



***Encephalophycus*, gen. nov., a new brown algal genus based upon *Colpomenia tuberculata*
D.A.Saunders (*Scytosiphonaceae*, *Phaeophyceae*)**

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The systematics and molecular phylogenetic relationships of the representatives of the brown algal family *Scytosiphonaceae* Ardissonne & Straforello (*Ectocarpales*, *Phaeophyceae*), especially those found in warm waters, are problematic and confused. Recent works on scytosiphonacean taxa combining information derived from morphological, anatomical, life history, and molecular phylogenetic studies have allowed taxonomic boundaries to be clarified (e.g. McDevit & Saunders 2017, Santiañez & Kogame 2017, 2019) and the descriptions of new genera (McDevit & Saunders 2017, Santiañez & al. 2018a, 2018b, Santiañez & Kogame 2022) and species (Lee & al. 2014a, Matsumoto & al. 2014, McDevit & Saunders 2017, Santiañez & al. 2018a, 2018b, Huisman & al. 2018, Hoshino & al. 2020). Despite renewed and continued efforts to address the incongruencies between the genus-to-species-level taxonomies and their molecular phylogenies, resolving the taxonomy and relationships of several warm water taxa—especially members of the genera *Rosenvingea* Børgesen (1914) and *Colpomenia* (Endlicher) Derbès & Solier (1851)—are still challenging. Between these genera, *Colpomenia* is relatively well-studied, and the taxonomy and phylogenetic relationships have been known to be among the most complicated, especially with the existence of cryptic species within the type *C. sinuosa* (Mertens ex Roth) Derbès & Solier (1851) (Lee & al. 2013).

Traditionally, the genus *Colpomenia* included species with hollow thalli that are sac-like (e.g. *C. sinuosa*), branching [e.g. *Colpomenia ramosa* W.R.Taylor (1945)], and finger-like [e.g., *Colpomenia bullosa* (D.A.Saunders) Yamada (1948)]. Recently, all known finger-like *Colpomenia* species [viz. *C. bullosa*, *C. durvillei* (Bory) M.E.Ramírez in Ramírez & Rojas (1991), and *C. wynnei* K.M.Lee, R.Riosmena-Rodríguez, Kogame & S.M.Boo (2014a)] have been transferred to the new genus *Dactylosiphon* Santiañez, K.M.Lee, S.M.Boo & Kogame in Santiañez & al. (2018b) based upon morphological, anatomical, life history, and molecular phylogenetic criteria. As such, the genus *Colpomenia* presently includes 10 taxonomically accepted species (Guiry & Guiry 2022): *C. claytoniae* S.M.Boo, K.M.Lee, G.Y.Cho & W.Nelson (2011, as ‘*C. claytonii*’), *C. ecuticulata* M.J.Parsons (1982), *C. expansa* (D.A.Saunders) Y.-P.Lee (2008), “*C. hasanainii*” Aisha & M.Shameel, *nom. inval.* (Aisha & M.Shameel 2012), *C. mollis* W.R.Taylor (1945), *C. nainativensis* Durairatnam (1962), *C. peregrina* Sauvageau (1927), *C. ramosa*, *C. sinuosa*, and *C. tuberculata* D.A.Saunders (1898). Of these, *C. tuberculata* is distinct in terms of both its morpho-anatomy and phylogenetic position.

Colpomenia tuberculata was first described by De Alton Saunders (1870–1940) based on a material from “near San Pedro, California”, USA (Saunders 1898: 164, pl. XXXII: figs 1–3). It was distinguished from other *Colpomenia* species in having coriaceous, rounded, deeply convoluted, wrinkled, and folded thalli (“brain-like masses”) with blunt tubercles covering the surfaces, especially in mature plants. The species also possesses 3–5 layers of cortical cells and 5–8 layers of larger medullary cells, as compared to *C. sinuosa* with 1–2 layers of pigmented cortical cells and 2 layers of large medullary cells. Saunders (1898) also noted that the tissue of *C. tuberculata* has a firmer texture and is much thicker than that of *C. sinuosa*. Subsequent observations on *C. not tuberculata* collected along the Pacific coast of North and South America consistently reported these distinguishing characters (e.g., Wynne & Norris 1976, Ramírez & Rojas 1991, Norris 2010, Quiroz-González & al. 2020), with the latter authors providing a summary of the morpho-



anatomical features of *C. tuberculata*. Accordingly, *C. tuberculata* has 3–7 cortical cell layers and 4–8 medullary cells layers (table 1, Quiroz-González & al. 2020). The coriaceous, tuberculate, and brain-like thallus, along with the rigid and thicker thallus walls composed of at least 3 layers of cortical cells and up to 8 layers of medullary cells of *C. tuberculata* is distinct from other *Colpomenia* species. While *C. sinuosa* is known to have a convoluted thallus, its surface is typically smooth and lacks protuberances. In cross-section, the thallus of *C. sinuosa* possesses only 1–2 layers of cortical cells (e.g. Saunders 1898, Wynne & Norris 1976, Parsons 1982, Boo & al. 2011). Similarly, other *Colpomenia* species have smooth surfaces and possess only 1–2 (–3) cortical cell layers and 3–6 (–7) layers of medullary cells (Wynne & Norris 1976, Parsons 1982, Boo & al. 2011, Santiañez & al. 2018b). These morpho-anatomical differences between *C. tuberculata* and other *Colpomenia* species suggest that the generic assignment of *C. tuberculata* may be incorrect. This is unsurprising in the *Scytosiphonaceae* as several taxa were incorrectly classified in several broadly circumscribed genera. As mentioned above, several new genera have been proposed in the *Scytosiphonaceae* to resolve these issues: 1) *Planosiphon* McDevit & G.W.Saunders (2017) to accommodate *Scytosiphon* and *Petalonia* species with compressed to flattened and non-constricted thalli that are hollow to partially hollow (McDevit & Saunders 2017, Santiañez & Kogame 2017); 2) *Dactylosiphon* Santiañez & al. to include finger-like species of *Colpomenia*; 3) *Pseudochnoospora* Santiañez, G.Y.Cho & Kogame (in Santiañez & al. 2018b) for *Chnoospora* which possesses thalli that are solid, decumbent, and entangled; and, more recently, 4) *Manzaea* Santiañez & Kogame (2022), for *Hydroclathrus* species that possesses a very thin, fibrous, and inter-adhesive thallus with thick-walled medullary cells.

Several molecular phylogenetic studies on *Colpomenia* species (Boo & al. 2011, Lee & al. 2012, 2013, 2014) and the family *Scytosiphonaceae* (Santiañez & al. 2018a, 2018b, 2020) have repeatedly shown that *C. tuberculata* is segregated from other *Colpomenia*. In *cox3* gene-based molecular phylogenetic trees, *C. tuberculata* formed a highly supported clade with the branching *C. ramosa* (Lee & al. 2012: fig. 1, Lee & al. 2014: fig.1, Santiañez & al. 2018b: fig. 1, Santiañez & Kogame 2019). In our recent molecular phylogenetic study on the relatively understudied scytosiphonacean genus *Iyengaria* Børgesen (1939) based on *rbcL* gene sequences, *C. tuberculata* formed a clade with *C. sinuosa* and *Iyengaria stellata* (Børgesen) Børgesen (1939) (the type and only species of the genus; Santiañez & al. 2020). This relationship is similarly observed in the molecular phylogenetic tree I newly generated based on GenBank-available *rbcL* sequences of scytosiphonacean taxa (Fig. 1). However, *C. tuberculata* was shown to be more closely related to *I. stellata* with moderate to high support (Posterior Probability: 0.99, Bootstrap Percentage: 87%) than to *C. sinuosa* (Santiañez & al. 2020). The close phylogenetic relationship of *I. stellata* and *C. tuberculata* is also reflected in the similar nature of their thalli. Additionally, I computed for the sequence divergences (*P*-distances) of members of the family *Scytosiphonaceae* based on GenBank-available *rbcL* sequences using MEGA v6 (Tamura & al. 2011). Sequence divergence between *C. tuberculata* and its closest relative *I. stellata* was 0.30; those with other *Colpomenia* species were between 0.040 to 0.046. Meanwhile, similar, or relatively higher sequence divergences, were observed between *C. tuberculata* and *Rosenvingea* (0.041–0.050), *Pseudochnoospora* (0.050), *Chnoospora* (0.62), and the recently described *Manzaea* (0.046). Based on *rbcL* sequences, the known range of genus-level divergences among brown algae were from 0.010 to 0.038 (Kawai & Hanyuda 2021). Taking into consideration the high sequence divergence and its phylogenetic position, and considering its distinct morphology (thick, coriaceous, and tuberculate thallus) and anatomy (3–7 layers and 4–8 layers of cortical and medullary cells, respectively), I believe *C. tuberculata* should be segregated from the genus *Colpomenia*. As such, I propose the recognition of a new genus as follows:

***Encephalophycus* Santiañez, *gen. nov.***

Description: Thallus hollow, rigid, and rounded to irregularly shaped and compressed; appearing brain-like due to deeply convoluted and folded surfaces; coriaceous surface possessing blunt protuberances (tubercles); walls composed of 3–7 layers of small cortical cells and 4–8 layers of larger, colourless medullary cells. Unilocular sporangium unknown; plurilocular sporangia uniseriate, sometimes with biseriate portions. Paraphyses present. Life history unknown.

Etymology: *encephalos*, brain and *phykos*, Greek, alga, seaweed; referring to the original description of “brain-like masses” of the type. While *phykos* is a Greek neuter noun, it is treated as masculine in accordance with botanical tradition (ICN Art. 62c; Turland & al. 2018).

Type: ***Encephalophycus tuberculatus*** (D.A.Saunders) Santiañez, *comb. nov.*

Basionym: *Colpomenia tuberculata* D.A.Saunders *Proceedings of the California Academy of Sciences. Series 3, Botany 1*: 164, pl. XXXII: figs 1–3, 1898.

Synonyms: *Colpomenia sinuosa* f. *tuberculata* (D.A.Saunders) Setchell & N.L. Gardner (1903); *Colpomenia sinuosa* f. *expansissima* Setchell & N.L. Gardner (1924).

Distribution: Warm waters of eastern Pacific Ocean. North America: Southern California to Mexico; South America: Ecuador (Galapagos Islands), Costa Rica, Peru, Chile (Wynne & Norris 1976, Ramírez & Rojas 1991, Miller 2022).

Remarks: *Encephalophycus* is similar to *C. ramosa* and *I. stellata* in possessing a crisp to coriaceous thalli but differs from them in lacking branches that are inter-adhesive (*C. ramosa*) or free (*I. stellata*). Additionally, *Encephalophycus* is different from *Iyengaria* in the number of cell layers in its cortex and medulla. *Encephalophycus* has 3–7 cortical and 4–8 medullary cell layers, while *Iyengaria* is known to possess 1–2 cortical and 6–8 medullary cell layers (Santiañez & al. 2020). Lee & al. (2013) illustrated some *C. sinuosa* morphotypes showing some protuberances. However, these do not have the deeply convoluted and folded surfaces of *E. tuberculatus*. Additionally, Lee & al. (2013) mentioned that all their *C. sinuosa* specimens have morpho-anatomical characters that agree well with the description of the species of Wynne & Norris (1976), Parsons (1982), and Boo & al. (2011), among others. *Encephalophycus* is usually epilithic, sometimes occurring as seaweed epiphyte, growing in mid to lower intertidal areas exposed to waves in cooler tropical to warmer temperate seas (Wynne & Norris 1976, Ramírez & Rojas 1991, Norris 2010, Quiroz-González & al. 2020).

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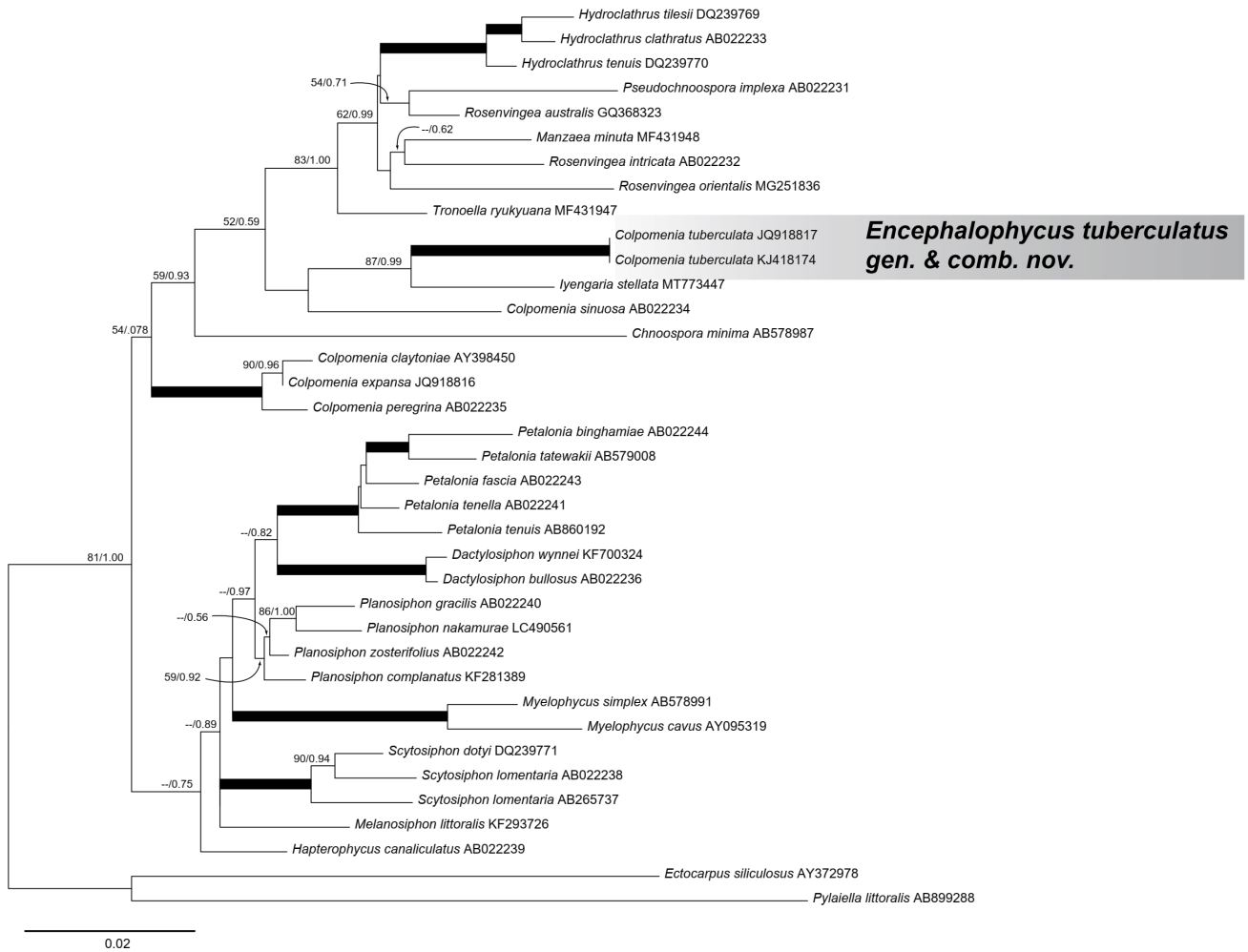


Fig. 1. Molecular phylogeny of the family Scytosiphonaceae based on *rbcL* sequence data. Values shown at node: Maximum Likelihood bootstrap percentages (BP) and Bayesian posterior probabilities (PP). Values below <50% BP and <0.50 PP not shown. Thickened branches are highly supported in all analyses (BP: $\geq 95\%$; PP: ≥ 0.97). Phylogenetic analyses (Maximum Likelihood and Bayesian Inference) followed those described in Santiañez & al. (2018a).