

Named after the finger-like (Greek: *dactylo*)- and sipho-nous thalli of the species belonging to this genus.

**Dactylosiphon bullosus** (D.A. Saunders) Santiañez, K.M. Lee, S.M. Boo et Kogame **comb. nov.**

**Basionym**

*Aspercoccus durvillei* Bory de Saint-Vincent 1828: Botanique, Cryptogamie. In (Duperrey, L.I. Eds): *Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de Sa Majesté, la Coquille, pendant les années 1822, 1823, 1824 et 1825*: 200, pl. 11: fig. 3 (as “*durvillaei*”).

**Synonyms**


**Type locality**

Concepcion, Chile.

**Distribution**

Temperate waters of the Pacific (Lee et al. 2012).

**Remarks**

The taxonomy and molecular phylogeny of *Dactylosiphon durvillei* (=*Colpomenia durvillei*) relative to other
elongate species of *Colpomenia* (= *Dactylosiphon*) has been reviewed in detail by Lee et al. (2012), where it is suggested that *C. phaeodactyla* may be conspecific with *C. durvillei*. Based on morphological and phylogenetic analyses on an elongate *Colpomenia* from Las Cuevas, Sonora, Mexico (near the type locality of *C. phaeodactyla*) and Chile, Lee et al. (2014a: 485) synonymized *C. phaeodactyla* with *C. durvillei* based on nomenclatural priority.


**Basionym**


**Type locality**

Hoedong, Jindo, Korea.

**Distribution**

Southern Korea and Japan (Lee et al. 2014a).

**Remarks**

*Dactylosiphon wynnei* is a recently described species (as *C. wynnei*) from Korea and Japan. It is unique among its congeners in possessing adventitious branchlets along the length of its contorted, mature elongate sacs.

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**References**


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**Bionotes**

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Kazuhiro Kogame is a Professor in the Faculty of Science, Hokkaido University, Japan. His research interests include taxonomy, phylogeny and life history of seaweeds.
Research article: A new Hydroclathrus species, *H. rapanuii*, is described from Easter Island; although not found in the island, we additionally proposed the recognition of two new genera, *Dactylosiphon* and *Pseudochnoospora*, based on three-gene phylogeny and known morphologies/anatomies.

**Keywords:** *Dactylosiphon* gen. nov.; Easter Island; Indo-Pacific Ocean; *Pseudochnoospora* gen. nov.; Scytosiphonaceae.