

## *Colpomenia wynnei* sp. nov. (Scytosiphonaceae, Phaeophyceae): a new species of marine algae from northeast Asia

KYUNG MIN LEE<sup>1</sup>, RAFAEL RIOSMENA-RODRIGUEZ<sup>2</sup>, KAZUHIRO KOGAME<sup>3</sup> AND SUNG MIN BOO<sup>1\*</sup>

<sup>1</sup>Department of Biology, Chungnam National University, Daejeon 305-764, Korea

<sup>2</sup>Programa de Investigación en Botánica Marina, Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, Apartado postal 19-B, La Paz, B.C.S. 23080, México

<sup>3</sup>Department of Natural History Sciences, Faculty of Science, Hokkaido University, Sapporo 060-0810, Japan

**ABSTRACT:** The taxonomic distinctiveness and distribution of the brown alga *Colpomenia phaeodactyla* are debatable. The type locality of this species is Puerto Peñasco, Mexico, and its distribution includes northeast Asia. We analyzed two gene sequences of specimens of so-called *C. phaeodactyla* from Korea, Japan and Mexico, in combination with morphological observations of the specimens. Analyses of 71 *cox3* and 23 *rbcL* sequences resulted in similar trees in which specimens under the name *C. phaeodactyla* consisted of two distinct clades. One clade comprised samples from Korea and Japan, and the other clade, from the Gulf of California, was identical to *C. durvillei*. Additional observations of the morphology and anatomy of the specimens agreed with the molecular data. On the basis of these results, we describe the new species *C. wynnei* for plants from Korea and Japan. *Colpomenia wynnei* was distinguished by finger-like sacs with adventitious branchlets when mature and was much contorted, the height of ascocysts being shorter than plurilocular sporangia. Both *cox3* and *rbcL* sequence data strongly supported the monophyly of *C. wynnei*, *C. bullosa* and *C. durvillei*, all being characterized by having elongate thalli. Based on both *cox3* and *rbcL* data sets, we herein propose to synonymise *C. phaeodactyla* with *C. durvillei*.

**KEY WORDS:** Biogeography, Brown algae, *Colpomenia*, *cox3*, Korea, *rbcL*, Taxonomy

### INTRODUCTION

Members of the brown algal family Scytosiphonaceae are distributed from intertidal to subtidal habitats and occur in most oceans, including tropical, warm and cold waters. Recent research on the family Scytosiphonaceae has revealed significant complexity in the phylogenetic relationships of genera and species, with paraphyly demonstrated in the genera *Chnoospora* J. Agardh, *Colpomenia* (Endlicher) Derbès et Solier, *Petalonia* Derbès et Solier, *Rosenvingea* Børgesen and *Scytosiphon* C. Agardh (Kogame *et al.* 1999; Cho *et al.* 2006; West *et al.* 2010). Moreover, biogeographic patterns in this family are interesting to study because some species are reportedly distributed on both the western and the eastern coastlines of the Pacific Ocean.

The genus *Colpomenia* is characterized by its habit of hollow, crisp thalli that are globular to convoluted to elongate-ovoid in shape. The genus is found worldwide across a wide latitudinal range. To date, 12 species are recognised, with a high diversity in temperate waters (Boo *et al.* 2011b; Guiry & Guiry 2013). Within *Colpomenia*, there are morphological groups, a globose thallus group and an elongate/tubular thallus group (Kogame *et al.* 1999; Boo *et al.* 2011b). Recently, we have focused on the taxonomy, biogeography, and genetic diversity of *Colpomenia* species (Cho *et al.* 2005, 2006; Boo *et al.* 2011b; Lee *et al.* 2012, 2013, 2014). Further revision, however, is needed for the taxonomy of the elongate species of *Colpomenia*: *C. bullosa*

(D.A. Saunders) Yamada, *C. durvillei* (Bory) M.E. Ramírez and *C. phaeodactyla* M.J. Wynne & J.N. Norris.

Wynne & Norris (1976) described *Colpomenia phaeodactyla* on the basis of specimens collected at Puerto Peñasco, Sonora, Mexico, which was previously identified as *C. sinuosa* f. *deformans* sensu Setchell & Gardner (Wynne 1972); however, *C. sinuosa* f. *deformans* is currently considered a synonym of *C. bullosa*. The distinguishing features of *C. phaeodactyla* are the delicate nature of the sacs and their clustered aspect from a common basal system. Conversely, *C. bullosa* has a firmer texture of the balloon-like sacs, and it usually has a solitary condition. In agreement with the proposal of M. Chihara, Wynne & Norris (1976) considered specimens in southern and central Japan as *C. phaeodactyla*, which was previously known as *C. bullosa*. Afterwards, this species was reported from the southern coast of Korea (Oak *et al.* 2002; Boo & Ko 2012).

The basionym of *Colpomenia durvillei* is *Asperococcus durvillei* Bory (Bory de Saint-Vincent 1828) with the type locality of Concepción, Chile. It was transferred to *Colpomenia* by Ramírez (in Ramírez & Rojas 1991; Wynne 1999). It had been called *C. bullosa* in central Chile (Alveal 1970) and *C. phaeodactyla* in central Chile and Peru (Santelices *et al.* 1989; Hoffmann & Santelices 1997; Norris 2010). Recently, Lee *et al.* (2012) recognized *C. durvillei* and confirmed its occurrence in Mexico as well as Chile and Peru based on *cox3* and *rbcL* data and morphological observations. Thus, at present, the distribution of *C. phaeodactyla* is limited to Baja California and Costa Rica in the eastern Pacific and to Korea and Japan in the western Pacific (Lee *et al.* 2012), but the distinctiveness of this species from other

\* Corresponding author (sboo@cnu.ac.kr).

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species in the genus, particularly *C. durvillei*, requires investigation.

During May 2010, collections of *C. phaeodactyla* were made from Mexico and Korea, and we found only small plants of elongate *Colpomenia* that were later confirmed as *C. durvillei* (Lee et al. 2012). Additional specimens were collected in February 2013. Our goals in the present study were to characterise specimens from Korea, Japan and Mexico by describing their morphology and anatomy and by addressing phylogenetic relationships with markers from plastid and mitochondrial markers. As a result of this investigation, we describe *C. wynnei* sp. nov. for specimens from Korea and Japan previously identified as *C. phaeodactyla*.

## MATERIAL AND METHODS

Representative specimens of so-called *Colpomenia phaeodactyla* were collected from intertidal zones on the southern coasts of Korea and Japan and in Puerto Peñasco, the type locality of the species, and Guaymas, Sonora, Mexico. Material for observation was pressed onto herbarium sheets, whereas material used in molecular studies was desiccated in silica gel. Tissues were sectioned using a freezing microtome (FX-801; Yamato Kohki Industrial Co. Ltd, Asaka, Japan). Photographs were taken with a DP-71 camera (Olympus Corp., Tokyo, Japan) attached to a BX-51 microscope (Olympus). Voucher specimens were deposited at the Herbarium of Chungnam National University, Daejeon, Korea (CNUK); the Herbarium of National Institute of Biological Resources, Incheon, Korea (KB); and the Herbarium of Faculty of Science, Hokkaido University, Sapporo, Japan (SAP).

Specimens used for the molecular study are summarised in Table S1. DNA extraction, PCR amplification and sequencing followed Boo et al. (2011b). Primer pairs for the amplification and sequencing of each gene were as follows; for *cox3*, F49–R20 and CAR4A (Boo et al. 2010, et al. 2011a; Kogame et al. 2005) and, for *rbcL*, NDRbcL2–RL960R and RL814F–RLrbcSR (Daugbjerg & Andersen 1997; Lee et al. 2012).

We newly updated 47 *cox3* and eight *rbcL* sequences in the GenBank database of the genus *Colpomenia* and other scytosiphonacean algae via the present study. Including published data for *Colpomenia*, a total of 71 *cox3* and 23 *rbcL* sequences were collated using Se-A1 v.2.0a11 (Rambaut 2002) and aligned visually.

Maximum likelihood (ML) phylogenetic analyses were performed with RAxML v.7.2.8 software (Stamatakis 2006) using the GTRGAMMA model. We used 200 independent tree inferences with the ‘number of run’ option with default optimized SPR rearrangement and 25 distinct rate categories to identify the best tree. Statistical support for each branch was obtained from 1000 bootstrap replications using the same substitution model and RAxML program settings.

Maximum parsimony (MP) trees were constructed for each data set with PAUP\* v.4.0b.10 (Swofford 2002) using a heuristic search algorithm with the following settings: 1000 random sequence additions, tree bisection-reconnection (TBR) branch swapping, MulTrees, all characters unordered

and unweighted and branches with a maximum length of zero collapsed. Bootstrap values for the resulting nodes were assessed using 1000 bootstrapping replicates with 10 random sequence additions, TBR, and MulTrees.

A statistical parsimony network of *cox3* haplotypes was created using TCS v. 1.21 software (Clement et al. 2000).

## RESULTS

### *Colpomenia wynnei* K.M. Lee, R. Riosmena-Rodriguez, K. Kogame & S.M. Boo sp. nov.

Figs 1–7

**DIAGNOSIS:** Thalli consisting of clusters of long, hollow sacs, ranging up to 23 cm in length and 2 cm in width, arising from an adherent colpomenioid base of up to 4 cm in diameter; sacs occasionally undulated or contorted and producing adventitious branches, 3–21 sacs arising from a single base; cortical layer composed of one to two layers of cuboidal cells, 10–15 µm in diameter; medullary layer consisting of three to four layers of spherical to subspherical cells with 15–80 µm in diameter; plurilocular sporangia 30–75 µm long, biseriate, forming dense, extensive sori over the erect sacs; ascocysts shorter than plurilocular sporangia, ovoid to obovoid, 15–20 µm long and 10–15 µm broad; tufts of colorless phaeophycean hairs arising from an outer medullary cell; unilocular sporangia unknown. GenBank accession KF700281 for *cox3*.

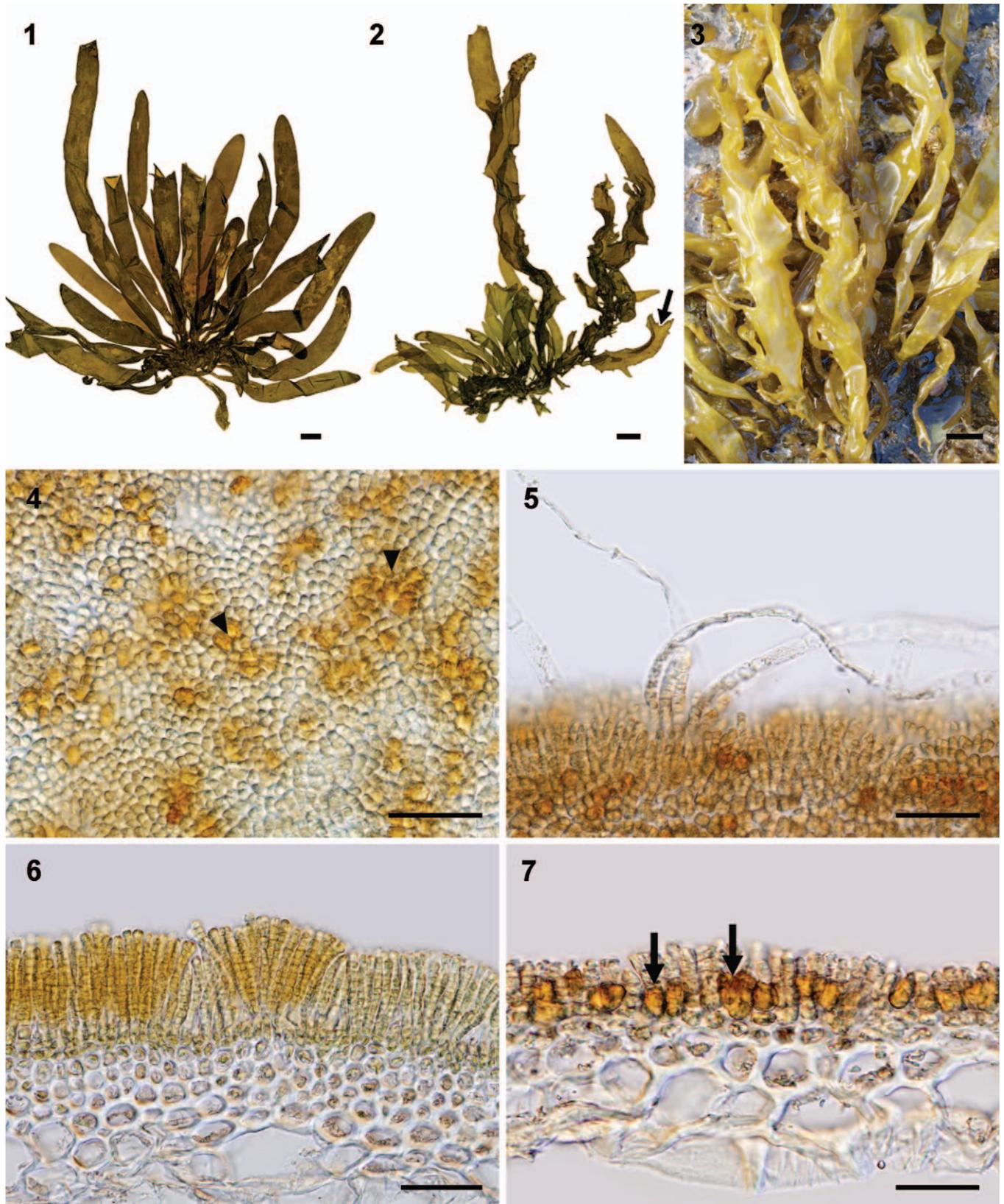
**HOLOTYPE:** CNU33055 deposited in CNUK, Herbarium of Chungnam National University, Daejeon, Korea. Epilithic on rocks covered with muddy sands in the lower intertidal zone off Hoedong, Jindo, Korea (34°25′17.17″N, 126°20′41.23″E). Collected 2 March 2013.

**ISOTYPES:** CNU33049 to 33054 and CNU33056 to 33058 deposited in CNUK, Daejeon, Korea.

**ETYMOLOGY:** The specific epithet ‘wynnei’ is chosen to honor Prof. Michael J. Wynne of University of Michigan, Ann Arbor, USA, for his great taxonomic contributions to the understanding of *Colpomenia* and other marine algae.

**PARATYPES:** CNU5863, 12 January 2005, CNU18315-17, 22 February 2005, CNU40329-38 and CNU40367-76, 8 April 2013, Hoedong, Jindo, Korea; NIBRAL6701, 23 February 2005, Haegeumgang, Geoje, Korea; NIBRAL103848, 9 December 2003, NIBRAL6703, 22 February 2005, NIBRAL6702, 14 January 2006, Sangjokam, Goseong, Korea.

Thalli consisted of 3–21 clusters of elongated and hollow sacs, up to 23 cm long and 2 cm broad, arising from an adherent colpomenioid base, occasionally undulated or contorted and producing adventitious branches (Figs 1–3). Cortical cells and ascocysts on the surface were polygonal and irregularly arranged (Fig. 4). Phaeophycean hairs were in tufts, colorless, arising from outer medullary cells (Fig. 5). Cortical layer was one to two cells thick, and cortical cells were cuboidal, 10–15 µm in diameter (Fig. 6). Medullary layer consisted of three to four layers of spherical to subspherical cells, 15–80 µm in diameter (Fig. 7). Plurilocular sporangia were biseriate, 30–75 µm long, and they formed dense and extensive sori over the erect sacs (Fig. 6). Ascocysts were ovoid to obovoid, 15–20 µm long and 10–15 µm broad, and shorter than the plurilocular



Figs 1–7. *Colpomenia wynnei* sp. nov.

sporangia (Fig. 7). Unilocular sporangia were not observed.

### Phylogeny of *cox3* and *rbcL*

A 623-nucleotide portion of *cox3* was aligned for all specimens including 30 from *Colpomenia wynnei* [17 from Korea and eight from Japan in the present study and eight in GenBank (HQ83371-5) under the name of *C. phaeodactyla*; see Table S1] analysed here. The tree produced by the ML analysis was based on the 71 *cox3* sequences (Fig. 8). Variable sites occurred at 282 positions (45.3%), and 222 positions (35.6%) were parsimoniously informative. It was found that *C. wynnei* from Korea and Japan differed by 45–57 base pairs (bp; 7.2–9.2%) from *C. bullosa* and by 49–56 bp (7.9–9.0%) from *C. durvillei* from Chile and Mexico. There was a 29–38 bp (4.7–6.1%) difference between *C. bullosa* and *C. durvillei*. One sequence from Katsura, Japan (SAP114608), was highly diverged from other sequences of *C. wynnei* by 16 bp (2.6%). Pairwise divergence within *C. wynnei* (not Katsura specimens) was in the range of up to 4 bp (0.6%). In the *cox3* tree (Fig. 8), *C. wynnei* formed a monophyletic group with strong support values (100% for both ML/MP). *Colpomenia wynnei* was sister to the clade of *C. bullosa* and *C. durvillei* (97/96% for ML/MP). The family Scytosiphonaceae, including 10 species of *Colpomenia* and other scytosiphonacean algae, was supported in the *cox3* tree (83/86% for ML/MP).

A 1085-nucleotide portion of the *rbcL* gene was compared across 23 sequences from eight species of *Colpomenia* and *Scytosiphon lomentaria* (Lyngbye) Link as the outgroup. Variable sites occurred at 96 positions (8.8%), and 52 positions (4.8%) were parsimoniously informative. *Colpomenia wynnei* differed by 4–6 bp (0.4–0.6%) from *C. bullosa* and *C. durvillei*, respectively. There was a difference of 2–3 bp (0.2–0.3%) between *C. bullosa* and *C. durvillei*. The *rbcL* sequences of *C. wynnei* were identical or differed up to 1 bp (0.1%). In the *rbcL* tree (Fig. 9), *C. wynnei*, *C. bullosa*, and *C. durvillei* formed a clade, but there was no resolution of the phylogenetic relationships among those three species.

## DISCUSSION

This study arose from repeated field collections of elongate *Colpomenia* populations, suggesting a distinct species from what is currently known in Korea and Japan. We describe a new *Colpomenia* species, *C. wynnei*, on the basis of comprehensive morphological observation and sequences of *cox3* and *rbcL*. Morphologically, *C. wynnei* is characterized by its finger-like sacs with adventitious branchlets when mature, much contorted, and the height of ascocysts shorter

than the plurilocular sporangia. All phylogenetic analyses of *cox3* and *rbcL* sequences consistently demonstrated the distinctness of *C. wynnei* from congeners. However, *C. wynnei* consistently formed a clade with *C. bullosa* and *C. durvillei* in both *cox3* and *rbcL* sequences. *Colpomenia wynnei* is dominant on the shore, covered with muddy sand on intertidal rock during winter to early spring. It is distributed in southern Korea and in central and southern Japan (see Fig. S1).

A morphological comparison of elongate species within *Colpomenia* is given in Table 1.

*Colpomenia bullosa*, described on the basis of specimens from Pacific Grove, California, USA, with the basionym *Scytosiphon bullosus* D.A. Saunders (Saunders 1898; Yamada 1948), is characterised usually by a solitary condition and a firmer texture of the balloon-like sacs. The cosmopolitan distribution of *C. bullosa* in Korea, Japan, Australia, New Zealand, and USA (Alaska to California) was confirmed by *cox3*, *rbcL* or ITS data (Cho *et al.* 2006; Kain *et al.* 2010; Lee *et al.* 2012). The erect phase, presumably introduced, was found in Northland, New Zealand, by Parsons (1982); whereas, only the crustose phase has been found in eastern Australia (Kain *et al.* 2010). Additional sampling of crustose brown algae may extend its distribution to temperate waters in central America or Europe.

*Colpomenia durvillei* is distinguished by erect, elongate thalli arising from a wide colpomenioid base, up to eight layers of cortical and medullary cells, and plurilocular sporangia with up to 18 locules (Ramírez & Rosas 1991; Lee *et al.* 2012). It is distributed from Baja California to central Chile (Lee *et al.* 2012). Compared to the smooth and extended sacs of *C. durvillei* in Mexico (as *C. phaeodactyla*; Wynne & Norris 1976), *C. wynnei* from northeast Asia is occasionally undulated or contorted with adventitious branches, as seen in previous studies (Oak *et al.* 2002; Boo & Ko 2012). Our fresh collections of *C. durvillei* from Puerto Peñasco, the type locality of *C. phaeodactyla*, and Guaymas, Mexico, correspond well in their morphological features with Chilean specimens, as described by Ramírez & Rojas (1991) and Lee *et al.* (2012). On the basis of both *cox3* and *rbcL* sequences, all specimens of *C. durvillei* from Mexico and Chile formed a well-supported clade (see Figs 8, 9). Based on repeated collections and observations of herbarium specimens including the isotype in MICH, we conclude that *Colpomenia phaeodactyla* from Baja California is the same as *C. durvillei* that we recognized again in Mexico as well as Chile and Peru (Lee *et al.* 2012), as in previous studies by Acleto (1973) and Ramírez & Rojas (1991). Indeed, both *cox3* and *rbcL* data confirmed that *C. phaeodactyla* by Wynne & Norris is identical to *C. durvillei*.

← **Fig. 1.** Image of the holotype specimen (CNU33055), a gametophytic thallus from Heodong, Jindo, Korea. Scale bar = 1 cm.

**Fig. 2.** Specimen (NIBRAL103848) showing erect sacs with adventitious branchlets (arrow) collected in Sangjokam, Goseong, Korea (9 December 2003). Scale bar = 1 cm.

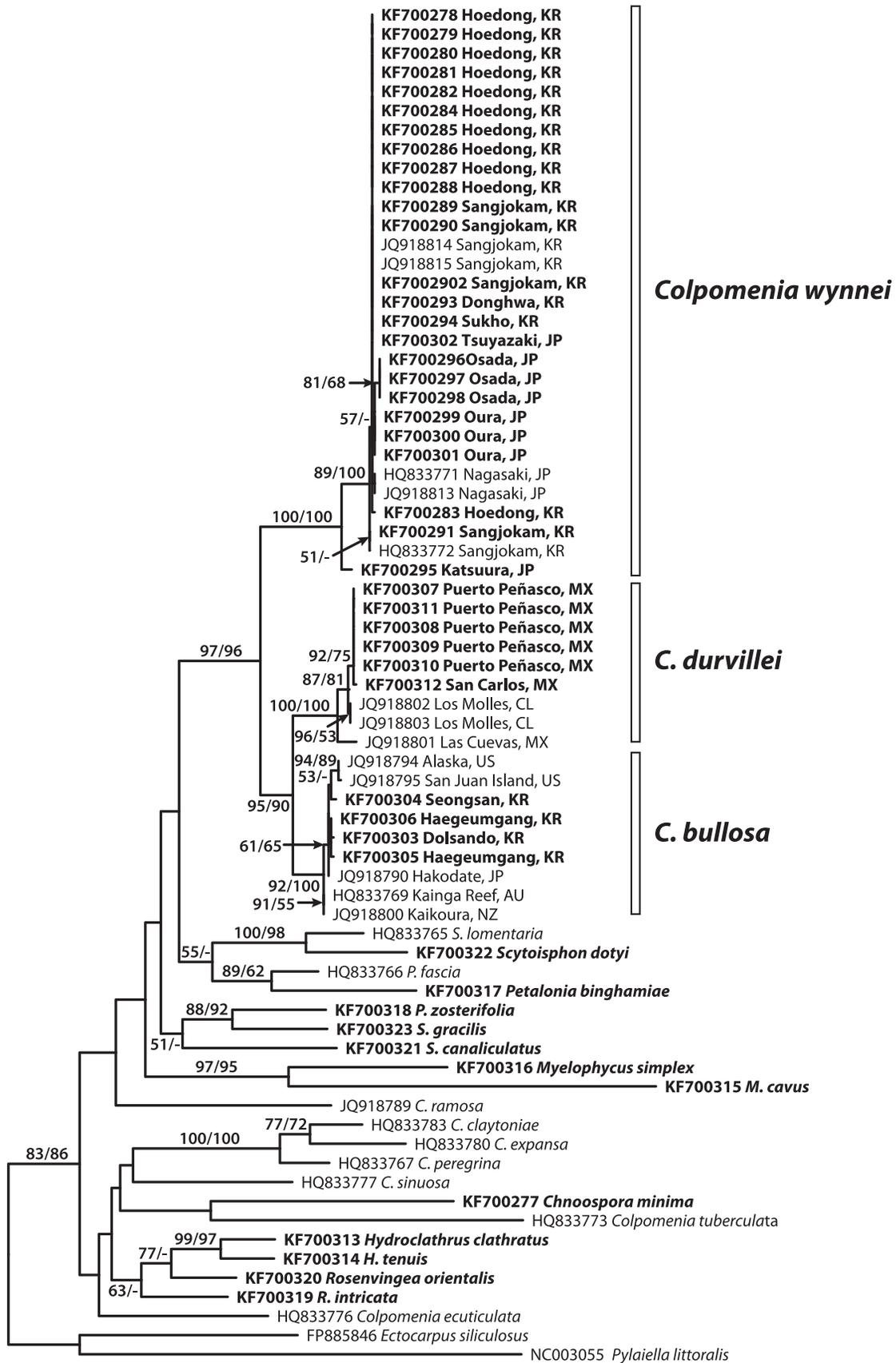
**Fig. 3.** A thallus growing on the rock in the intertidal zone. Scale bar = 1 cm.

**Fig. 4.** Cortical cells and ascocysts (arrowheads) in surface view. Scale bar = 50 µm.

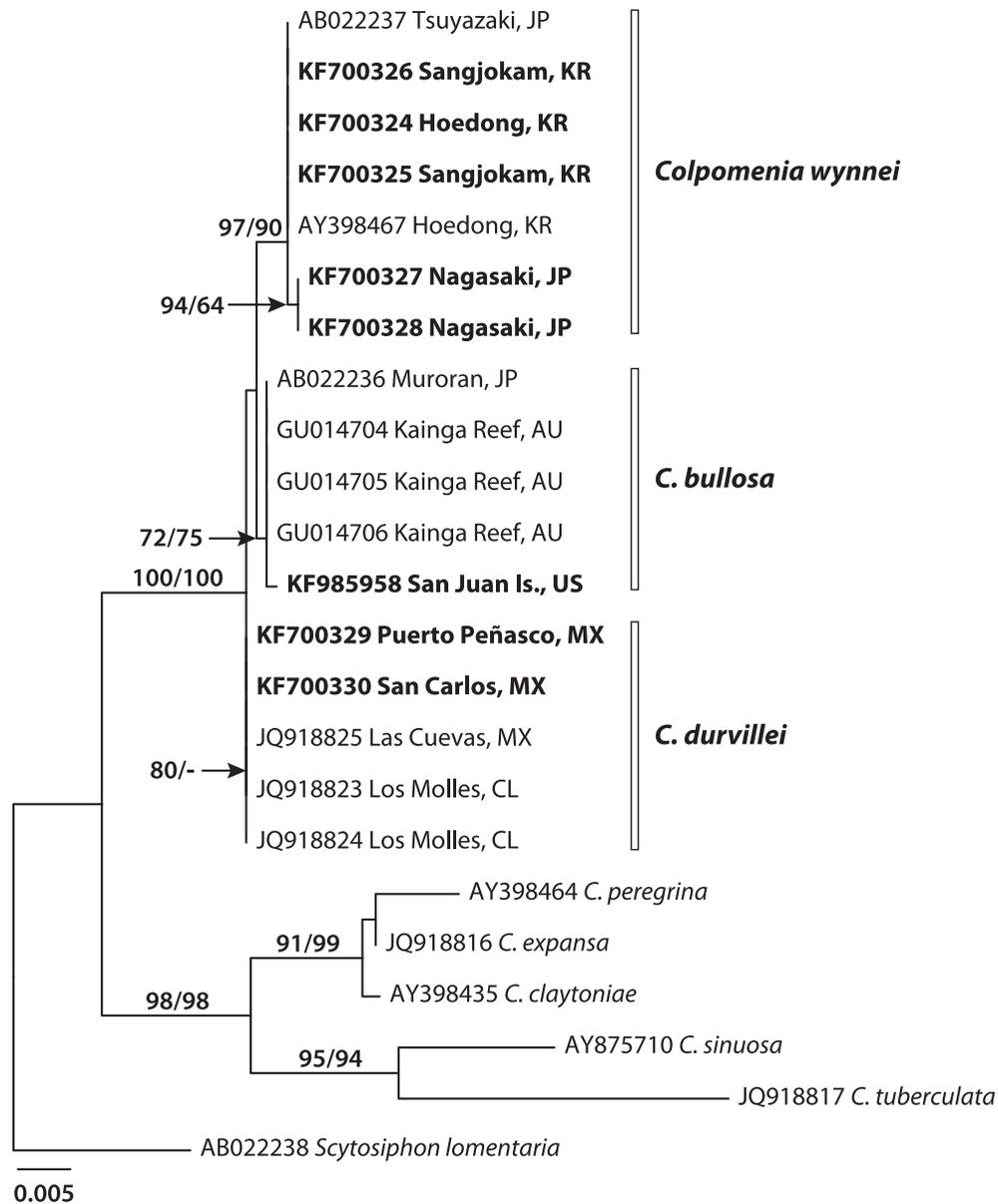
**Fig. 5.** Tufts of phaeophyceean hair cells. Scale bar = 50 µm.

**Fig. 6.** Cross section of thallus with plurilocular sporangia. Scale bar = 50 µm.

**Fig. 7.** Cross section of ascocysts (arrows). Scale bar = 20 µm.



0.05



**Fig. 9.** Maximum likelihood tree based on *rbcL* sequences in the genus *Colpomenia* (*C.*) and *Scytosiphon lomentaria* using the GTRGAMMA evolution model [ $-\ln L = 2183.09$ ; base frequencies  $\pi_A = 0.294129$ ,  $\pi_C = 0.161130$ ,  $\pi_G = 0.218032$ ,  $\pi_T = 0.326708$ ; shape parameter ( $\alpha$ ) = 0.020013]. The numbers above or below the branches are bootstrap values from the maximum parsimony and maximum likelihood (MP/ML). Sequences generated in the present study are in bold.

Based on above results, we update the taxonomy of *C. durvillei* as follows: *Colpomenia durvillei* (Bory) M.E. Ramírez in Ramírez & Rojas 1991 [in Bol. Mus. Nac. Hist. Nat. (Santiago de Chile) 42: 17]. Lectotype: d'Urville, PC Herb. Bornet-Thuret, TA 5284 (see illustration of Type at fig. 10 in Ramírez & Rojas 1991), Concepción, Chile. Basionym: *Asperococcus durvillei* Bory in Duperrey 1828

(in Voy. Coquille 200, pl. 11, fig. 3). Taxonomic (heterotypic) synonym: *Colpomenia phaeodactyla* M.J. Wynne & J.N. Norris 1976 (Smithson. Contrib. Bot. 35: 6, figs 4, 5, 11c). Holotype: J.N. Norris 3629 (US)!, 22 January 1973, Playa Estacion, Puerto Peñasco, Sonora, Mexico.

Network analysis of 30 *C. wynnei* specimens revealed seven *cox3* haplotypes (Fig. S2). Interestingly, we found

**Fig. 8.** Maximum likelihood tree based on *cox3* sequences of the Scytosiphonaceae using the GTRGAMMA evolution model [ $-\ln L = 5802.29$ ; base frequencies  $\pi_A = 0.217799$ ,  $\pi_C = 0.141699$ ,  $\pi_G = 0.223061$ ,  $\pi_T = 0.417441$ ; shape parameter ( $\alpha$ ) = 0.252955]. The numbers above or near the branches are bootstrap values from the maximum parsimony and maximum likelihood (MP/ML). Sequences generated in the present study are in bold.

**Table 1.** Morphological comparisons of elongate species of *Colpomenia*.

	<i>C. wynnei</i> sp. nov.	<i>C. bullosa</i>	<i>C. durvillei</i>
Thallus shape	finger-like, arising from a colpomenioid base of up to 4 cm in diameter, undulated or contorted sacs with adventitious branchlets	finger-like, branched at the colpomenioid base of up to 3 cm in diameter	finger-like, branched at the colpomenioid base of up to 3 cm in diameter
Thallus size	up to 23 cm tall, about 2 cm in width	usually up to 30 cm in length, 3 cm in width	up to 15 cm in length, 0.8 cm in width
Cortex	1–2 layers of cuboidal cells	2–3 layers of angular cells	1–3 layers of angular cells
Medullary structure	3–4 layers of spherical to subspherical cells	3–5 layers of cuboidal cells	up to 5 layers of cuboidal cells
Paraphyse	shorter than as plurilocular sporangia	1–2 celled, same height or longer than plurilocular sporangia	rare, same height or longer than plurilocular sporangia
Phaeophycean hairs	arising from an outer medullary cell	hair pits scattered	occur occasionally
Plurilocular sporangia	biseriate, 10–16 locules	uni- to biseriate, 12–15 locules	uni- to biseriate, about 18 locules
Habitat	epilithic, intertidal	epilithic, intertidal	epilithic, intertidal, semiexposed
Type locality	Hoedong, Jindo, Korea	Pacific Grove, California, USA	Concepcion, Chile
Geographical distribution	southern Korea, Japan	temperate waters of the Pacific	Sonora, Mexico, Central to northern Chile
References	This study	Saunders (1898); Lee <i>et al.</i> (2012); this study	Lee <i>et al.</i> (2012); this study

one haplotype collected in Katsuura, Japan, to be highly divergent with 13 missing haplotypes (the sequence divergence up to 2.6%) from others. This may indicate the description of a new species based on specimen from Katsuura after enough sampling, but this is beyond the present study. The genetic diversity of *C. wynnei* was lower than those of other *Colpomenia* species (up to 4.6% in *C. claytoniae*, 3.1% in *C. durvillei*, 3.7% in *C. peregrina* and 7.4% in *C. sinuosa*; Boo *et al.* 2011b; Lee *et al.* 2012, 2013, 2014, b). Its low genetic diversity is due to its limited distribution in northeast Asian waters, compared to ubiquitous distribution of other species over marine ecoregions.

Despite the fact that phylogenetic relationships within the Scytosiphonaceae have been investigated using multiple gene sequences (e.g. nuclear SSU rDNA, LSU rDNA and ITS, and plastid *rbcL*, RuBisCo spacer and *psaA*), from this and previous studies, it is obvious that the polyphyly and paraphyly present among scytosiphonacean genera has yet to be resolved (Kogame *et al.* 1999; Cho *et al.* 2006; Kain *et al.* 2010; Boo *et al.* 2011b; Kogame *et al.* 2011). Our mitochondrial *cox3* phylogeny showed a well-supported family (83/86% in ML and MP) consisting of the genera *Chnoospora*, *Colpomenia*, *Hydroclathrus*, *Myelophycus*, *Petalonia*, *Rosenvingea* and *Scytosiphon*. Only *Hydroclathrus* and *Myelophycus* are strongly supported, as in previous studies (Cho *et al.* 2003, 2006). However, despite adding most of species (10 out of 12; except *C. mollis* Taylor and *C. nainativensis* Durairatnam), the monophyly of *Colpomenia* was not resolved. Although several species of *Hydroclathrus*, *Iyengarina*, *Jolyana* and *Rosenvingea* in the Scytosiphonaceae have not yet been included in molecular analyses, a taxonomic revision of the family should be carried out with a broad perspective with as many taxa as possible, and the results of such a study will likely result in significant nomenclatural changes. Cryptic diversities were shown in

*C. sinuosa*, *Scytosiphon lomentaria* (Lyngbye) Link and *Petalonia fascia* (O.F. Müller) Kuntze that probably represent multiple species (Cho *et al.* 2007; Kogame *et al.* 2011; Lee *et al.* 2013, 2014).

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#### SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at <http://dx.doi.org/10.2216/13-232.1.s1>.

#### REFERENCES

- ACLETO C. 1973. Les algas marines del Perú. *Sociedad Peruana de Botánica* 6: 1–64.  
 ALVEAL K. 1970. Estudios ficecológicos en la región costera de Valparaíso. *Revista de Biología Marina Valparaíso* 14: 7–88.

- BOO G.H., LINDSTROM S.C., KLOCHKOVA N.G., YOTSUKURA N., YANG E.C., KIM H.G., WAALAND J.R., CHO G.Y., MILLER K.A. & BOO S.M. 2011a. Taxonomy and biogeography of *Agarum* and *Thalassiophyllum* (Laminariales, Phaeophyceae) based on sequences of nuclear, mitochondrial, and plastid markers. *Taxon* 60: 831–840.
- BOO S.M. & KO Y.D. 2012. *Marine plants from Korea*. Korean Institute of Ocean Sciences & Technology, Marine & Extreme Genome Research Centre Program, Seoul. 233 pp.
- BOO S.M., KIM H.S., SHIN W., BOO G.H., CHO S.M., JO B.Y., KIM J.H., YANG E.C., SIVER P.A., WOLFE A.P., BHATTACHARYA D., ANDERSEN R.A. & YOON H.S. 2010. Complex phylogeographic patterns in the freshwater alga *Synura* provide new insights on ubiquity versus endemism in microbial eukaryotes. *Molecular Ecology* 19: 4328–4338.
- BOO S.M., LEE K.M., CHO G.Y. & NELSON W. 2011b. *Colpomenia claytoniae* sp. nov. (Scytosiphonaceae, Phaeophyceae) based on morphology and mitochondrial *cox3* sequences. *Botanica Marina* 54: 159–167.
- BORY DE ST. VINCENT J.B. 1828. Botanique, Cryptogamie. In *Voyage autour de monde, exécuté par ordre du Roi, sur la corvette de Sa Majesté, la Coquille, pendant les années 1822, 1823, 1824 et 1825* (Ed. by L.I. Duperrey), pp. 97–200. Bertrand, Paris.
- CHO G.Y., BOO S.M., NELSON W. & CLAYTON M.N. 2005. Genealogical partitioning and phylogeography of *Colpomenia peregrina* (Scytosiphonaceae, Phaeophyceae) based on plastid *rbcL* and nuclear ribosomal DNA internal transcribed spacer sequences. *Phycologia* 44: 103–111.
- CHO G.Y., KOGAME K. & BOO S.M. 2006. Molecular phylogeny of the family Scytosiphonaceae (Phaeophyceae). *Algae* 21: 175–183.
- CHO G.Y., KOGAME K., KAWAI H. & BOO S.M. 2007. Genetic diversity of *Scytosiphon lomentaria* (Scytosiphonaceae, Phaeophyceae) from the Pacific and Europe based on RuBisCo large subunit and spacer, and ITS nrDNA sequences. *Phycologia* 46: 657–665.
- CHO T.O., CHO G.Y., YOON H.S., LEE W.J. & BOO S.M. 2003. New record of *Myelophycus cavus* (Scytosiphonaceae, Phaeophyceae) in Korea and taxonomic position of the genus on the basis of a *rbcL* phylogeny. *Nova Hedwigia* 76: 381–397.
- CLEMENT M.D., POSADA D. & CRANDALL K.A. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657–1669.
- DAUGBJERG N. & ANDERSEN R.A. 1997. Phylogenetic analyses of the *rbcL* sequences from haptophytes and heterokont algae suggest their chloroplasts are unrelated. *Molecular Biology and Evolution* 14: 1242–1251.
- GUIRY M.D. & GUIRY G.M. 2013. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. <http://www.algaebase.org>; searched on 25 May 2013.
- HOFFMANN A. & SANTELICES B. 1997. *Flora Marina de Chile Central (Marine Flora of Central Chile)*. Ediciones Universidad Católica de Chile, Santiago. 434 pp.
- KAIN (JONES) J.M., BUCHANAN J., BOO S.M. & LEE K.M. 2010. *Colpomenia bullosa* crust masquerading as *Ralfsia verrucosa* (Phaeophyceae) in southern Australia. *Phycologia* 49: 617–627.
- KOGAME K., Horiguchi T. & MASUDA M. 1999. Phylogeny of the order Scytosiphonales (Phaeophyceae) based on DNA sequences of *rbcL*, partial *rbcS*, and partial LSU nrDNA. *Phycologia* 38: 496–502.
- KOGAME K., UWAI S., SHIMADA S. & MASUDA M. 2005. A study of sexual and asexual populations of *Scytosiphon lomentaria* (Scytosiphonaceae, Phaeophyceae) in Hokkaido, northern Japan, using molecular markers. *European Journal of Phycology* 40: 313–322.
- KOGAME K., KURIHARA A., CHO G.Y., LEE K.M., SHERWOOD A.R. & BOO S.M. 2011. *Petalonia tatewakii* sp. nov. (Scytosiphonaceae, Phaeophyceae) from the Hawaiian Islands. *Phycologia* 50: 563–573.
- LEE K.M., MANSILLA A., NELSON W.A. & BOO S.M. 2012. *Colpomenia durvillei* (Scytosiphonaceae, Phaeophyceae): its distribution and relationships with other elongate species of the genus. *Botanica Marina* 55: 367–375.
- LEE K.M., BOO S.M., KAIN (JONES) J.M. & SHERWOOD A.R. 2013a. Cryptic diversity and biogeography of the widespread brown alga *Colpomenia sinuosa* (Scytosiphonaceae, Phaeophyceae). *Botanica Marina* 56: 15–25.
- LEE K.M., BOO G.H., COYER J.A., NELSON W.A., MILLER K.A. & BOO S.M. 2014. Distribution patterns and introduction pathways of the cosmopolitan brown alga *Colpomenia peregrina* using mt *cox3* and *atp6* sequences. *Journal of Applied Phycology* 26: 491–504.
- NORRIS J.N. 2010. Marine algae of the northern Gulf of California: Chlorophyta and Phaeophyceae. *Smithsonian Contributions to Botany* 94: 1–276.
- OAK J.H., KEUM Y.S., HWANG M.S. & OH Y.S. 2002. New records of marine algae from Korea I. *Algae* 17: 145–151.
- PARSONS M.J. 1982. *Colpomenia* (Endlicher) Derbès et Solier (Phaeophyta) in New Zealand. *New Zealand Journal of Botany* 20: 289–301.
- RAMBAUT A. 2002. *SeAl, v.2.0*. Institute of Evolutionary Biology, Ashworth Laboratories, Edinburgh.
- RAMIREZ M.E. & ROJAS V.G. 1991. El genero *Colpomenia* (F.C. Mertens ex Roth) Derbès et Solier (Phaeophyceae), en Chile. *Boletín del Museo Nacional de Historia Natural, Chile* 42: 11–24.
- SANTELICES B., RAMIREZ M.E. & ABBOTT I.A. 1989. A new species and new records of marine algae from Chile. *British Phycological Journal* 24: 73–82.
- SAUNDERS DE A. 1898. Phycological memoirs. *Proceedings of the California Academy of Sciences, Third Series, Botany* 1: 147–168.
- STAMATAKIS A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- SWOFFORD D.L. 2002. *PAUP\*: phylogenetic analysis using parsimony (\*and other methods)*. Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- WEST J.A., ZUCCARELLO G.C., PEDROCHE, F.F. & DE GOËR, S.L. 2010. *Rosenvingea orientalis* (Scytosiphonaceae, Phaeophyceae) from Chiapas, Mexico: life history in culture and molecular phylogeny. *Algae* 25: 187–195.
- WYNNE M.J. 1972. Studies on the life forms in nature and in culture of selected brown algae. In *Contributions to the systematics of benthic algae of the North Pacific* (Ed. by M. Kurogi and I.A. Abbott), pp. 133–145. Japanese Society of Phycology, Kobe.
- WYNNE M.J. 1999. Concerning the names of two phaeophycean algae: *Colpomenia durvillei* (Bory de Saint-Vincent) M.E. Ramirez and *Utriculidium durvillei* Skottsberg. *Cryptogamie Algologie* 20: 289–293.
- WYNNE M.J. & NORRIS J.N. 1976. The genus *Colpomenia* Derbès et Solier (Phaeophyta) in the Gulf of California. *Smithsonian Contributions to Botany* 35: 1–18.
- YAMADA Y. 1948. *Marine algae*. In *Icones of the marine animals and plants of Hokkaido. No.1* (Ed. By Y. Yamada & S. Kinoshita), pp. 1–18. Hokkaido Fisheries Scientific Institution, Hokkaido.

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