Cryptogamie, Algologie, 2017, 38 (2): 79-132
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Phylogenetic analyses support recognition of ten new genera, ten new species and 16 new combinations in the family Kallymeniaceae (Gigartinales, Rhodophyta)

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Abstract – The current study presents the most detailed multigene phylogenetic assessment of the red algal family Kallymeniaceae to date emphasising the floras of Australia (220 specimens), Europe (19 specimens) and North America (54 specimens). Toward a natural classification and in light of our phylogenetic results, we propose numerous taxonomic changes including the recognition of ten new genera: *Austrokallymenia* Huisman & G.W.Saunders; *Glaphyrymeniopsis* Kraft & G.W.Saunders; *Huonia* G.W.Saunders; *Leiomenia* Huisman & G.W.Saunders; *Metacallophyllis* A.Vergés & L.Le Gall; *Nothokallymenia* A.Vergés & L.Le Gall; *Rhipidomenia* G.W.Saunders; *Thalassiodianthus* G.W.Saunders & Kraft; *Tytthomenia* G.W.Saunders; and *Verlaquea* L.Le Gall & A.Vergés. The proposals of new genera are accompanied by 16 new combinations of which half are for species from the formerly species-rich genus *Kallymenia*. Approximately 50 undescribed genetic species were uncovered, of which only ten are now formally named, five of which are type species for new genera: *Glaphyrymeniopsis mollis* Kraft & G.W.Saunders, *Huonia sandersonii* G.W.Saunders, *Leiomenia lacunata* Huisman & G.W.Saunders, *Thalassiodianthus incrassatus*

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doi/10.7872/crya/v38.iss2.2017.79

G.W.Saunders & Kraft and *Tytthomenia barrettii* G.W.Saunders. The remaining five are *Austrokallymenia rebeccae* G.W.Saunders & Kraft, *A. roensis* Huisman & G.W.Saunders, *Leiomenia imbricata* Huisman & G.W.Saunders, *Meredithia compaginata* G.W.Saunders, and *Verlaquea fimbriata* G.W.Saunders. Also described and illustrated for the first time are reproductive features of the northeastern-Pacific *Euthora timburtonii* Clarkston & G.W.Saunders, which has been known until now only from molecular studies of vegetative thalli. Despite advances made by our work, the need for considerably more taxonomic investigation in this diverse family is demonstrated, particularly within the presently constituted genus *Callophyllis*.

COI-5P / DNA barcode / Gigartinales / Kallymeniaceae / LSU / phylogeny / *rbc*L / Rhodophyta / systematics / taxonomy

INTRODUCTION

When Womersley (1994) treated the Kallymeniaceae in the first volume of his monograph of southern Australian Rhodophyta, he was presenting the last broad-brush treatment of the family based wholly on morphological (alpha) taxonomy. Crediting it with "some 18 genera", he detailed the morphology of eight, of which four were among the 12 covered in Kylin's (1956) survey of the red algal genera known at the time of his posthumously published "*Die Gattungen der Rhodophyceen*". Kylin (1928) himself had earlier established the family Kallymeniaceae (as the "Callymeniaceae") for a diverse group of foliose, lacerate or variously branched red algae with triphasic life histories, isomorphic gametophytes and tetrasporophytes, presumably multiaxial thallus construction, and regularly cruciate tetrasporangia. So broad a circumscription would apply to any number of non-members of the family but, as in the best-defined of rhodophyte families, Kylin regarded its truly diagnostic characters to lie in the complex processes leading to zygote formation and the subsequent development of the embryo that becomes the diploid carposporophyte phase of the life history. Members were paradigm exemplars of Kylin's order Cryptonemiales because their carpogonial and, when present, separate auxiliary-cell apparatuses were borne in highly modified side branchlets of cortical filaments, the supporting and auxiliary cells being the basal cells of these systems and the laterals on these basal cells being either one- or two-celled distinctively shaped "subsidiary" cells or short filaments. On supporting cells, one or more of these could develop into a three-celled carpogonial branch. In most genera, supporting and auxiliary cells with their subsidiary cells were in separate branch systems (i.e. nonprocarpic), presumed fertilization being followed by formation of a fusion cell from which connecting filaments radiated to seek out, fuse with, and diploidize distant auxiliary cells to initiate the carposporophyte phase.

Following Kylin (1956), eight genera were added to the family prior to Womersley's (1994) monograph, these also based wholly on morphological criteria: *Austrophyllis* Womersley & R.E.Norris (1971), *Beringia* Perestenko (1975), *Cirrulicarpus* Tokida & T.Masaki (1956), *Hommersandia* G.I.Hansen & S.C.Lindstrom (1984), *Kallymeniopsis* Perestenko (1977), *Meredithia* J.Agardh (1892; resurrected by Guiry & Maggs 1984), *Thamnophyllis* R.E.Norris (1964), and *Velatocarpus* Perestenko (1986).

As often happens with foliose red algae from a number of distant families, precise details of cystocarp development in the Kallymeniaceae can be missing or difficult to interpret, so that vegetative characters are applied by most individuals when attempting to identify genera and species. Important features tend to focus on thallus structure as seen in cross- and longitudinal-sections or stained whole-mount squashes of blade tissue. Interior details tend to center on the medulla, which can be: virtually pseudoparenchymatous throughout [as in *Euthora* J.Agardh (Clarkston & Saunders, 2012); Figs 58, 59]; predominantly composed of inflated subisodiametric cells interspersed with varying numbers of pigmented or non-pigmented narrow filaments (*Austrophyllis*, *Callophyllis* Kützing, *Pugetia* Kylin, *Thamnophyllis*); a mostly filamentous medulla bounded by several layers of inflated subcortical cells (e.g. *Kallymenia* J.Agardh, *Cirrulicarpus*, *Hormophora* J.Agardh); or one that is filamentous throughout with an abrupt transition to a shallow, two- or three-layered small-celled cortex (*Glaphyrymenia* J.Agardh). The only genera with an unambiguously diagnostic anatomy are the Australian *Glaphyrymenia* and *Polycoelia* J.Agardh, the latter with a single central layer of rectilinear, thick-walled cells surrounded by a deep cortex of narrow, small-celled anticlinal filaments (Womersley, 1994, fig. 77M). Another distinctive feature of the medulla in several genera (e.g. *Cirrulicarpus, Hormophora, Kallymenia, Thamnophyllis*) is the varying presence of stellate cells (Womersley, 1994, figs 73A, F; 75B; 77B, K) in which the central portion is markedly inflated and issues radiating long narrow arms. In some species these cells are refractive or stain very darkly, termed "ganglionic" by Womersley (1994, fig.78B). *Austrophyllis*, *Callophyllis* and several other genera apparently lack these distinctive medullary inclusions altogether.

In light of the above, it seemed inevitable that the genus-level taxonomy of the group would undergo an explosion of molecularly-assisted taxonomic modifications, beginning with the addition of *Austropugetia* R.L.Moe, *Leniea* R.L.Moe, and *Varimenia* R.L.Moe (all *in* Hommersand *et al.*, 2009; sequence data cited as unpublished in that study), *Psaromenia* D'Archino, W.A.Nelson & Zuccarello (2010), *Salishia* Clarkston & G.W.Saunders (2012), *Stauromenia* D'Archino & W.A.Nelson (in D'Archino *et al.*, 2012), *Rhytimenia* Huisman & G.W.Saunders (*in* Huisman *et al.*, 2016), and *Judithia* D'Archino & S.-M.Lin and *Wendya* D'Archino & S.-M.Lin (both in D'Archino *et al.*, 2016). With the exception of *Rhytimenia*, from the tropical Indo-Pacific, these new taxa were confined to cool- and cold-temperate waters, as is typical of most of the family's members.

The current state of taxonomic affairs is summarized easily with the Kallymeniaceae currently assigned some 32 genera, many of which are considered to have worldwide distribution, and 171 species (Guiry & Guiry, 2016). For the most part the genera contain few species with *Austropugetia, Crossocarpus* Ruprecht*, Glaphyrymenia, Hormophora, Judithia, Leniea, Psaromenia, Rhizopogonia* Kylin*, Stauromenia, Varimenia,* and *Wendya* all being monotypic and *Austrophyllis, Beringia, Ectophora* J.Agardh*, Erythrophyllum* J.Agardh*, Hommersandia*, *Nereoginkgo* Kylin*, Polycoelia* J.Agardh, *Rhytimenia* and *Velatocarpus* presently credited with just two species. Only *Callophyllis* (60), *Kallymenia* (47), *Meredithia* (10) and *Pugetia* (8) currently contain more than four species, with *Callophyllis* and *Kallymenia* being by far the largest and most widespread genera with at least one or more species in warm-temperate to tropical waters (Guiry & Guiry, 2016).

Unfortunately, the molecular studies cited in the previous paragraph, as well as other works exploring this family with molecular tools (e.g. Harper & Saunders, 2002; D'Archino *et al.*, 2011; Schneider *et al.*, 2014), routinely resolve the larger genera as paraphyletic and or polyphyletic. This conundrum has not been

addressed in the literature to date and has become exacerbated by the explosion of overlooked species being uncovered as a result of routine DNA barcode surveys (e.g. Schneider *et al.*, 2014). As the species-rich genera are nothing more than form constructs of no taxonomic value, overlooked species acquire meaningless genus-level assignments based on their closest match in databases such as BOLD (Barcode of Life Database) and GenBank. These assignments persist in the literature and add to the taxonomic confusion. Schneider *et al.* (2014) tried to avoid this by simply using the generic placeholder "*Kallymeniac*" in front of equally temporary and unsatisfactory form species names such as sp.1LH, sp.2LH, etc.

Recent DNA barcode surveys have only further aggravated the problems outlined above as centers of kallymeniacean richness in the cool- to cold-temperate western and eastern Pacific, the northeastern Atlantic, South African and Australasian regions are explored. New Zealand is particularly endowed with new and segregate taxa that are being highlighted and described as a result of molecular-assisted studies by D'Archino, Nelson, Zuccarello and colleagues. The family is also proving to be well represented along coasts of the southern half of Australia, although only two of the three currently recognized species of *Callophyllis* are common enough to be major drift elements throughout the year (G.T. Kraft, personal observations). Our recent collections from Lord Howe Island, Tasmania, and Western Australia have revealed a wealth of undiscovered or misclassified species that molecular studies are only now focused on addressing (e.g. Schneider *et al.*, 2014). In Europe, where members of the Kallymeniaceae for the most part have been well known and long named, some from as early as the mid 18th century, recent anatomical analyses have yielded taxonomic insights that question the definitions and composition of familiar genera (e.g. Vergés & Rodríguez-Prieto, 2006a). A number of such species have now been treated molecularly and their true generic placements established in the results given below.

Our goal in this paper was to use DNA barcoding [COI-5P (Saunders, 2005) with *rbc*L-3P as a secondary marker (Saunders & Moore, 2013)] to identify as many kallymeniacean species as possible with an emphasis on Australia and western Europe. We do not treat taxonomically all of the species-level diversity that was uncovered but rather attempt to include every genetic species encountered during our surveys in a contemporary genus-level taxonomic framework, i.e. one based on the principle of monophyly as determined through molecular phylogenetic analyses and buttressed by anatomical features when possible. This has resulted in the resurrection of *Euhymenia* Kützing [previously subsumed in *Kallymenia* (Schneider & Wynne, 2007)] and description of ten new genera. These generic changes have necessitated the description of ten new species and 16 transfers of species currently misplaced in other genera. We provide the barcode records for many (~ 40) temporarily designated genetic groups and place them in a phylogenetic context to assist future researchers in exploring and naming these remaining species.

MATERIALS & METHODS

Sample collection & anatomy

Kallymeniacean specimens were collected from many locations (with emphasis on Australia and western Europe) by scuba, dredging, snorkelling, and from the intertidal or as drift (Table S1). A subsample of each specimen was cleaned,

dried in silica gel for DNA extraction and to function as a voucher (Saunders & McDevit, 2012). Where feasible a further portion was preserved by pressing fresh material or by fixation in 4-5% formalin/sea water for later anatomical observations. Preparations for anatomical studies were made by hand-sectioning, whole-mount squashes or thin-slicing in a cryostat (CM1850, Leica) then stained with acidified 1% aniline blue before mounting in 30-50% corn syrup. Habit views were reproduced with a HP Officejet 6500A scanner (Hewlett-Packard, Palo Alto, CA, USA). Herbarium abbreviations followed the online Index Herbariorum http://sweetgum.nybg.org/ih/ (Thiers, 2017).

Molecular sequencing and analysis

Specimens used for molecular analyses are listed in Table S1 (doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1), along with their collection details, voucher details and their BOLD and GenBank accession numbers for LSU, *rbc*L, *rbc*L-3P and COI-5P.

For specimens processed at UNB (voucher numbers beginning with B0, CCMP, CL, G0, and GWS, as well as the specimens from Tristan da Cunha in Table S1) DNA extraction (Saunders & McDevit, 2012) and marker amplification for LSU, *rbc*L, *rbc*L-3P and COI-5P followed published protocols (Saunders & Moore, 2013). For COI-5P, the actual primer pair used for amplification of each specimen is listed with the BOLD and GenBank accessions (Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1). Sequence data were edited and contigs produced in Geneious 9.1.3 (http://www.geneious.com; Kearse *et al.,* 2012).

For specimens processed at the Muséum national d'Histoire naturelle (voucher numbers beginning with LLG, PC, and RMAR in Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1), total DNA was extracted using a DNeasy Plant Mini Kit (QIAGEN, Hilden, Germany) according to the manufacturer's instructions except that the extraction buffer was prepared as follows: 1M tris-base, 1M tris-HCl, 0.05M Na_2EDTA, 0.2M NaCl, 2.5M potassium acetate, 1% Tween 20, and 0.2 mg/ml Pro K (Saunders, 1993). The LSU and COI-5P were amplified as outlined above. The *rbc*L was amplified in three fragments (total of 1647 bp) using the following primer combinations: F-*rbc*Lstart / R-753, F-577 / R1381, and F-993 / R-rbcS start (Freshwater & Rueness, 1994). Purification and sequencing reactions were performed by *Genoscope* (www.genoscope.fr, Evry, France) with contigs edited and assembled with the software Codoncode (Dedham, MA).

The ClustalW plugin for Geneious version 9.1.3 was used to align the sequences generated here (and those produced previously by our respective labs; Table S1) and included data from other labs as downloaded from GenBank (accession numbers indicated directly in Figs 1, 2). Three single gene alignments were prepared for phylogenetic analyses: LSU (131 sequences, 2863 bp), *rbc*L (143 sequences, 1358 bp) and CO1-5P (124 sequences, 664 bp). These included representatives of the Dumontiaceae and Rhizophyllidaceae (Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1) as outgroup taxa (Saunders *et al.*, 2004; Dixon *et al.*, 2015). Single gene alignments were analyzed independently with maximum likelihood (ML, model GTR+I+G) using RAxML (Stamatakis *et al.*, 2008) with partitioning by codon for *rbc*L and COI-5P, in Geneious 9.1.3. Since no conflicts were detected between single gene topologies, a final LSU + *rbc*L + COI-5P concatenated alignment was constructed and analyzed as outlined for the single gene alignments but with partitioning by gene and then codon for *rbc*L and COI-5P. Support was assessed with 500 bootstrap replicates.

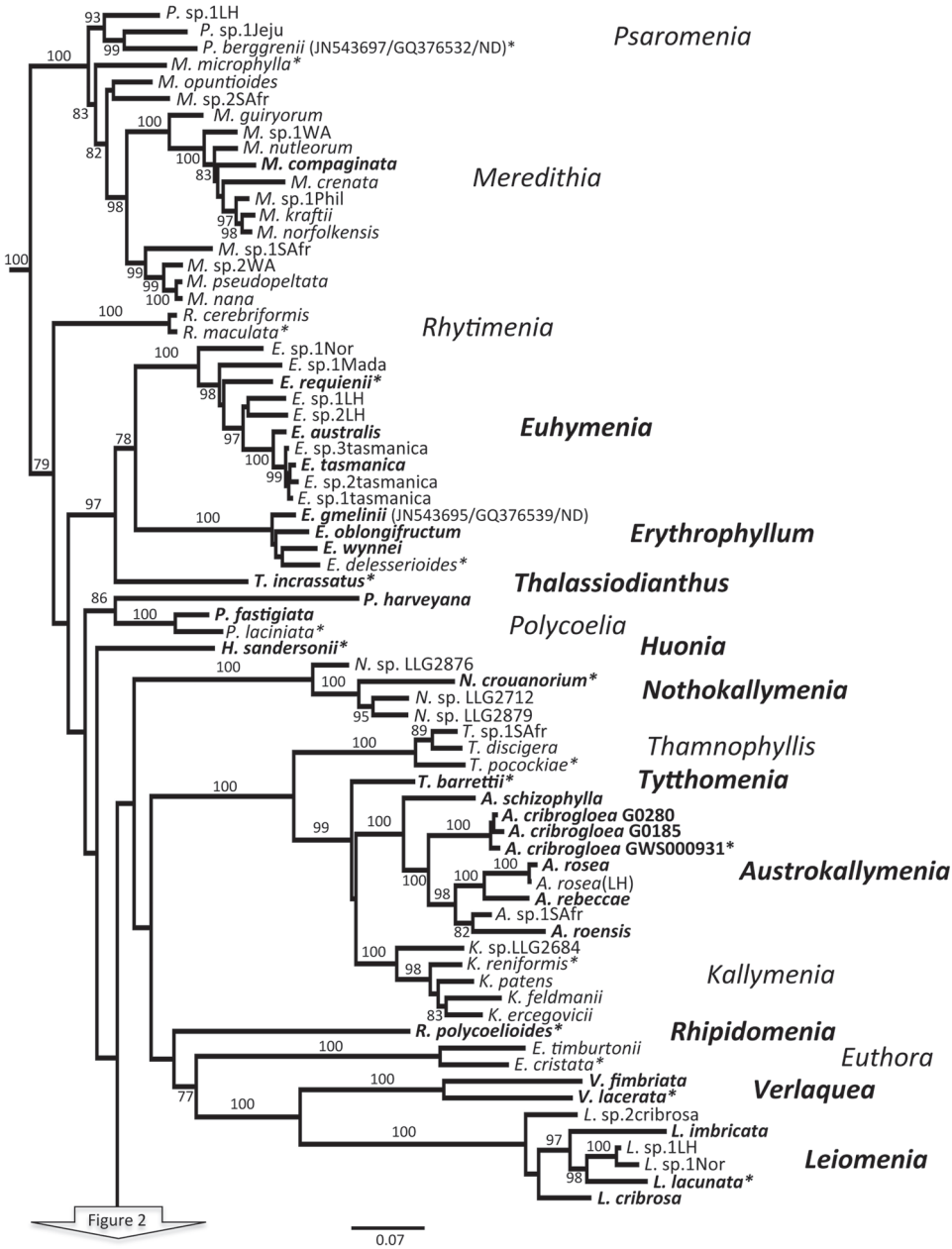


Fig. 1. Maximum likelihood phylogeny of our multigene alignment. Outgroup taxa were pruned to facilitate presentation. Taxa in bold type were resurrected, transferred or newly named as a result of our analyses. Generitypes indicated with an asterisk. Bootstrap support values > 75 % included. Scale equals substitutions per site.

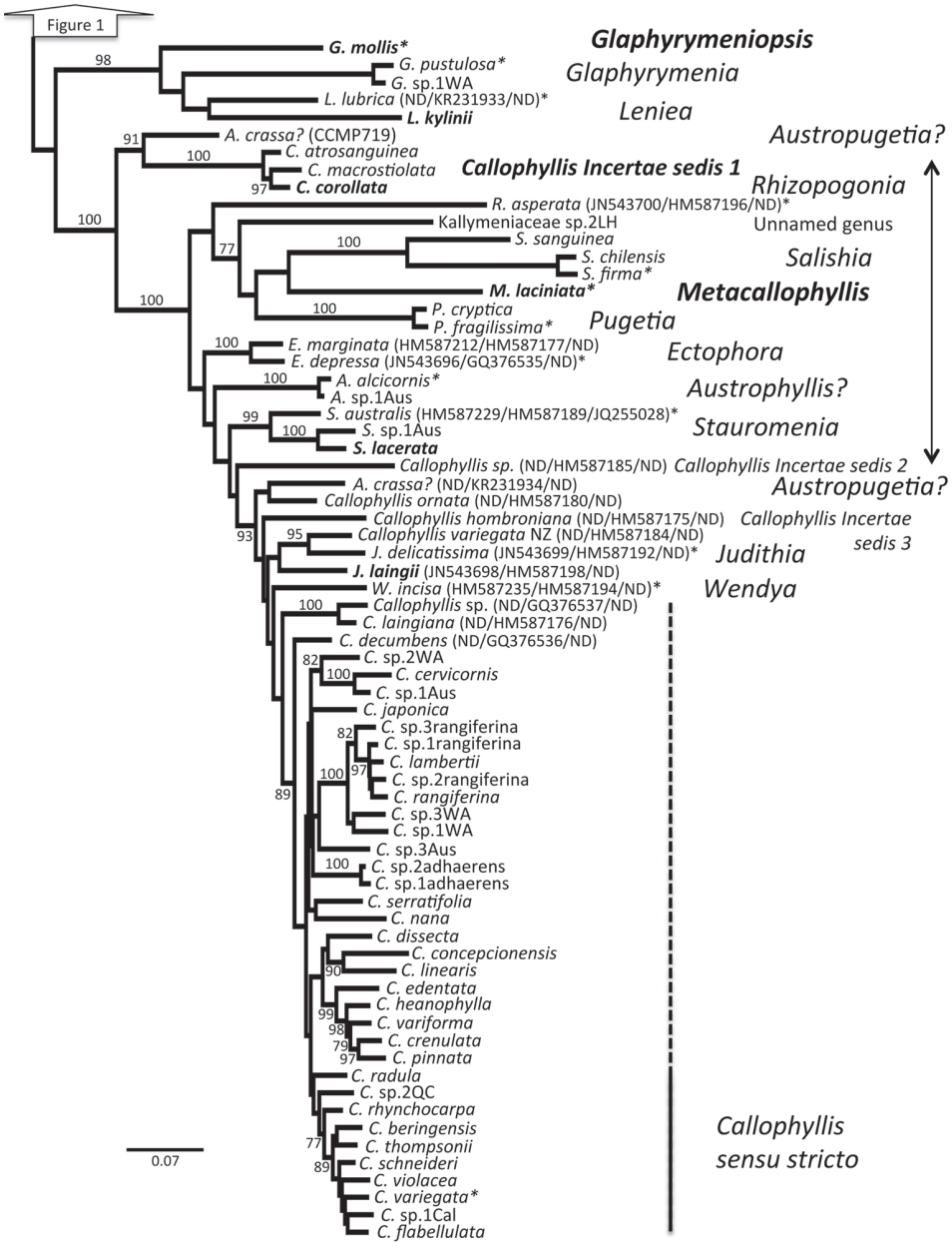


Fig. 2. Continuation of Figure 1 – consult for legend details.

RESULTS AND DISCUSSION

DNA barcode results

A total of 196 specimens had COI-5P newly determined as part of ongoing DNA barcode surveys of Kallymeniaceae that primarily emphasized Australia (n = 144), but which also included critical collections from Europe, Saint Helena, Ascension and Tristan da Cunha Islands, and South Africa (Table S1 doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1). An additional 11 Australian collections were assigned to genetic groups on the basis of *rbc*L-3P data where COI-5P amplification failed (Table S1). The net result was *ca* 60 genetic species groups for Australia whereas only *ca* 20 were expected (Millar & Kraft, 1993; Womersley, 2004), as well as the uncovering of cryptic diversity within the European and South African regions sampled (Table S1). We do not deal with all of the novel genetic species in this report, although we provide these records (Table S1) to facilitate future research. We largely generated LSU and *rbc*L for at least one representative of each genetic group that we uncovered in the Kallymeniaceae (Table S1) and combined these with representative data from GenBank in an effort to establish a contemporary genus-level taxonomic overview for the family (Figs 1, 2).

Phylogenetic results, anatomical observation, and description of novel taxa

Phylogenetic analysis of our concatenated alignment resolved at least 36 genus-level lineages, most of which were expanded, revised or resurrected versions of existing genera or which are new taxa that we formally describe below (Figs 1, 2). Not surprisingly, the more speciose genera such as *Callophyllis*, *Kallymenia* and *Pugetia* proved to be highly para/polyphyletic. We deal with each genus-level lineage below, beginning in order of treatment from the top of Figure 1 to the bottom of Figure 2, providing the necessary taxonomic proposals and comments for each lineage. In presenting the various taxa, detailed lists of synonyms are not provided as these are comprehensively provided on AlgaeBase (www.algaebase.org).

Psaromenia D'Archino, W.A.Nelson & Zuccarello

Type species: *Psaromenia berggrenii* (J.Agardh) D'Archino, W.A.Nelson & Zuccarello, 2010.

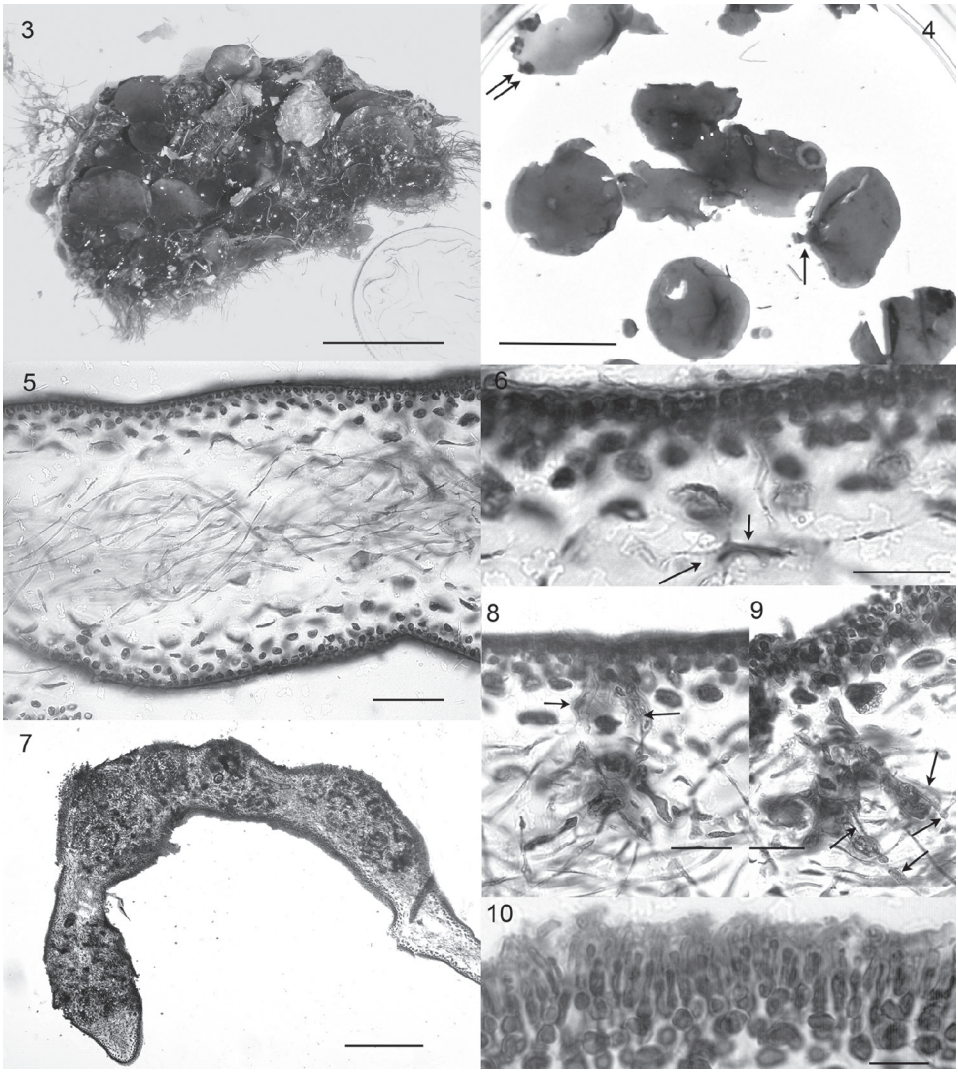
Remarks: *Psaromenia* was established for the New Zealand-endemic *Kallymenia berggrenii* J.Agardh largely on the basis of molecular data that allied it closer to the type of *Meredithia* (discussed below) than to that of *Kallymenia*. In addition to the type, Schneider *et al.* (2014) provided evidence for two additional species assignable to this genus, one each from Jeju Island, South Korea and Lord Howe Island, Australia (*P.* sp.1Jeju and *P.* sp.1LH, respectively; Fig. 1). As with most kallymeniacean genera we anticipate that additional overlooked species remain to be discovered. Given the heteromorphic life history for *Meredithia microphylla* (J.Agardh) J.Agardh (Guiry & Maggs, 1984), D'Archino *et al.* (2010) speculated that *P. berggrenii* may also have this pattern, which combined with the deep divergence and strong alliance of these two genera in molecular analyses (Fig. 1) could be considered grounds for recognition of a separate family. We consider proposal of a distinct family premature pending exploration of the life history patterns in additional species of *Meredithia* (Schneider *et al.*, 2014) and *Psaromenia*.

Meredithia J.Agardh

Type species: *Meredithia microphylla* (J.Agardh) J.Agardh, 1892.
Remarks: As recently as 2010, *Meredithia* was regarded as a monospecific genus confined to the North Atlantic and Mediterranean (e.g. D'Archino *et al.*, 2010). Schneider *et al.* (2014) radically altered that view when they reported 12 genetic species groups including the generitype, *M. microphylla,* plus a resurrected Australian *M. nana* J.Agardh [considered by Womersley (1994) to be a species of *Cirrulicarpus*], and ten novel species of which they formally described seven. Subsequently, additional overlooked species have been uncovered in the North Atlantic (Le Gall, unpublished observations), as have three additional species during short collecting trips by members of the Saunders' lab to South Africa (*M.* sp.1SAfr and *M.* sp.2SAfr; Fig. 1) and the Cocos (Keeling) Islands (northwest of tropical Western Australia). Only the last mentioned is formally described below (as *M. compaginata* G.W.Saunders; Fig. 1), but all indications point to considerably more diversity yet to be uncovered for this genus of typically hard-to-differentiate red blades (e.g. Ballantine *et al.*, 2015). The recently described *Meredithia pulchella* Ballantine, H.Ruiz & J.N.Norris for which only LSU sequence data are available was not included in our analyses, but is a close sister to *M. crenata* C.W.Schneider, C.E.Lane & G.W.Saunders (data not shown).

Meredithia compaginata G.W.Saunders, *sp. nov.* **Figs 3-10**

Description: Thalli typically clustering in small populations on coral rubble (Fig. 3); individual fronds stipitate, the stipes 0.5-0.8 mm wide and tall and fanning above to clearly peltate blades, the blades round to oval, dorsally depressed, 0.25-1.20 cm across, with smooth to irregularly crenulate margins; compound thalli resulting from up to four orders of marginal blades (Fig. 4). Blade sections 140-210 µm thick; medulla filamentous, the filaments predominantly longitudinally aligned, at times obliquely to transversely, the cells rectilinear, 3-6 µm wide (Fig. 5). Outer medullary cells stellate, lightly staining, some with crystalline inclusions, the cells periclinally elongated, 15-25 µm long, 7-10 µm tall, flanked on both surfaces by a 2- or 3-layered inner cortex of ovoid cells 7-10 µm wide by 5-7 µm tall (Fig. 6), and 1(-2) outer cortical layers with those of ventral surface layers larger, 5-8 µm in diam., and less darkly staining than those on the dorsal surface, 4-6 µm in diam. (Fig. 5). Cystocarps protuberant, in irregular patches near margins (Fig. 4), projecting more on the dorsal than the ventral surface and causing the blades to recurve toward the substratum; carposporophytes composed of numerous pockets of carposporangia separated by sterile filaments (Fig. 7). Supporting cells polycarpogonial, producing 2-4 three-celled carpogonial branches, the details difficult to discern (Fig. 8). Postfertilization events unclear, but chains of cells appear to grow from the carpogonial branch system and connect to medullary filaments (Fig. 9). Thalli dioecious; elongated spermatangial mother cells scattered across both surfaces, the spermatangia single and terminal, 2.5 µm in diam. (Fig. 10). Tetrasporophytes not found.
Type collection: Coll. *G.W. Saunders & K. Dixon*, December 9, 2013, Blue Holes (inner east lagoon), Cocos (Keeling) Islands, Australia, 12.15365°S, 96.88007°E, subtidal 5 m on coral rubble. Holotype, UNB [GWS037856, BOLD ABMMC19028-13, cystocarpic (Figs 4-9)]. Isotypes, UNB [GWS037854; GWS037855, spermatangial (Figs 3, 10)].
Etymology: From the Latin *compaginatus* meaning packed closely one on top of the other in reference to the imbricate habit of thalli as higher-order blades overlap those of lower orders.



Figs 3-10. *Meredithia compaginata* G.W.Saunders, *sp. nov.* **3.** Living habit of isotype collection growing on coral rubble (GWS037855). **4.** Habit of holotype (GWS037856) including simple stipitate (arrow) blades, a compound thallus to four orders (center of image) and clustered marginal cystocarps (double arrows). **5.** Vegetative cross-section showing cortical development on dorsal (top) and ventral (bottom) surfaces (GWS037856). **6.** Transition between isodiametric cells of the inner cortex and elongate cells (arrows) of the outer medulla (GWS037856). **7.** Ventral arching of a blade caused by the aggregated marginal cystocarps (GWS037856). **8.** Two trichogynes (arrows) extending toward the thallus surface from carpogonial branches borne on obscured supporting cell (GWS037856). **9.** Procarpic development of early gonimoblast filaments (arrow) directed thallus-inwardly from the supporting-cell (now the auxiliary-cell) complex (GWS037856). **10.** Dense surface palisade of elongate mother cells with terminal spermatangia (GWS037855). Scale bars: 3, 4 = 1 cm; 5, = 50 µm; 6, 8, 9 = 20 µm; 7 = 400 µm, 10 = 10 µm.

Holotype DNA Barcode: KX808100 (COI-5P).
Additional specimens examined: See Table S1 (doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1).
Distribution: Known from the type locality and nearby sites on the Cocos (Keeling) Islands (Table S1).
Remarks: Remarkably another Australian species is assignable to *Meredithia*, this time from the Cocos (Keeling) Islands (see Schneider *et al.*, 2014). This species was only collected at two sites on coral rubble in shallows of the sheltered inner lagoon. This species has a distinctive habit with small cup-like blades growing from margins of up to four orders of overlapping blades. Unlike the type species, *M. microphylla*, and the Bermudan *M. crenata*, both of which are monocarpogonial, *M. compaginata* is polycarpogonial, although it is dioecious as presumably is *M. microphylla* (Guiry & Maggs, 1984) but not *M. crenata* (Schneider *et al.*, 2014). Details of postfertilization events, including a sure identification of auxiliary cells, are unknown for any member of *Meredithia* (Schneider *et al.*, 2014), but in *M. compaginata* we observed filaments composed of proximally long and distally short cells radiating from the carpogonial-branch complex and connecting to gametophytic medullary cells in a way similar to the procarpic *Callophyllis concepcionensis* Arakaki, Alveal & Ramírez (Lin *et al.*, 2012) and as reported for *Rhytimenia* (Huisman *et al.*, 2016) and *Stauromenia* (D'Archino *et al.*, 2012). More study along the lines of the detailed histological observations of Lin *et al.* (2012) is definitely warranted, but it is noteworthy that observations for *M. nana* could be reinterpreted in light of observations here [compare Hansen (1977; fig. 23) to Fig. 8 here].

Rhytimenia Huisman & G.W.Saunders

Type species: *Rhytimenia maculata* (Weber Bosse) Huisman & G.W.Saunders, 2016 (in Huisman *et al.*).
Remarks: *Rhytimenia* remains a deeply diverging lineage in the Kallymeniaceae (Fig. 1). In addition to the type species, we include the closely allied *R. cerebriformis* (N'Yeurt & Payri) Should be L.Le Gall & Vergés (Huisman *et al.* 2016) in our phylogenetic analyses (Fig. 1).

Euhymenia Kützing

Revised description: Member of the Kallymeniaceae with foliose blades; medulla lax, with an interconnected network of slender filaments and stellate cells; inner cortex typically one or two layers of periclinally elongated cells internal to two or three layers of smaller cortical cells that decrease in size towards the surface. Nonprocarpic; supporting cells either mono- or polycarpogonial, also carrying up to ten subsidiary cells; supporting cell, carpogonial branch cells and subsidiary cells typically elongate to some degree. Fusion cells, where known, prominent, deeply lobed, incorporating the supporting and subsidiary cells and issuing long connecting filaments. Auxiliary cell systems formed by the auxiliary cell bearing up to six subsidiary cells. Gonimoblast filaments develop from the auxiliary cell or from the connecting filament near the site of fusion with the auxiliary cell.
Lectotype species: *Euhymenia requienii* (J.Agardh) Kützing, 1843.
Representative DNA barcode: KJ083090 (COI-5P).
Remarks: Our molecular analyses have resolved species traditionally assigned to the genus *Kallymenia* in multiple independent lineages (Figs 1, 2), which is consistent with all published molecular studies to date (citations throughout this manuscript). Although thus far a predominantly Australian clade, our inclusion for the first time

of the Mediterranean *Kallymenia requienii* (J.Agardh) J.Agardh requires resurrection of Kützing's (1843) *Euhymenia*, which was based on three species [*E. requienii, E. reniformis* (Turner) Kützing and *E. lactuca* (C.Agardh) Kützing] formerly placed in *Kallymenia,* none of which Kützing designated as the type. *Kallymenia reniformis* (Turner) J.Agardh is now the type species of the genus *Kallymenia* itself, whereas *K. lactuca* (C.Agardh) Rabenhorst is currently regarded a synonym of *Cryptonemia lomation* (Bertoloni) J.Agardh (Guiry & Guiry, 2016). *Euhymenia requienii* is thus here designated as the lectotype species for this genus.

In addition to the type species, we have uncovered nine additional genetic groups, including the Australian *Cirrulicarpus australis* Womersley & R.E.Norris [which Womersley (1994, p. 241) erroneously synonymized with *C. nanus* (J.Agardh) Womersley], the Australian *Kallymenia tasmanica* Harvey in J.D. Hooker (which is a complex of four closely allied genetic groups in need of further study), and unnamed species yet to be morphologically characterized from Lord Howe Island (*E.* sp.1LH and *E.* sp.2LH), Norfolk Island (*E.* sp.1Nor) and Madagascar (*E.* sp.1Mada) (Fig. 1). Where details are known these species share elongate carpogonial-branch and subsidiary cells, as well as auxiliary-cell assemblages that resemble supporting cell complexes save for a lack of carpogonial branches (examples in Womersley & Norris, 1971; Rodriguez-Prieto & Hommersand, 2009).

Euhymenia australis* (Womersley & R.E.Norris) G.W.Saunders, *comb. nov.

Basionym: *Cirrulicarpus australis* Womersley & R.E.Norris, *Australian journal of botany,* Suppl. 2: 19, 20, figs 39-43, 90 (1971).
Holotype: MEL 1005814 (Womersley & Norris, 1971; Guiry & Guiry, 2016).
Representative DNA barcode: KF280926 (COI-5P).
Remarks: Womersley & Norris (1971) indicated that their placement of *E. australis* in *Cirrulicarpus* was largely owing to its gross morphological similarities to the generitype, *Cirrulicarpus gmelinii* (Grunow) Tokida & T.Masaki, from the subarctic northern Pacific, both species being branched in contrast to foliose, but otherwise similar to *Kallymenia* in anatomical details. Throughout this paper we maintain that being branched versus foliose can lack taxonomic utility at the genus level in the Kallymeniaceae and, at times, even the species level [e.g. in *Erythrophyllum delesserioides* J.Agardh, for which GWS has a genetically verified broadly foliose specimen (as opposed to the typical narrowly linear habit of the species); image available in BOLD – public record ABMMC544-06]. Indeed, many of our *E. tasmanica* specimens (see below) of this normally broadly foliose species could be considered deeply lobed, if not actually 'branched' (images available in the BOLD public dataset DS-KALLGE1).

Our phylogenetic analyses failed to ally *Cirrulicarpus australis* with the type species of either *Cirrulicarpus* or *Kallymenia,* thus necessitating transfer to *Euhymenia* owing to its close affiliation with the type species of that genus (Fig. 1). As stated above, *C.* (= *Euhymenia*) *australis* had been synonymized with *C. nanus* (J.Agardh) Womersley (1973), a move disputed by Hansen (1977) but which Womersley (1994, p. 242) himself later erroneously argued was based on her observational errors. The distinctness of *E. australis* from *C. nanus* and return of the latter to *Meredithia* were confirmed by Schneider *et al.* (2014).

Although *Euhymenia australis* is polycarpogonial whereas *E. tasmanica* (Womersley, 1994) and *E. requienii* (Vergés & Rodríguez-Prieto, 2006a) are monocarpogonial, this trait is a variable feature in other genera (e.g. *Meredithia,* discussed above). In describing the cells of the carpogonial and auxiliary-cell branch systems, Womersley & Norris (1971, pp. 12, 13, 19) provided virtually identical

descriptions of anatomy for *Cirrulicarpus australis* and *Kallymenia tasmanica,* as would be expected for two species so closely allied in the *Euhymenia* clade of our phylogenetic analyses (Fig. 1). Fortunately, one of our two specimens of *E. australis* was female (GWS028939; Table S1), and we confirmed features of supporting and auxiliary cell complexes (data not shown) as outlined in Womersley & Norris (1971).

Euhymenia tasmanica* (Harvey) G.W.Saunders, *comb. nov.

Basionym: *Kallymenia tasmanica* Harvey, *Flora Tasmaniae* 2: 325 (1859).
Lectotype: TCD, Herb. Harvey Alg. Aust. Exsicc. 418 (Womersley, 1994, p. 236; Guiry & Guiry, 2016).
Representative DNA barcode: HM917794 (COI-5P).
Remarks: As indicated above, this morphospecies actually encompasses a complex of four genetic groups for which further taxonomic study is needed (Fig. 1). Genetically verified collections are confined to southern Australia, predominantly the island state of Tasmania (Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1).

Erythrophyllum J.Agardh

Type species: *Erythrophyllum delesserioides* J.Agardh, 1872.
Remarks: A closely related lineage encompasses the type of *Erythrophyllum*, *E. delesserioides*, which has priority, and the type of *Cirrulicarpus*, *C. gmelinii*, necessitating synonymization of the latter genus (Fig. 1). *Beringia wynnei* Clarkston & G.W.Saunders and *Kallymeniopsis oblongifructa* (Setchell) G.I.Hansen also belong to this lineage necessitating their transfer to *Erythrophyllum*. It is highly likely that other North Pacific species, including *Crossocarpus lamuticus* Ruprecht (see Norris *et al.*, 1960, p. 35; Perestenko, 1975), generitype of the family Crossocarpaceae, belong in this lineage. Should these two genera prove synonymous as proposed here, *Crossocarpus* would have nomenclatural priority (Guiry & Guiry, 2016) necessitating transfer of all of the species assigned to *Erythrophyllum* to it and inevitably relegating the Crossocarpaceae to synonymy with the Kallymeniaceae. In addition, the remaining species of *Beringia*, *Kallymeniopsis* and *Velatocarpus* need to be examined for their likely inclusion in *Erythrophyllum*. *Hommersandia maximicarpa* G.I.Hansen & S.C.Lindstrom and *H. palmatifolia* (Tokida) Perestenko ex O.N.Selivanova & G.G.Zhigadlova [the synonymy of these two species (Perestenko, 1986) remains an unresolved issue (Guiry & Guiry, 2016)] are likely allied to *Erythrophyllum*, but differ sufficiently in post-fertilization development to possibly justify the continued recognition of *Hommersandia* as distinct at the genus level (Hansen & Lindstrom, 1984). However, substantially differing patterns of post-fertilization development characterize species within other genera such as *Callophyllis* (Lin *et al.*, 2012), and molecular data are necessary to determine whether *Hommersandia* is generically distinct from *Erythrophyllum*. More research is needed on these species from North Pacific, especially Russian, coastal waters.

***Erythrophyllum gmelinii* (Grunow) Yendo**

Basionym: *Kallymenia gmelinii* Grunow, *Algae Novara* 72 (1870).
Remarks: *Kallymenia gmelinii* is the type of the genus *Cirrulicarpus*, which is here synonymized with *Erythrophyllum*. Yendo (1915) first transferred this species to *Erythrophyllum* owing to vegetative similarities with *E. delesserioides*, but in emphasizing reproductive features Tokida & Masaki (1956) reassigned it to their new genus *Cirrulicarpu*s (see Hansen, 1977) on the grounds that its cystocarps are located in rings rather than papillae and its tetrasporangia are intercalary rather than

terminal, characters that clearly lack importance at the genus level. The alliance of *Cirrulicarpus* and *Erythrophyllum* was foreshadowed, but not formally proposed, by Norris *et al.* (1960).

Other species from Australia currently assigned to *Cirrulicarpus* have been returned to *Meredithia* (*Meredithia nana*; Schneider *et al.*, 2014) or are assigned here to the resurrected genus *Euhymenia* (*E. australis*) and the new genus *Rhipidomenia* [for *C. polycoelioides* (J.Agardh) Womersley]. This leaves the orphaned species *C. carolinensis* G.I.Hansen and *C. ruprechtianus* (E.S.Zinova) Perestenko *incertae sedis* and in need of further taxonomic study.

Erythrophyllum oblongifructum* (Setchell) G.W.Saunders, *comb. nov.

Basionym: *Iridaea oblongifructa* Setchell, *Zoe* 5: 123, 124 (1901).
Holotype: UC 94395 (Setchell 1901, p. 123; Guiry & Guiry, 2016).
Representative DNA barcode: KX808086 (COI-5P).
Remarks: Hansen (1997) transferred this species to *Kallymeniopsis* from *Kallymenia* indicating that "morphological data supporting this transfer will be provided in a paper to follow". Those data regrettably did not eventuate, but they would have undoubtedly been correct inasmuch as Hansen recognized a close alliance between this taxon and its North Pacific counterparts (Fig. 1) in *Kallymeniopsis,* a genus that we consider a likely synonym of *Erythrophyllum.*

Erythrophyllum wynnei* (Clarkston & G.W.Saunders) G.W.Saunders, *comb. nov.

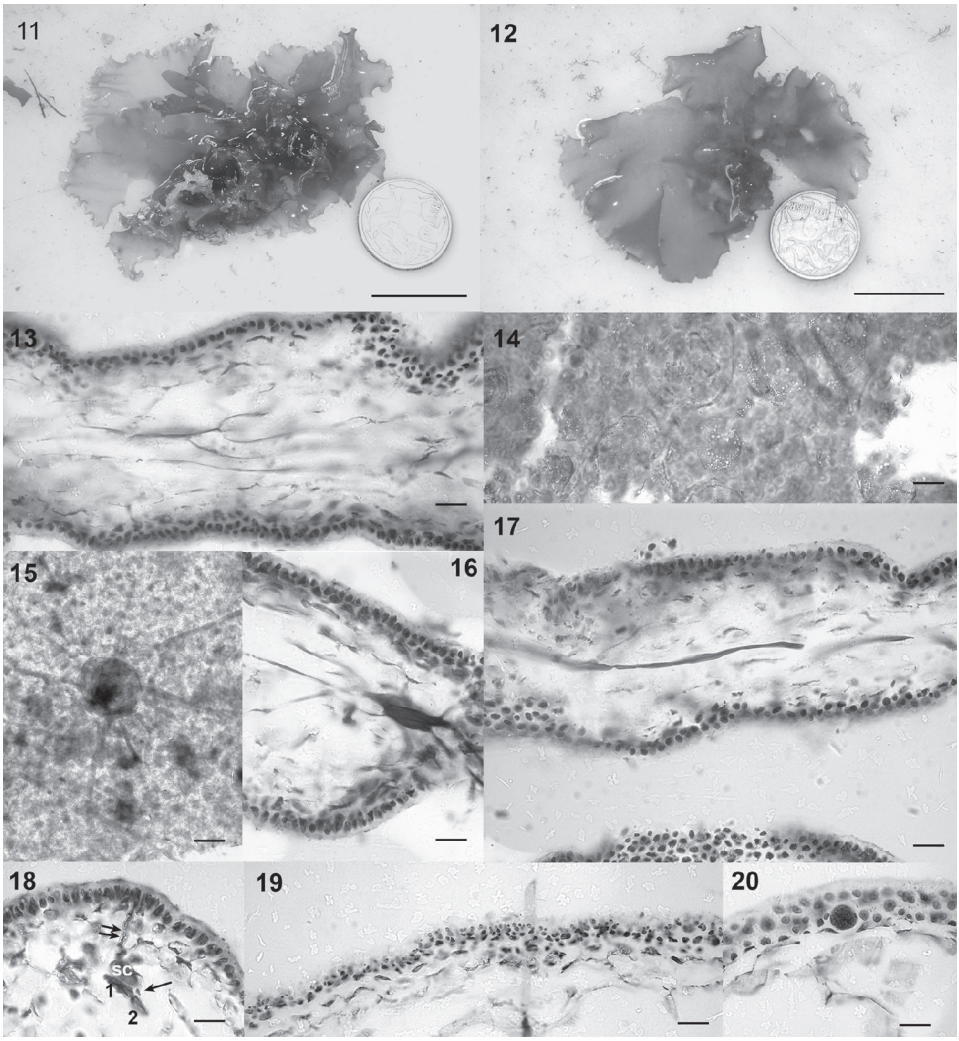
Basionym: *Beringia wynnei* Clarkston & G.W.Saunders, *Phycologia* 51: 57, 58, figs 46-51 (2012).
Holotype: UNB GWS004493 (Clarkston & Saunders, 2012; Guiry & Guiry, 2016).
Holotype DNA barcode: JF903287 (COI-5P).
Remarks: This recently described species is locally common subtidally at exposed sites from northern Haida Gwaii to Bamfield, British Columbia. It also extends to northern Oregon (based on COI-5P data for an unpublished specimen sent by G. Hansen to GWS for identification) thus being similar to *E. delesserioides* and *E. oblongifructum* in its biogeographical distribution.

Thalassiodianthus* G.W.Saunders & Kraft, *gen. nov.

Description: Member of the Kallymeniaceae with foliose blades; medulla of filaments interspersed with a partially interconnected network of stellate cells; inner cortex typically one or two layers of periclinally elongate cells that subtend one or two layers of smaller isodiametric outer cortical cells. Supporting cells typically monocarpogonial (occasionally with two carpogonial branches), apparently lacking subsidiary cells; auxiliary cells and post-fertilization stages not observed. Spermatangia borne singly or in pairs on surface spermatangial mother cells, appearing to develop in advance of carpogonial branches.
Etymology: From the Greek *thalassa* for sea and *dianthus* in reference to the carnation-like appearance of individuals in the field.
Type species: *Thalassiodianthus incrassatus* G.W.Saunders & Kraft, *sp. nov.*

Thalassiodianthus incrassatus* G.W.Saunders & Kraft, *sp. nov. **Figs 11-20**

Description: Blades single or clustered, non-stipitate, 3-6 cm in height, 8-10 cm wide, lobed with ruffled margins that at times impart the appearance of a carnation (Figs 11, 12). Blades in long section 125-200 μm thick (Fig. 13), increasing to 220-250 μm at the margins. Medulla sparsely filamentous (Fig. 13), the orientations



Figs 11-20. *Thalassiodianthus incrassatus* G.W.Saunders & Kraft, *gen. et sp. nov*. **11-12.** Living habits of the holotype (Fig. 11, GWS034310) and an isotype (Fig. 12, GWS032487) from Norfolk Island. **13-18.** Anatomical observations of isotype GWS032486. **13.** Shallow dorsal and ventral cortexes and the broad, laxly filamentous medulla in long-section cut *ca* 10 mm proximal to a leading blade margin. **14.** Tangential section focused on angularly subisodiametric inner cortical cells as seen through ventral surface layers. **15.** A ganglionic stellate medullary cell visible through the cortex. **16.** The dark central body and radiating stellate arms of a ganglionic medullary cell seen in long-section. **17.** One of the periclinally oriented stellate arms of a ganglionic cell in long-section. **18.** Supporting cell (sc) with elongated basal (1) and hypogynous (2) cells, the minute carpogonium (arrow) bearing a contorted trichogyne (double arrows). **19.** Single and paired spermatangia on surface-cortical mother cells (GWS034310). **20.** Cruciate tetrasporangium lodged deeply in the slightly thickened outer cortex (GWS032487). Scale bars: 11,12 = 2.5 cm; 13, 14, 16-20 = 20 µm; 15 = 40 µm.

longitudinal to oblique, occasionally transverse, the medulla bordered on both sides by one or two layers of periclinally compressed cortical cells (Fig. 14) 2.5-8.0 µm in height and 14-40 µm in diam., these internal to one or two surface layers of (sub-) isodiametric cells 5-8 µm in diam. (Fig. 13). Central ganglionic medullary cells in surface view commonly isodiametric, 25-75 µm in diam., extending laterally into a partially interconnected network of darkly staining and branching narrow arms (Figs 15, 16) 7-12 µm in width (Fig. 17); ganglionic cells flattened in long-sections, 6.5-17.0 µm tall by 25-75 µm in overall length (Fig. 16). Supporting cells typically monocarpogonial (rarely with two carpogonial branches), developing in and adjacent to the thickened blade margins, the basal and hypogynous cells elongate, the terminal conical carpogonia with long trichogynes (Fig. 18); position of auxiliary cells and post-fertilization events not observed. Gametophytes monoecious; spermatangial mother cells cutting off one or two terminal spermatangia 2.5-3.0 µm in diam. these aggregated in patches near the margins (Fig. 19). Tetrasporophytes isomorphic to gametophytes; tetrasporangia scattered across the outer cortex (Fig. 20), typically (sub-) spherical and regularly cruciate, 15-20 × 17-20 µm.

Type collection: Coll. *G.W. Saunders & K. Dixon*, November 27, 2012, Little Organ, Norfolk I., 29.00254°S, 167.95161°E, subtidal, 17 m on invertebrate. Holotype, UNB [GWS034310, BOLD OZSEA3196-13, cystocarpic/spermatangial (Figs 11, 19)]. Isotypes, UNB [GWS032486, cystocarpic/spermatangial (Figs 13-18); GWS032487, tetrasporangial (Figs 12, 20)].

Etymology: From the Latin *incrassatus* in reference to the thickened margins.

Holotype DNA barcode: KT307586 (COI-5P).

Additional specimens examined: See Table S1 (doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1).

Distribution: Known from the type locality of Norfolk Island, as well as Lord Howe Island and nearby Balls Pyramid, New South Wales, Australia (Table S1).

Remarks: This is just one of the many blade-like kallymeniacean taxa known at these two remote island locations that would likely have been assigned to *Kallymenia* were standard morpho-taxonomic concepts of that genus to be followed. However, our molecular phylogeny resolves this species as distinct from but sister to *Erythrophyllum* and *Euhymenia* rather than *Kallymenia*, necessitating the designation of a separate genus (Fig. 1).

Polycoelia J.Agardh

Type species: *Polycoelia laciniata* J.Agardh, 1849.

Remarks: Prior to this study *Polycoelia* was considered monospecific [allowing for the uncertain status of *Polycoelia van-hoevellii* Weber Bosse (Womersley & Norris, 1971)], but we uncovered two additional species, one each from Australia and South Africa (Fig. 1). The first genetic group with representative collections from South Australia and Tasmania closely matches the type species, *Polycoelia laciniata* (Table S1), in habit and anatomical details. The second is an Australian species represented by a single Tasmanian specimen morphologically consistent with *Polycoelia fastigiata* Harvey (1859), which has its type locality in that state and which Womersley (1994) synonymized with *P. laciniata*. We have thus resurrected *P. fastigiata* for this genetic group (Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1), but it requires further study.

Our South African addition to *Polycoelia* is a morphological match to *Pugetia harveyana* (J.Agardh) R.E.Norris. Norris (1964) completed detailed anatomical studies on the type material and additional collections in transferring *Kallymenia harveyana* J.Agardh to *Pugetia*, but Clarkston & Saunders (2012)

revisited the type, as well as Norris's study, and concluded that transfer to another genus may be warranted following further study. We were fortunate to have a single cystocarpic collection in UNB from Western Cape, South Africa, that was a match to this species (Table S1), and its inclusion in molecular analyses indicates, as anticipated, that it does not belong in *Pugetia* but rather allies with *Polycoelia* (Fig. 1). It is interesting that Womersley (1994, p. 247) considered *Polycoelia laciniata* similar to *Pugetia* spp. However, *Pugetia* has undergone considerable taxonomic reduction since that time. Although, *P. laciniata* does match *Pugetia* as restricted by Clarkston & Saunders (2012) in being nonprocarpic, it is a better match to their segregate procarpic genus *Salishia* for the shape of the cells in its carpogonial branch. This combination of features noted for *Polycoelia laciniata* (Womersley, 1994), but not a perfect match with either *Pugetia* or *Salishia*, also characterizes *P. harveyana* in support of our molecular results. Consequently we recommend interim inclusion of this species in *Polycoelia* (Fig. 1). However, there is some genetic divergence between *P. harveyana* and the type *P. laciniata* (Fig. 1), and the former lacks the highly distinctive single-layered central medulla of the latter (Womersley 1994, fig. 77m), which may warrant separate genera following further study. Our interim taxonomic change renders *Polycoelia*, like *Euhymenia* above and *Thamnophyllis* below, a genus with species characterized by either largely entire foliose or deeply branched thalli. Our work here, and that of colleagues (D'Archino *et al.*, 2016), is rapidly reducing the number of species assigned to *Pugetia*, which is becoming a genus more and more limited to the west coast of North America.

Polycoelia harveyana* (J.Agardh) G.W.Saunders, *comb. nov.

Basionym: *Kallymenia harveyana* J.Agardh, *In systemata algarum hodierna adversaria*, 40 (1844).
Lectotype: LD, Herb. Agardh 090097 (Clarkston & Saunders, 2012, p. 51; Guiry & Guiry, 2016).
Representative DNA barcode: KX808013 (COI-5P).

Huonia* G.W.Saunders, *gen. nov.

Description: Member of the Kallymeniaceae with foliose blades; medulla filamentous, with an interconnected network of stellate cells, these variously slender or slightly swollen, or transformed into and bearing secondarily derived filaments of slightly to highly swollen cells full of starch-like inclusions; inner cortex typically one or two layers of periclinally compressed cells bearing 1-2 layers of smaller isodiametric outer cortical cells. Female and postfertilization structures unknown.
Etymology: Named for the Huon River, which opens into the only channel where this genus has been collected.
Type species: *Huonia sandersonii* G.W.Saunders, *sp. nov.*

Huonia sandersonii* G.W.Saunders, *sp. nov. **Figs 21-25**

Description: Thalli consisting of dark red individual blades, these typically procumbent to excentrically peltate, borne on a stipe 2.0-2.5 mm wide by 4-5 mm long and anchored by a prominent crustose holdfast (Fig. 21). Blades oval to reniform, to 9 cm wide by 6 cm tall, at times slightly lobed or dissected, the margins smooth when intact. Blades in section 170-300 µm (Fig. 22), thickening to 500-550 µm at the margins. Medulla at first glance appearing to be composed of spherical to oval cells, 4-10 µm wide by 4-20 µm long, filled with starch-like inclusions (Fig. 22). On closer inspection, most clearly seen at the margins, an interconnected

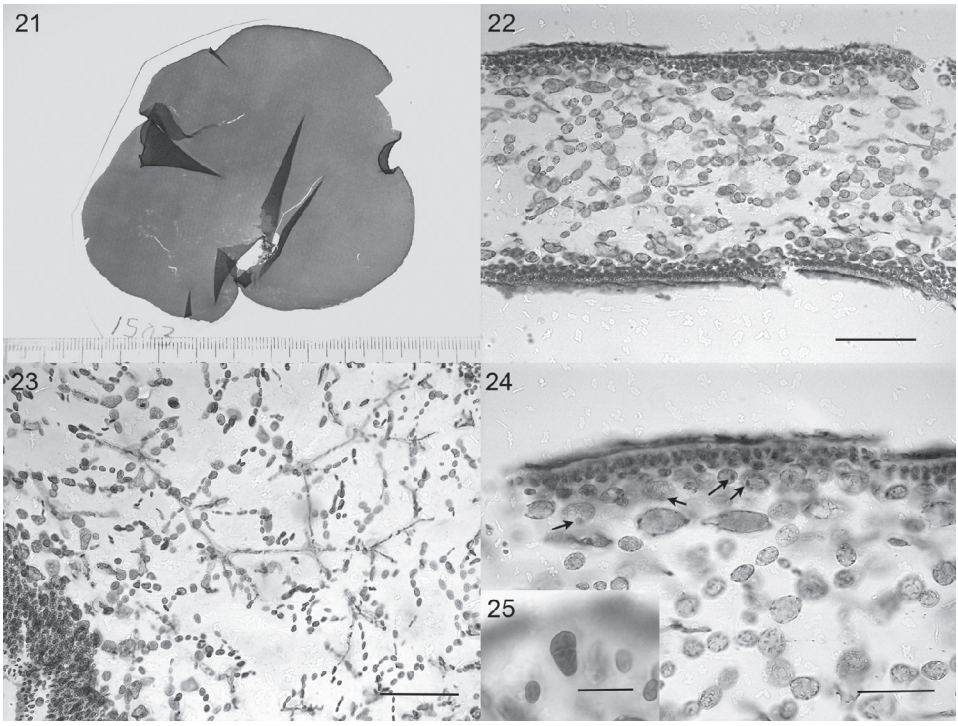
network of medullary filaments linked through stellate cells is revealed which variously transform into and or bear the secondarily derived filaments of the spherical cells (Fig. 23). Inner cortex composed of three or four layers of progressively smaller cells 10-50 µm wide by 7-20 µm high and containing one or two crystalline inclusions, the outer layer subtending an outer cortex of one or two layers of ovoid cells 3-4 µm wide by 7-8 µm tall (Fig. 24). Tetrasporangia decussate to regularly cruciate, 12-13 µm wide by 15-18 µm high, scattered in outer cortex (Fig. 25). Gametangia unknown.

Type collection: Coll. *G.W. Saunders*, November 28, 2002, Arch Rock, where the Huon River estuary opens into D'Entrecasteaux Channel, Tasmania, Australia, 43.2938°S, 147.1352°E, subtidal, 10 m on rock. Holotype, UNB [GWS001503, BOLD ABMMC1573-07 (Fig. 21)].

Etymology: Named in appreciation of Dr. Craig Sanderson who has graciously supported our collecting efforts in southern Tasmania and first introduced GWS, along with his long time collaborator GTK, to dive sites around the type locality.

Holotype DNA barcode: KX807996 (COI-5P).

Additional specimens examined: See Table S1 (doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1).



Figs 21-25. *Huonia sandersonii* G.W.Saunders, *gen. et sp. nov*. **21.** Dried-pressed holotype specimen (GWS001503). **22.** Shallow, evenly developed ventral and dorsal cortexes and broad medulla of moniliform filaments in long-section proximal to an inflated margin (GWS005970). **23.** The laxer and broader moniliform medulla within an inflated margin (GWS005970). **24.** Detail of the transition between cortex and medulla, most cells with dark-staining bodies (arrows) of unknown nature and function (GWS005970). **25.** A mature, decussate-cruciate tetrasporangium in the outer cortical layer (GWS002618). Scale bars: 21 = centimeter ruler; 22, 23 = 80 µm; 24 = 40 µm; 25 = 16 µm.

Distribution: Known from the type locality and nearby localities in D'Entrecasteaux Channel, south of Hobart, Tasmania (Table S1).
Remarks: This species is assigned to one of three new monospecific genera (see *Rhipidomenia* and *Tytthomenia* below) from the southeast corner of Tasmania, a flora in which novel red-algal taxa are more the norm than the exception (e.g. Scott *et al.*, 2013). Again, this species would most likely have been assigned to *Kallymenia* on strictly morphological grounds, but our molecular phylogeny resolves it as a distant, relatively deep lineage (Fig. 1).

Nothokallymenia A.Vergés & L.Le Gall, *gen. nov.*

Description: Member of the Kallymeniaceae with foliose blades; medulla filamentous and lax, the slender filaments intermixed with a network of ganglionic and deeply staining refractive cells that issue long narrow arms; inner cortex typically one or two layers of periclinally compressed cells bearing two or three layers of smaller outer cortical cells that diminish in size outwardly. Nonprocarpic, carpogonial branch system monocarpogonial, with 3-6 subsidiary cells enlarged and lobed. Fusion cell prominent, deeply lobed, incorporating the supporting and subsidiary cells, and forming numerous connecting filaments that attach to the supporting cell of the auxiliary cell system, which has up to six subsidiary cells. Gonimoblast filaments borne on the connecting filaments, forming a protruding gonimoblast.
Etymology: Named for the Greek *notho* owing to the similarity in habit of its type species to that of *Kallymenia, K. reniformis*, with which it grows sympatrically.
Type species: *Nothokallymenia crouaniorum* (A.Vergés & L.Le Gall) A.Vergés & L.Le Gall, *comb. nov.*

Nothokallymenia crouaniorum (A.Vergés & L.Le Gall) A.Vergés & L.Le Gall, *comb. nov.*

Basionym: *Kallymenia crouaniorum* A.Vergés & L.Le Gall in Robuchon *et al.*, *European journal of phycology* 49: p. 505, figs 1-23 (2014).
Holotype: PC0171066 (Robuchon *et al.*, 2014, 505, fig. 1; Guiry & Guiry, 2016).
Representative DNA barcode: KM896877 (*rbc*L).
Remarks: In our molecular phylogeny, three Mediterranean specimens (LLG2712, LLG2879, LLG2876) collected in Port-Cros national Park joined *Nothokallymenia crouaniorum* in a well-supported lineage. These represent three additional species assignable to this novel genus (Fig. 1).

Thamnophyllis R.E.Norris

Type species: *Thamnophyllis pocockiae* R.E.Norris, 1964.
Remarks: Our molecular analyses restrict this genus to three species from southern Africa: the type, *T. pocockiae*, *T. discigera* (J.Agardh) R.E.Norris, and an undescribed foliose species (*Thamnophyllis* sp.1SAfr; Fig. 1). The last-mentioned is based on a cystocarpic specimen (Table S1) for which details of the carpogonial and auxiliary-cell systems are a good match to the other species in this genus, thus supporting the molecular results (data not shown). As with *Euhymenia* and *Polycoelia* above, branched and foliose taxa are united in a single lineage diminishing the taxonomic utility of this character. Two species from Australia/New Zealand previously attributed to *Thamnophyllis* [viz. *T. lacerata* Womersley & R.E.Norris and *T. laingii* (J.Agardh) R.E.Norris] resolve elsewhere in our phylogeny (Fig. 2) and require transfer to two relatively novel genera of similar provenance (see *Stauromenia* and

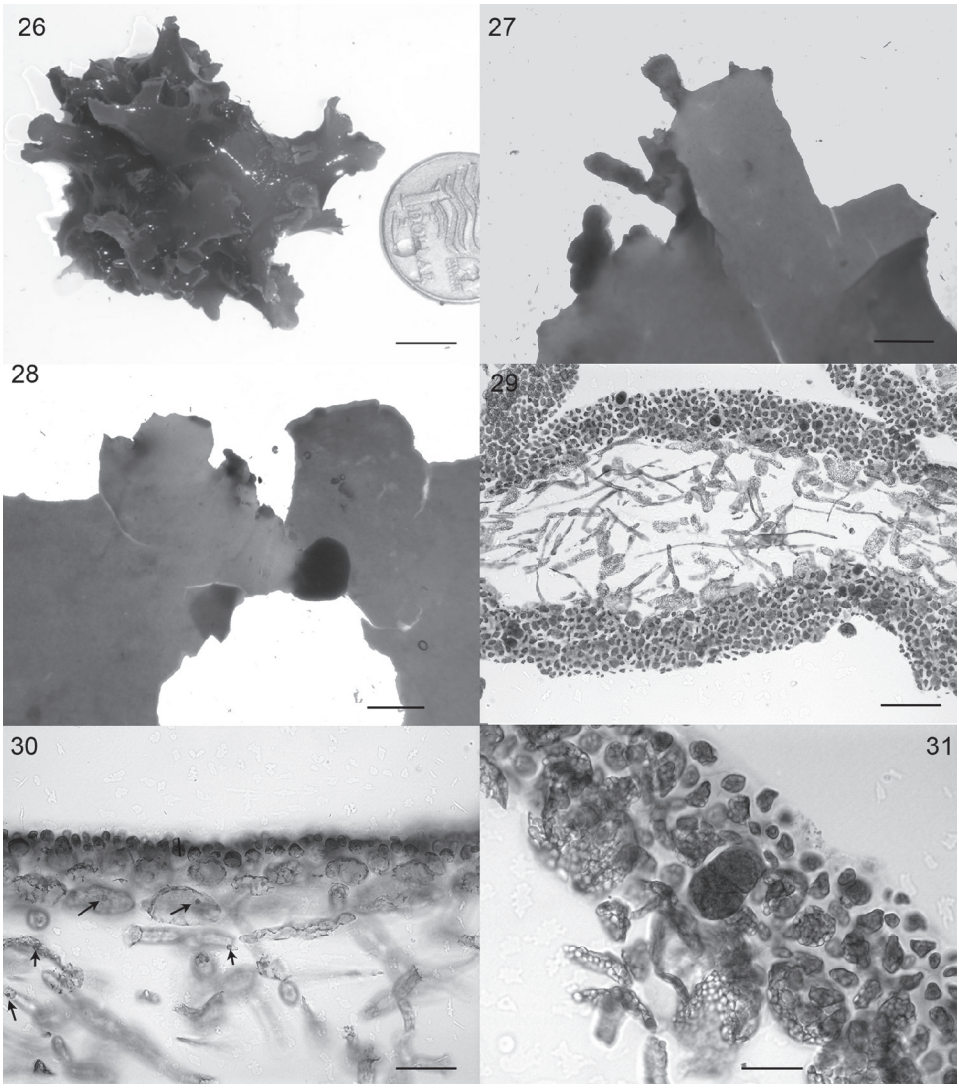
Judithia below, respectively; Figs 1, 2). Consequently this study represents the first time that bona fide representatives of *Thamnophyllis* were included in phylogenetic analyses, as all previous studies (references throughout this manuscript) have used species that we now know belong to other kallymeniacean genera.

Tytthomenia G.W.Saunders, *gen. nov.*

Description: Member of the Kallymeniaceae with foliose blades; medulla loosely filamentous, the filaments consisting of interconnected networks of weakly staining stellate cells that typically issue long thin arms parallel to the thallus surface that are cross-connected by filaments of irregularly shaped and sized cells; inner cortex typically two or three layers of horizontally elongate to subspherical cells bearing one or two layers of smaller isodiametric outer cortical cells. Female, postfertilization structures and spermatangia unknown.
Etymology: From the Greek *tytthes* for little and *hymen* in reference to the small membranous blades of individuals of the type and only species.
Type species: *Tytthomenia barrettii* G.W.Saunders, *sp. nov.*
Remarks: This genus joins two additional monospecific genera described from the rich flora of southeast Tasmania (see *Huonia* above and *Rhipidomenia* below).

Tytthomenia barrettii G.W.Saunders, *sp. nov.* **Figs 26-31**

Description: Thalli small, up to 5 cm, composed of procumbent to weakly erect blades (Fig. 26) that form projections (at times gall-like structures) at the margins (Fig. 27), the margins variously anastomosing to other blades, forming secondary attachments to substratum, or developing into further marginal blades (Fig. 28). Blades 275-325 µm thick in section; medulla lax (fully intact sections difficult to obtain) with an interconnected network of weakly staining stellate cells, these typically with long thin arms 3-6 µm wide running parallel to the blade surface and laterally connected by cells and filaments of highly variable size and shape (Fig. 29), the peripheral cells ultimately bearing an inner cortex of two or three layers of progressively smaller cells 12-30 µm tall by 15-70 µm long, the outer cortex consisting of one or two layers of small isodiametric cells 6-10 µm in diam. that do not completely cover the subsurface cells (Fig. 30). Cells of the inner cortex and medulla commonly containing darkly staining inclusions (Fig. 30). Tetrasporangia cruciate, 17-20 by 25-27 µm, scattered in the cortex on both surfaces (Fig. 31). Gametangia unknown.
Type collection: Coll. *N. Barrett*, January 22, 2010, Reef west of Verona Sands boat launch, Huon River, Tasmania, Australia, 43.2750° S, 147.1257° E, subtidal 17 m on rock. Holotype, UNB [GWS015382, BOLD ABMMC7559-10 (Figs 26-28)]. Isotypes, UNB [GWS015391, tetrasporangial (Figs 29-31), GWS015503, GWS015505].
Etymology: Named for Professor Neville Barrett of the University of Tasmania who has generously supported our fieldwork during Craig Sanderson's absences and who furthered our research in southeast Tasmania. He further collected the holotype specimen during one of our dives under his guidance.
Holotype DNA barcode: HM917737 (COI-5P).
Distribution: Presently only known from the type locality in Tasmania.
Remarks: The marginal outgrowths on blades of this species are occasionally spinose, as happens in *K. spinosa* Womersley & R.E.Norris, but that species differs in having larger (3-7 cm), cuneate and stipitate blades, a dense medulla of slender filaments, and large darkly staining refractive cells (Womersley & Norris, 1971). This is the second monotypic genus that we describe for southeastern Tasmania



Figs 26-31. *Tytthomenia barrettii* G.W.Saunders, *gen. et sp. nov*. **26-28.** From the holotype (GWS015382). **26.** The decumbent living habit. **27.** Linear proliferations and gall structure from blade margins. **28.** A gall-like growth at a blade margin bearing another blade. **29.** A long-section of a tetrasporic isotype blade (GWS015931) showing the mixture of inflated cells and narrow filaments in the medulla. **30.** Detail of the transistion between ovoid inner-cortical cells and filaments of the outer medulla (isotype GWS015931); darkly staining inclusions of unknown function (arrows) occur in both cortical and medullary cells. **31.** A cruciately divided mature tetrasporangium in the cortex of isotype GWS015931. Scale bars: 26 = 1 cm; 27, 28 = 1 mm; 29 = 100 μm; 30 = 50 μm; 31 = 20 μm.

(see *Huonia,* above) that likely would also have been assigned to *Kallymenia* in the absence of molecular data. In this case, *T. barrettii* is at least sister to the lineage including *Austrokallymenia* and *Kallymenia* in contrast to the distant *Huonia* (Fig. 1).

Austrokallymenia Huisman & G.W.Saunders, *gen. nov.*

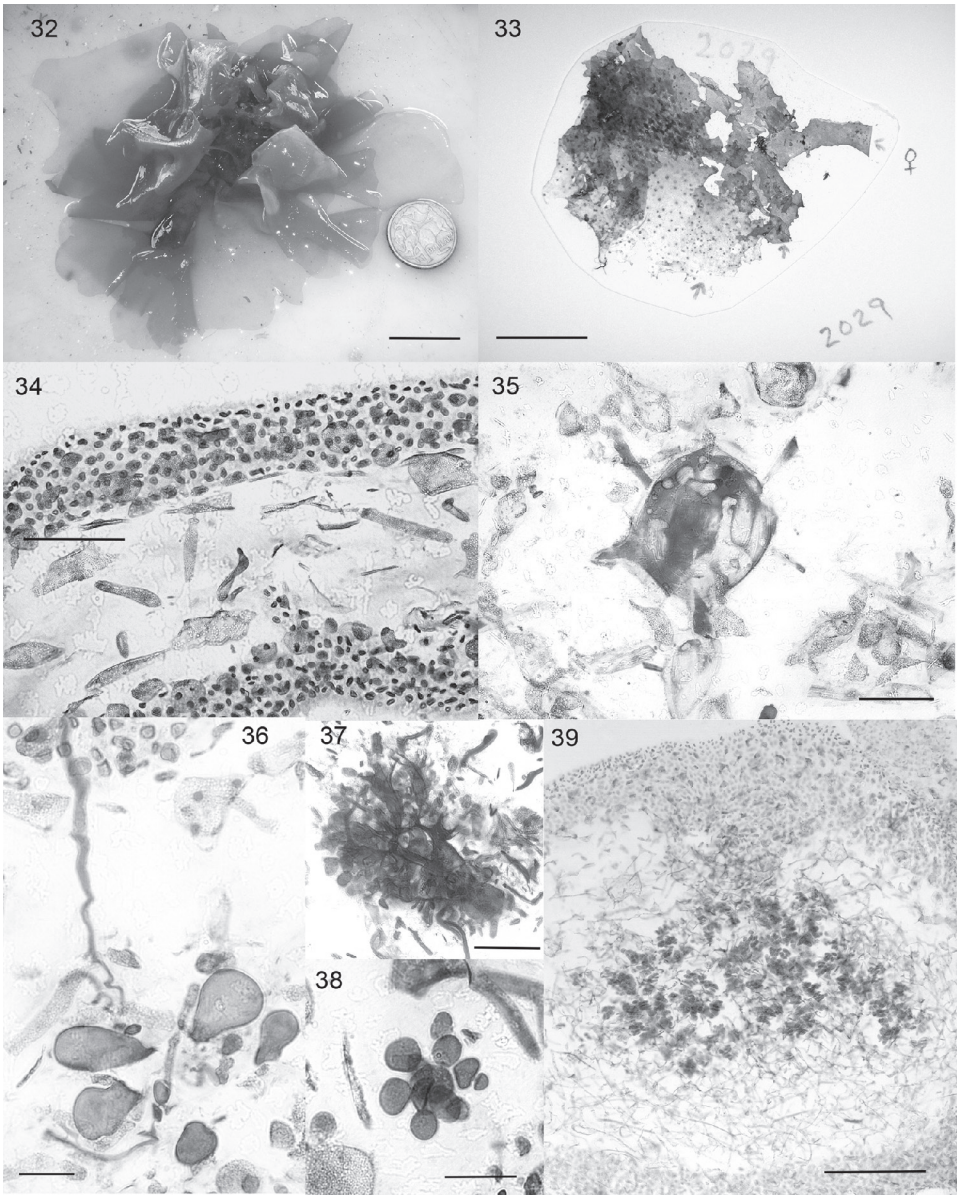
Description: Member of the Kallymeniaceae with foliose thalli, the blades solidly membranous or apparently obligately perforate, the medulla primarily of sparse filaments and stellate cells with elongate, slender arms. Supporting cells polycarpogonial and lacking subsidiary cells, bearing 3-16 carpogonial branches, these generally with relatively large ovate to pyriform basal cells. Nonprocarpic, fusion cell prominent, incorporating the supporting and basal cells of carpogonial branches. Auxiliary cells with 5-8 single- or (rarely) two-celled subsidiary laterals. Carposporophytes embedded in the medulla and distributed widely across blades, composed of clusters of carposporangia separated by sterile filaments. Spermatangia arising from outer cortical cells or from spermatangial mother cells borne on outer cortical cells. Tetrasporangia scattered in the cortex, subspherical to ellipsoidal, cruciately or irregularly zonately divided, basally or laterally pit-connected.
Etymology: From Latin *australis* (southern) and the Greek *calli* (beautiful) and *hymen* (a membrane), in reference to the southern hemisphere distribution of the included species and the habit of the thallus. The name also alludes to the affinities of the genus with *Kallymenia*.
Type species: *Austrokallymenia cribrogloea* (Womersley & R.E.Norris) Huisman & G.W.Saunders, *comb. nov.*
Remarks: Our molecular analyses resolve several Australian species in a clade sister to the one that includes European species of *Kallymenia*, including the generitype *K. reniformis* (Fig. 1). Consequently we transfer two of them represented in our molecular analyses, *K. cribrogloea* Womersley & R.E.Norris and *K. rosea* Womersley & R.E.Norris, to the new genus *Austrokallymenia* and describe the two new species *A. rebeccae* G.W.Saunders & Kraft and *A. roensis* Huisman & G.W.Saunders for specimens collected from Lord Howe and Norfolk Islands, and Rottnest Island, respectively. *Kallymenia schizophylla* J.Agardh and an undescribed species from South Africa (*A.* sp.1SAfr) also join this lineage (Fig. 1). The new genus is morphologically and reproductively similar to *Kallymenia* and our decision to erect a new genus is driven primarily by our molecular analyses. One possibly distinctive character is the morphology of the carpogonial branches, which in *Austrokallymenia* tend to have ovate to pyriform basal cells that are considerably larger than hypogynous cells, but the consistency of this feature requires further study.

Austrokallymenia cribrogloea (Womersley & R.E.Norris) Huisman & G.W.Saunders, *comb. nov.*

Basionym: *Kallymenia cribrogloea* Womersley & R.E.Norris, *Australian journal of botany,* Suppl. 2: 7, figs 6-12, 78-80 (1971).
Holotype: AD A35158 (Womersley, 1994, p. 235; Guiry & Guiry, 2016).
Representative DNA barcode: HM918159 (COI-5P).
Remarks: The obligately perforate *Austrokallymenia cribrogloea* proves to be a complex of at least three genetic groups, which span from Western Australia to New South Wales (Fig. 1, Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1). Further study is needed.

Austrokallymenia rebeccae G.W.Saunders & Kraft, *sp. nov.* Figs 32-39

Description: Thalli typically single, composed of procumbent to semi-erect, non-perforate blades 6-18 cm in diam. that are irregularly lobed and smooth-margined (Figs 32, 33). Blades delicate and difficult to section, 300-325 µm wide; medulla with few 3-7 µm wide periclinal and anticlinal to oblique filaments, the latter traversing the medulla from side to side (Fig. 34), the cells occasionally inflating to



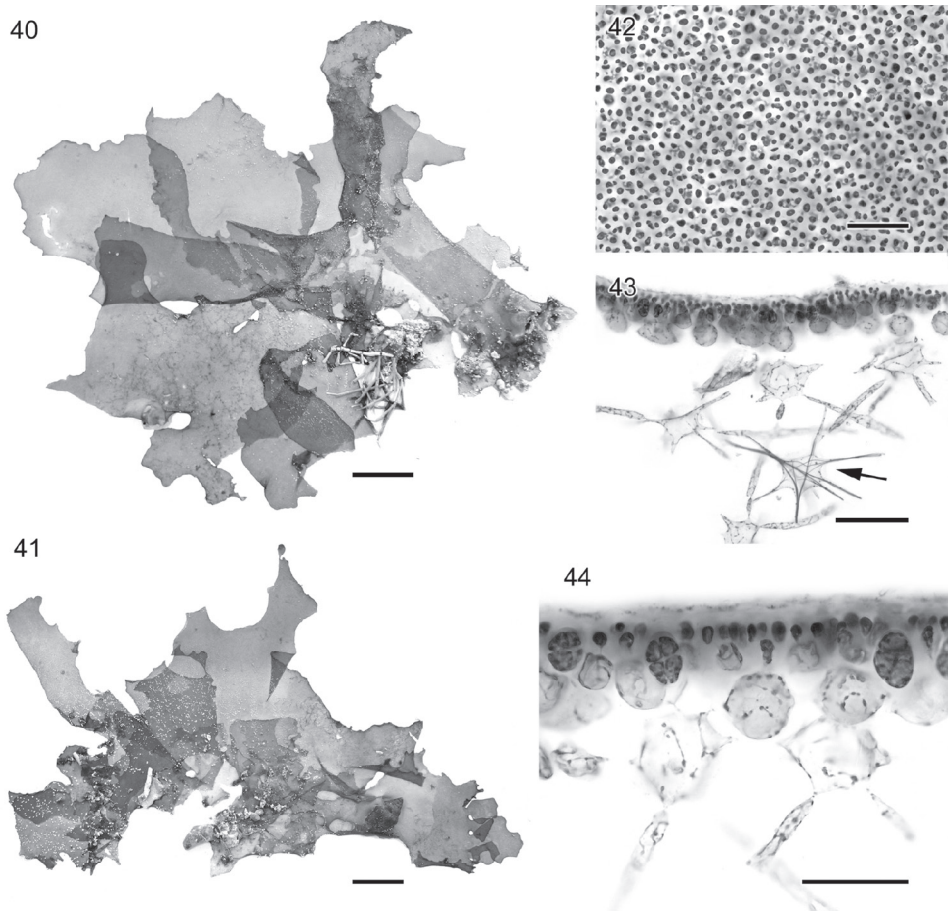
Figs 32-39. *Austrokallymenia rebeccae* G.W.Saunders & Kraft, *sp. nov*. **32.** Living habit of a Norfolk Island paratype specimen (GWS034990). **33.** Pressed habit of the cystocarpic holotype from Lord Howe Island (GWS002029). **34.** Mixture of inflated and narrowly elongate medullary cells in cross-section (GWS034990). **35.** A subspherical outer-medullary cell with short stellate arms in surface view (GWS002029). **36.** Polycarpogonial, basal cells ovate to pyriform and significantly larger than their associated hypogynous cells and carpogonia (GWS034990). **37.** Fusion of the presumably diploidized supporting cell with other elements of the polycarpogonial system to form a complex of radiating connecting filaments (GWS034990). **38.** An auxiliary cell surrounded by single-celled and two-celled subsidiary laterals (GWS034990). **39.** The mixture of carposporangial and sterile filaments of a deeply embedded carposporophyte (GWS002029). Scale bars: 32, 33 = 2.5 cm; 34, = 100 μm; 35, 37, 38 = 50 μm; 36 = 25 μm; 39 = 200 μm.

20 µm diam. and forming loose interlaced networks; outer-medulla/inner-cortex typically two or three layers of flattened to inflated cells 15-115 µm wide by 12-30 µm tall (Fig. 34), the larger innermost cells appearing stellate in surface view (Fig. 35); outer cortex is one or two incomplete layer(s) of smaller isodiametric to slightly wider than tall outer-cortical cells 5-10 µm wide by 3-6 µm tall (Fig. 34). Supporting cells with three to as many as eight carpogonial branches, each three-celled with a large ovate to pyriform basal cell subtending a much smaller spherical hypogynous cell and terminated by a conical carpogonium with a long spiralled trichogyne (Fig. 36). Post-fertilization details were difficult to determine, but a substantial fusion cell was formed in the polycarpogonial complex that issued multiple connecting filaments (Fig. 37). Auxiliary cells bore 5-8 single- or (rarely) two-celled subsidiary laterals (Fig. 38). Carposporophytes embedded in the medulla (Fig. 39) and distributed widely across blades, composed of clusters of carposporangia separated by sterile filaments; cystocarps typically protruding primarily on one or the other surface. Male structures and tetrasporangia unknown.
Type collection: Coll. *G.T. Kraft*, January 30, 2004, Yellow Rock, Lord Howe Island, New South Wales, Australia, 31.515°S, 159.0344°E, drift. Holotype, UNB [GWS002029, BOLD ABMMC5076-09, cystocarpic (Figs 33, 35, 39)].
Etymology: Named by the first author for Rebecca Harrington Kraft in sincere thanks for her masterful organization of numerous collection excursions, including the trip to Lord Howe that resulted in collecting this holotype specimen.
Holotype DNA barcode: HM915972 (COI-5P).
Additional specimens examined: See Table S1 (doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1).
Distribution: This species has only been genetically verified from the type locality, Lord Howe I., and the relatively nearby Norfolk I., Australia (Table S1).

Austrokallymenia roensis Huisman & G.W.Saunders, ***sp. nov.*** **Figs 40-44, S3***

Description: Thallus (Figs 40, 41) foliose, rose red, non-perforate, sprawling, 8-10 cm in maximum dimension, the blades sometimes wider than long, membranous, with numerous marginal pads attaching to the substratum and linking adjacent blades. Blades irregularly lobed, smooth-surfaced, c. 400 µm thick. Medulla (Fig. 43) of sparse filaments 5-12 µm diam., these often crossing between inner cells of the dorsal and ventral cortexes; stellate cells large, (central bodies 60-70 µm in diam.) and lightly staining. Ganglionic cells present, occasionally with several linear inclusions crossing the cell body (Fig. 43, arrow) and extending into the narrow arms. Cortex of three or four layers of similar-sized cells. Inner cortical cells stellate, 35-50 µm in diam. centrally, bearing numerous radiating arms; outer cortex 1-3 layers of progressively smaller cells, those at the surface small (4-6 µm in diam.), rounded, deeply pigmented (Figs 42, 43). Tetrasporangia scattered in the cortex, subspherical to ellipsoidal, regularly cruciately divided (Fig. 44), 20-25 µm tall by 15-18 µm wide, basally or laterally pit-connected. Other reproductive structures not observed.
Type collection: Coll. *J.M. Huisman*, January 27, 2014, Roe Reef, Rottnest Island, Western Australia, Australia, 31.9743°S, 115.5417°E, epilithic on undercut reef at 15-m depth. Holotype, PERTH [08709289, BOLD ABMMC19608-14, tetrasporangial (Figs 40, 41)].
Etymology: The epithet refers to the subtidal type locality (Roe Reef) north of Rottnest Island, Western Australia. The reef itself was named for John Septimus Roe, an explorer and the first Surveyor-General of Western Australia.
Holotype DNA barcode: KX808094 (COI-5P).

* See doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.2.



Figs 40-44. *Austrokallymenia roensis* Huisman & G.W.Saunders, *sp. nov*. (all PERTH 08709289). **40- 41.** Two specimens mounted on the holotype sheet (PERTH 08709289). **42.** Surface view of thallus. **43.** Section of thallus showing medulla of sparse stellate cells and a ganglionic cell with linear inclusions (arrow). **44.** Section of thallus showing cruciately divided tetrasporangia scattered in the cortex. Scale bars: 40, 41 = 1 cm; 42, 44 = 50 μm; 43 = 100 μm.

Distribution: Known only from the type locality and collection from Western Australia.
Remarks: Of the known Australian species previously referred to *Kallymenia*, *Austrokallymenia roensis* appears to be most similar to *K. rubra*, a seemingly rare species known with certainty only from two locations in South Australia. *Kallymenia rubra* differs, however, in being stipitate with a discoid holdfast (Womersley & Norris, 1971, p. 13-15, figs 26-31, 86; Womersley, 1994), whereas *A. roensis* forms a sprawling thallus with multiple marginal attachments. Structurally, *K. rubra* has darkly staining ganglionic cells in the medulla and outer cortical cells that form a palisade, which further serve to distinguish it from *A. roensis*. Unfortunately only tetrasporangial plants are known for *A. roensis* and we are thus unable to make comparisons of its gametophyte features with those of other non-perforate species. Our decision to recognise it as new is supported by its autonomy in molecular analyses (Fig. 1) and the absence of morphologically comparable taxa within the region.

Specimens of the type collection bore several epiphytic thalli of *Tanakaella itonoi* Huisman & Gordon-Mills, a species previously known only as an epiphyte of *Kallymenia* (= *Leiomenia*) *cribrosa* Harvey and *Thamnophyllis* (= *Stauromenia*) *lacerata* (Huisman & Gordon-Mills, 1994).

Austrokallymenia rosea* (Womersley & R.E.Norris) Huisman & G.W.Saunders, *comb. nov.

Basionym: *Kallymenia rosea* Womersley & R.E.Norris, *Australian journal of botany,* Suppl. 2: 9, 10, figs 13-18, 81, 82 (1971).

Holotype: NSW 287229 (Womersley & Norris, 1971, p. 11; Guiry & Guiry, 2016).

Representative DNA barcode: KX808001 (COI-5P).

Remarks: Our collections of *Austrokallymenia rosea* from Lord Howe Island [Table S1; *A. rosea* (LH)] may be a cryptic sibling species [1.2% divergence in COI-5P from mainland and Norfolk Island populations; Fig. 1; *A. rosea* (LH)]. Further study is necessary.

Austrokallymenia schizophylla* (J.Agardh) G.W.Saunders, *comb. nov.

Basionym: *Kallymenia schizophylla* J.Agardh, *Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar, Stockholm* 5: 48 (1848).

Lectotype: LD, Herb. Agardh 24572 (Norris 1964, p. 97, 100, pl. 2A). This species was described by J. Agardh based on material sent to him by Harvey, collected from South Africa at 'Cap b. Spei, in sinu tabulari' [Cape of Good Hope, Table Bay]. In addition to the lectotype in LD, there are several Harvey specimens in TCD labelled 'CBS', one of which (TCD0000157) also has *Kallymenia schizophylla* in Harvey's hand and 'vera' [true] (see http://plants.jstor.org/stable/10.5555/al.ap.specimen.tcd0000157). The habit illustration in Stegenga *et al.* (1997, pl. 98, fig. 3) is a good representation and a figure of a pressed specimen is included in Braune & Guiry (2011, fig. 163:5).

Representative DNA barcode: KX808009 (COI-5P).

Remarks: *Austrokallymenia schizophylla* and a second, undescribed species from South Africa (*A.* sp.1SAfr; Fig. 1, Table S1 (doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1)) extend the range of this genus from Australia to southern Africa.

Kallymenia J.Agardh

Type species: *Kallymenia reniformis* (Turner) J.Agardh, 1842.

Remarks: The genus *Kallymenia* is greatly reduced in our system. Of the numerous species included in our phylogenetic analyses, it retains only *K. ercegovicii*, *K. feldmannii*, *K. patens*, *K. reniformis*, and an undescribed species (LLG2684) from the Port-Cros national parc, Marseille, France (Fig. 1, Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1). These species are all polycarpogonial with the carpogonial complex lacking subsidiary cells, and are nonprocarpic with the auxiliary cell system having associated subsidiary cells. As recognized here, all species are restricted to the Mediterranean Sea except *K. reniformis*, which is distributed in the northeast Atlantic from Macaronesia to the northern United Kingdom. As such, the genus may be endemic to this region having recently diversified in the Mediterranean Sea. Other regions reported to have species of *Kallymenia* require further study to test this hypothesis [e.g. the Caribbean Sea (Littler & Littler, 2000), Hawaii (Abbott, 1999)].

Rhipidomenia G.W.Saunders, *gen. nov.*

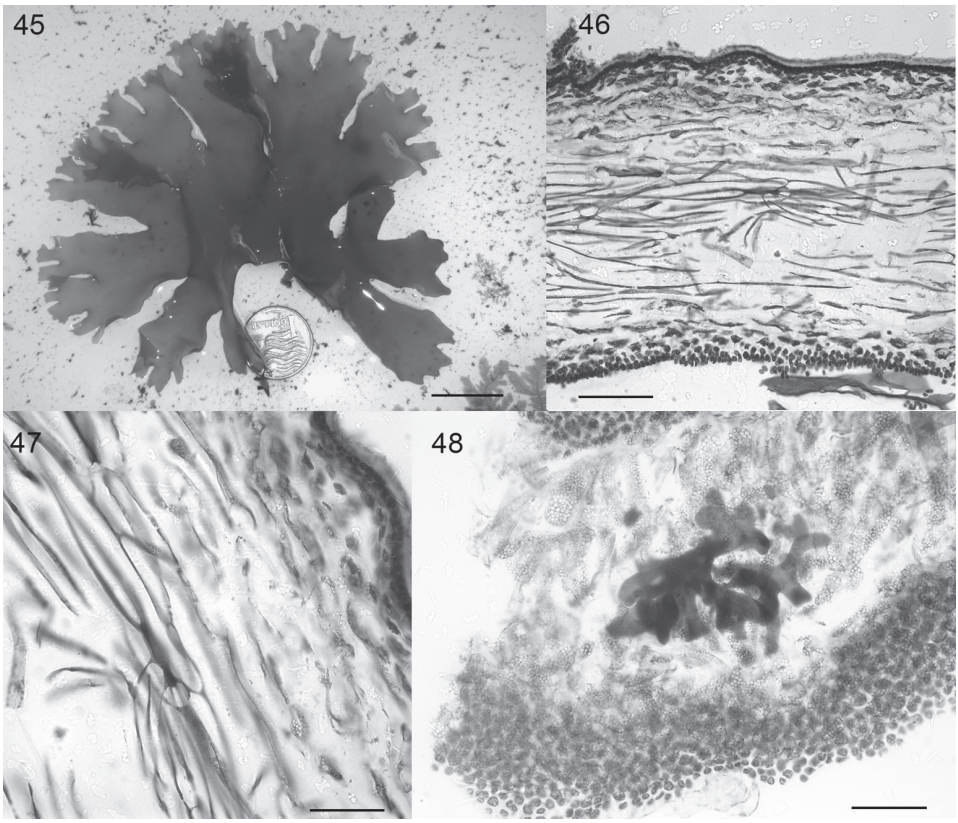
Description: Member of the Kallymeniaceae with complanate, subdichotomous blades (Fig. 45); medulla loose, composed of predominantly longitudinally aligned, secondarily pit-connected filaments (Fig. 46) and occasional stellate cells bearing numerous moderately staining narrow arms (Fig. 47). Supporting cells monocarpogonial, themselves lobed and usually bearing four lobed subsidiary cells; basal cells of carpogonial branches lobed similar to subsidiary cells, the hypogynous cells elongate, carpogonia conical, the supporting-cell complex forming a lobed fusion cell following presumed fertilisation (Fig. 48). Auxiliary cells in separate complexes (*i.e.* the species is nonprocarpic), bearing *ca* eight single-celled or, frequently, two-celled subsidiary laterals.
Etymology: From the Greek *rhipidos* for fan and *hymen,* in reference to the flattened membranous, spreading and basally attenuated fronds.
Type species: *Rhipidomenia polycoelioides* (J.Agardh) G.W.Saunders, *comb. nov.*
Remarks: This is the final of three novel monospecific genera along with *Huonia* and *Tytthomenia* that we describe from the species-rich waters of southeastern Tasmania.

Rhipidomenia polycoelioides (J.Agardh) G.W.Saunders, *comb. nov.*

Basionym: *Kallymenia polycoelioides* J.Agardh, *Species genera et ordines algarum, seu descriptiones succinctae specierum, generum et ordinum, quibus algarum regnum constituitur. Volumen tertium: de Florideis curae posteriores. Part 1*: 687 (1876).
Holotype: LD, Herb. Agardh 24843 (Womersley, 1994, p. 242; Guiry & Guiry, 2016).
Representative DNA barcode: HM917766 (COI-5P).
Remarks: Womersley (1994) transferred this seldom-collected species from *Kallymenia* to *Cirrulicarpus* with some hesitation, calling for further taxonomic study in light of its subdichotomous (as is typical of *Cirrulicarpus*) rather than foliose habit and a "soft", non-cartilaginous texture which is more typical of *Kallymenia*. Our study shows that it fails to join with either of those genera in phylogenetic analyses (Fig. 1), thus necessitating its removal to a new genus. As with those of Womersley (1994), our collections are few and restricted to southeastern Tasmania, the site of all records to date. The material sequenced matches the protologue description (Agardh, 1876) and observations of Womersley (1994) in regard to habit, vegetative anatomy, and the lobed fusion cells (Figs 45-48).

Euthora J.Agardh

Type species: *Euthora cristata* (C.Agardh) J.Agardh, 1847.
Remarks: Justification for *Euthora* as a genus distinct from *Callophyllis* had preoccupied taxonomists for over a century until Harper & Saunders (2002, and references therein) generated molecular data favouring the recognition of *Euthora*. This judgment was later supported by Clarkston & Saunders (2010) and is confirmed in the present study (Fig. 1). *Euthora* currently includes the widely distributed type species, *E. cristata* (C.Agardh) J.Agardh, the little-known *E. tristanensis* Baardseth from the south Atlantic, and the recently described northeastern Pacific *E. timburtonii* Clarkston & G.W.Saunders. The last-mentioned was described only from non-reproductive material (Clarkston & Saunders, 2010). Fertile collections made and accessed by one of the current authors (GTK) that predated the formal description of *E. timburtonii*, however, now allow us to provide many of its reproductive details.



Figs 45-48. *Rhipidomenia polycoelioides* (J.Agardh) G.W.Saunders, *comb. nov*. **45.** A typical, regularly dichotomous thallus from near the type locality (GWS015417). **46.** The narrow cortexes and densely filamentous medulla of a blade in long-section (GWS015417). **47.** A cell with dark contents, slightly inflated central portion and very fine arms in the central medulla. **48.** The apparent fusion product of a supporting cell and its highly lobed subsidiary cells following presumed fertilization. No traces of carpogonial branches or trichogynes are evident (GWS015422). Scale bars: 45 = 2.5 cm; 46 = 100 μm; 47, 48 = 50 μm.

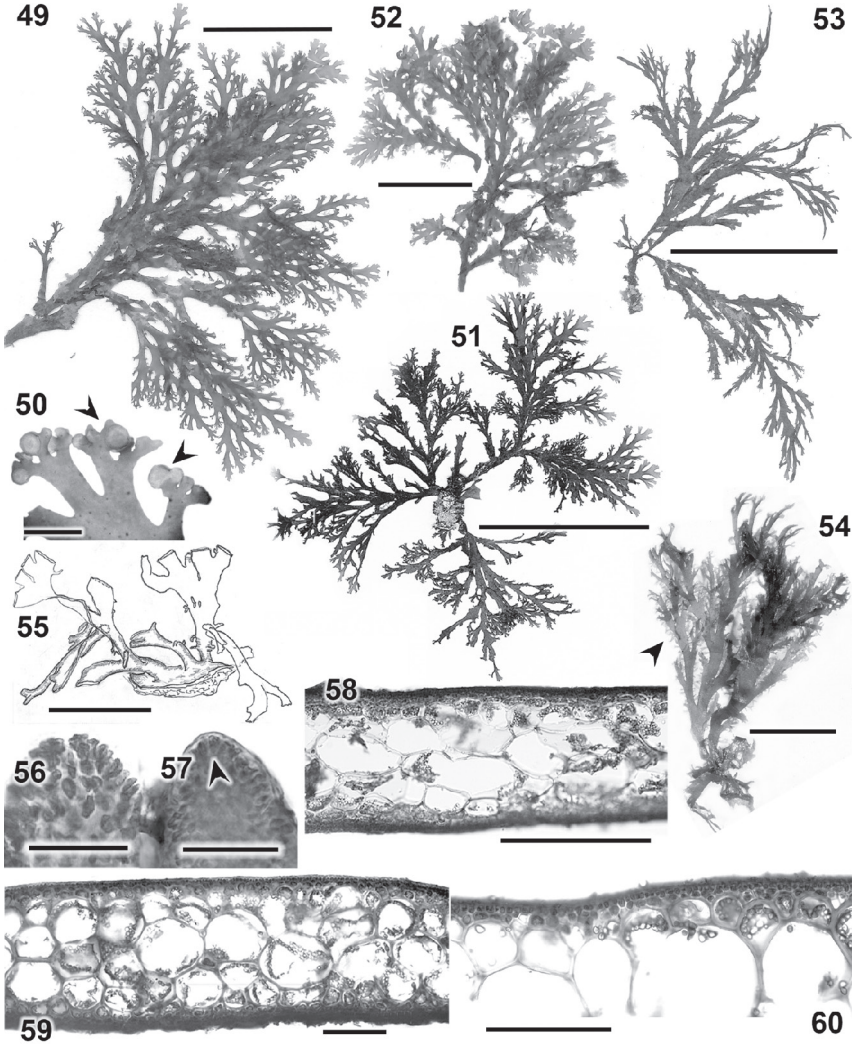
Euthora timburtonii Clarkston & G.W.Saunders

Formal proposal of this distinctive species was based on 28 collections of non-reproductive thalli from nine localities in British Columbia (Clarkston & Saunders, 2010). Populations had been known for some time, however, by workers dredging primarily at Salmon Bank (48.43698°N, 123.010483°W) off the southeastern end of San Juan Island in the Puget Sound of Washington, but even though fruiting material was known the specimens had been mostly filed as "*Rhodophyllis* sp." and not further dealt with taxonomically. In October of 1977 GTK was privileged to spend time with Professor Richard Norris at the Friday Harbor Marine Laboratories, at which time he also made collections of the unnamed species at Salmon Bank, including cystocarpic, spermatangial and tetrasporangial material. Mistaking the single subsidiary cells on the supporting cells as generative auxiliary cells, he also regarded the species as a member of the Cystocloniaceae (then the Rhodophyllidaceae), only as a new member of the genus *Calliblepharis* because of the uniformly "cellular" cross-sections.

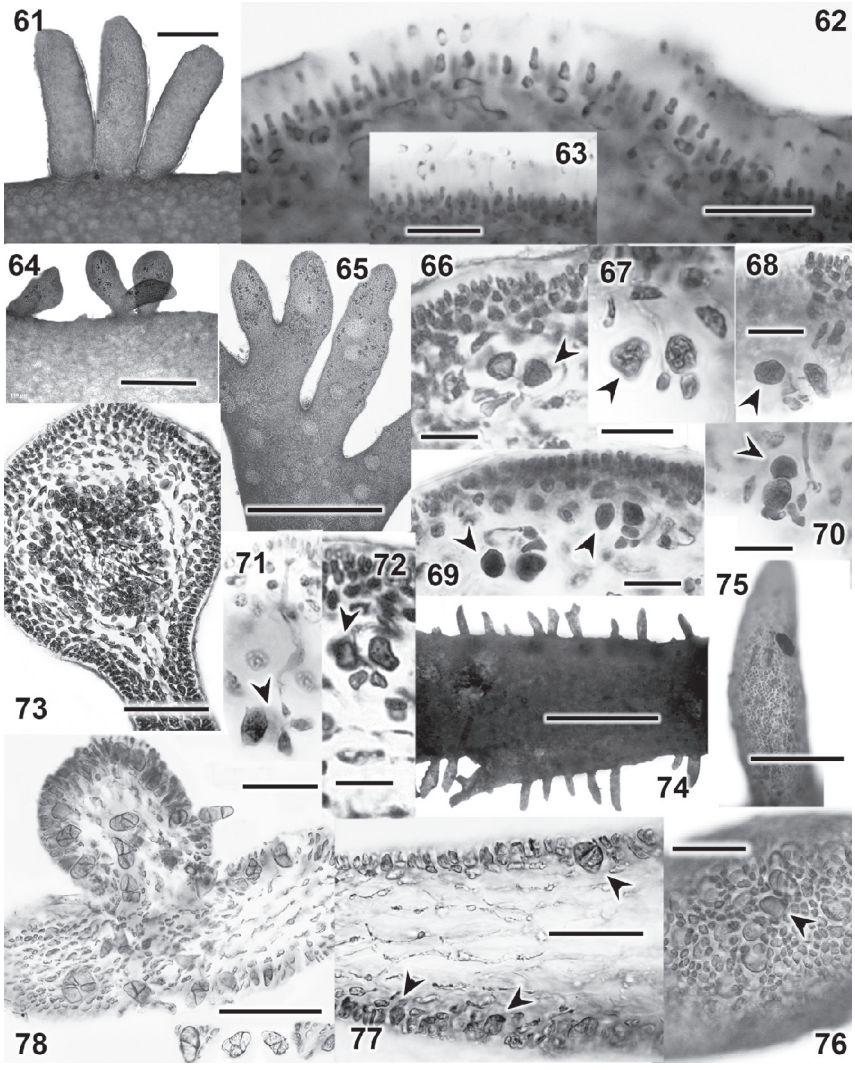
Additional kind gifts and loans of collections by Professors Norris and Michael Wynne (MICH) also from northwestern Washington have included cystocarpic, spermatangial and tetrasporangial plants, and this fertile material is fully concordant with the genus *Euthora* as defined molecularly by Clarkston & Saunders (2010).

Material examined: 1) Salmon Bank, San Juan Island, Washington (48.43698°N, 123.010483°W), coll. *R.E. Norris*, February 13, 1965, dredged. HO [K- REN 5141, spermatangial, tetrasporangial, vegetative (as "*Rhodophyllis*" sp.)]; coll. *M.J. Wynne*, June 20, 1968, dredged from 14.5 m. HO [K-Wynne #1903, vegetative (as "*Rhodophyllis*")]; coll. *G.I. Hansen*, July 7, 1969, dredged from 14.5-18 m. HO [K-Hansen 123, cystocarpic, tetrasporangial (as "*Rhodophyllis* sp.")]; coll. *M. Harlin*, 24 November, 1969, dredged from 11.5-18 m. HO [K-Harlin 1227, tetrasporangial (as "*Rhodophyllis*")]; coll. *R.E. Norris*, *G. & C. Kraft,* October 27, 1977, dredged from 12-15 m. HO [K-GEN-6396, female, tetrasporangial, vegetative (as "*Calliblepharis*? *sp. nov.*")]. 2) Partridge Point, West Beach, Whidbey Island, Washington (48.31°N, 122.73°W), coll. *R.E.* Norris, January 31, 1965, drift. HO [K-REN 5141a, vegetative (as *Rhodophyllis* sp.)]; coll. *R.E. Norris*, November 26 1966, drift. [K-REN 5318, cystocarpic, tetrasporangial (as "*Rhodophyllis* new species?")]; coll. *M.J. Wynne*, November 9 1968, drift. HO [K-Wynne 2352, vegetative (as "*Rhodophyllis*")].

Observations: Thalli 3-15 cm in length, distal fronds fanning to 7-11 cm wide in mature plants, the fronds planar and the axes flattened throughout (Figs 49, 51-54), mostly 1-3 mm in width, the branching pinnate to four orders, alternate to sub-opposite, the distal axes generally broader than those proximally (Figs 49, 51, 52) except in tetrasporangial fronds (Figs 53, 54); margins smooth except when cystocarps (Fig. 50), short marginal laterals bearing tetrasporangia (Figs 54, 74), spermatangia (Fig. 61) or procarps (Fig. 64) are present. Thalli arise as single or more typically multiple individuals from an extensive encrusting holdfast (Fig. 55). Apices domed and either seemingly multiaxial (Fig. 56) or more convincingly uniaxial (Fig. 57). Distal long-sections cellular throughout, 150-300 µm thick, the cells of the central medulla elongate and grading peripherally to progressively smaller cells (Fig. 58). Medullary cells in cross-section isodiametric (Fig. 59), the transition from medulla to the two-layered cortex abrupt (Fig. 60), the peripheral medullary cells often loaded with starch grains (Fig. 60). Spermatangia forming across the surfaces of perpendicular cylindrical dwarf laterals 150-225 µm in diam. by 550-660 µm long (Fig. 61). Spermatia ovoid, 3-4 µm long, budding off singly from a confluent layer of mother cells (Fig. 62), rounding as they pass out of the cuticle (Fig. 63). Gametophytes dioecious, the procarps concentrated in simple to forked marginal papillae (Fig. 64) or in ultimate branchings of main and lateral axes (Fig. 65). Carpogonial branches three-celled, the basal and hypogynous cells wedge-shaped (Figs 66, 69), globular (Fig. 67), rectilinear (Figs 69, 70) or irregularly contoured (Figs 71, 72), the carpogonial branches oriented either towards the thallus interior (Figs 66, 68, 69, 72), laterally (Figs 67, 70, 71) or the frond surface (Fig. 69). Supporting cells globular, bearing a single subsidiary cell of similar size (9-17 µm diam.) and shape in addition to the single carpogonial branch (Figs 66-72). Diploidization and gonimoblast initiation not observed; mature cystocarps globular (Figs 50, 73), 250-400 µm in diam., the carposporophyte consisting of a carposporangial mass (150-250 µm in diam.) traversed by pockets of sterile gametophytic cells and surrounded by a non-ostiolate pericarp of uniformly "cellular" construction (Fig. 73). Tetrasporangial fronds (Fig. 54) lined by mostly simple marginal projections 180-400 µm in length and 80-100 µm in width (Figs 74, 75), the tetrasporangia developing flush with the branch surface and not overlain by surface cortical cells at maturity (Fig. 76). Tetrasporangia basally attached to subsurface cortical cells (Fig. 77), at maturity 25-40 µm tall by 15-23 µm wide and irregularly cruciately divided (Fig. 78).



Figs 49-60. *Euthora timburtonii* Clarkston & G.W.Saunders. Habit and vegetative features. **49.** Thallus with young and mature cystocarps (K-REN-5318). **50.** Distal axis with terminal and lateral globular cystocarps (arrowheads) (K-REN-5318). **51.** Large thallus densely invested with procarps but not yet cystocarpic (K-GEN-6396a). **52.** Habit of a spermatangial thallus (K-REN-5166A). **53.** Dried habit of a tetrasporophytic thallus (K-GEN-6396b). **54.** Wet habit of a thallus fringed with perpendicular tetrasporangial laterals (arrowhead) (K-GEN-6396b). **55.** Portion of proximal thallus showing a thick basal crust anchoring several erect axes (K-GEN-6396a). **56-57.** Apices of a tetrasporophyte showing apparent multiaxial (Fig. 56) and probable uniaxial (Fig. 57, arrowhead) construction (K-GEN-6396a). **58.** Longitudinal section of a distal axis, the medullary cells ovoid to elongate in profile (K-GEN-6396a). **59.** Axis cross-section, the medullary cells nearly spherical in outline throughout (K-GEN-6396a). **60.** Detail of surface and inner cortical layers, the cells with numerous spherical starch grains (K-GEN-6396a). Scale bars: 49, 52, 54 = 25 mm; 50 = 1 mm; 51, 53 = 50 mm; 55 = 10 mm; 56, 57 = 50 µm; 58 = 250 µm; 59, 60 = 100 µm.



Figs 61-78. *Euthora timburtonii* Clarkston & G.W.Saunders. Reproductive features. **61.** A male gametophyte with cylindrical marginal processes covered by spermatangia (K-REN-5166A). **62-63.** Details of terminal spermatangia budded off singly into the cuticle from surface mother cells (K-REN-5166A). **64.** Marginal processes that produce procarps on a female gametophyte (K-REN-5318). **65.** Numerous procarps visible as darkly staining bodies in the cortex of branched lateral. Light-colored ovoid bodies are epiphytic diatoms (K-REN-5318). **66-72.** Various configurations of pre-fertilization procarps, the supporting cells all bearing a single subspherical subsidiary cell (arrowheads) and a three-celled carpogonial branch (K-REN-5318). **73.** Cross-section of a non-ostiolate mature cystocarp, the carposporophyte consisting of a central mass of carposporangia intermixed with sterile gonimoblast filaments and cells (K-REN-5318). **74.** Nearly perpendicular and unbranched marginal laterals that contain tetrasporangia (K-GEN-6396b). **75-76.** Details of a tetrasporangial lateral, the tetrasporangia visible from the surface due to the absence of overlying cortical cells (arrowhead) (K-GEN-6396b). **77.** Long-section of a lateral at early stages (arrowheads) of tetrasporangial formation (K-GEN-6396b). **78.** Mature, irregularly cruciate tetrasporangia (K-GEN-6396b). Scale bars: 61 = 250 µm; 62, 63, 66-72 = 25 µm; 64, 65 = 500 µm; 73, 75, 78 = 100 µm; 74 = 1 µm; 76, 77 = 50 µm.

Remarks: *Euthora timburtonii* conforms to the morphological criteria set out by Lindstrom (in Guiry & Guiry, 2016) for the genus *Euthora*, including possession of a uniformly pseudoparenchymatous medulla and frequent indications at branch apices of uniaxial construction (Fig. 57). Plants are monocarpogonial, the carpogonial branches three-celled, the supporting cells bearing a single nearly spherical subsidiary cell of similar size and shape to the basal cells of the carpogonial branches. Evidence of separate auxiliary cell complexes and of connecting filaments has not been seen. Carposporangia form in clusters between groups of sterile gonimoblast filaments, and protuberant cystocarps lack or have a poorly developed ostiole. *Euthora timburtonii* was morphologically differentiated from *E. cristata* by its lesser degree of branch tapering, flattened rather than terete/subterete cross-sections, and confinement of small unpigmented cells among large medullary cells to the basal regions of thalli rather than being clearly visible throughout the fronds (Clarkston & Saunders, 2010).

Verlaquea L.Le Gall & A.Vergés, *gen. nov.*

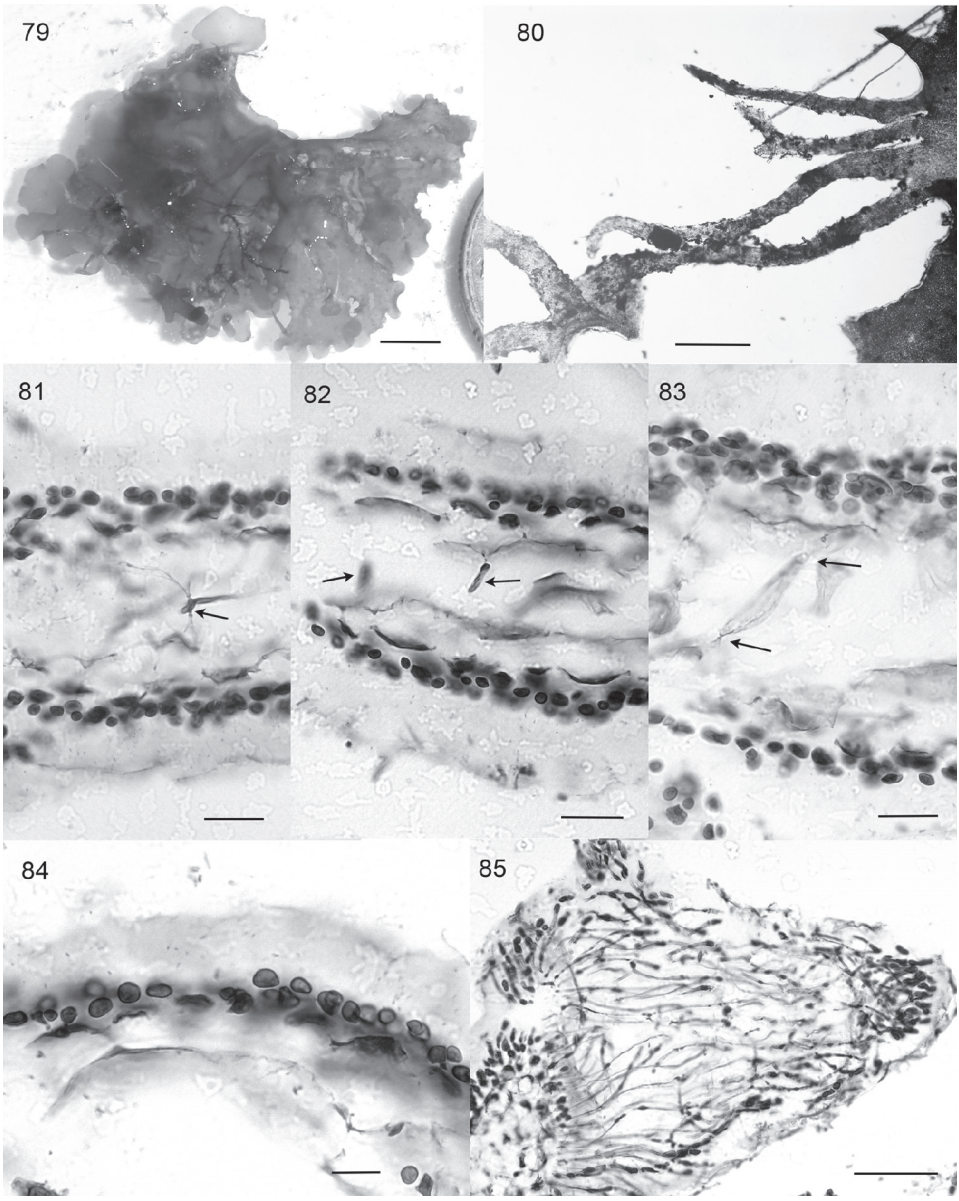
Description: Member of the Kallymeniaceae with erect thalli. Fronds composed of a cortex up to four cell layers and a narrow and lax medulla; cells of inner cortical layers stellate or trapezoidal; medulla with scarce filaments and conspicuous hyaline cells with an enlarged body cell and short arms in the distal parts. Carpogonial cell system polycarpogonial. Gonimoblast filaments forming from vegetative cells and producing branched chains of carposporangia intermixed with sterile filaments.
Etymology: In honour of recently retired Professor Marc Verlaque for his outstanding contributions to the knowledge of the European marine flora.
Type species: *Verlaquea lacerata* (Feldmann) L.Le Gall & A.Vergés, *comb. nov.*

Verlaquea lacerata (Feldmann) L.Le Gall & A.Vergés, *comb. nov.*

Basionym: *Kallymenia lacerata* Feldmann, *Bulletin de la société d'histoire naturelle de l'Afrique du nord* 33: 10 (1942).
Holotype: PC, Feldmann No. 4877 (PC0508517) (Rodríguez-Prieto & Hommersand, 2009, p. 147; Guiry & Guiry, 2016).
Representative DNA barcode: KJ083058 (COI-5P).
Distribution: Mediterranean Sea (Rodríguez-Prieto & Vergés, 2001).
Remarks: *Kallymenia lacerata* is removed from the genus *Kallymenia* because of differences in cortical and medullary structure, and significant differences in carposporophyte formation, which is strongly supported in our molecular analyses (Fig. 1). Specimens of *Verlaquea lacerata* have four cortical layers, cells of the innermost layer being large and closely crowded together but leaving space for the medullary cells and filaments. Medullary cells are scarce, have a large central body and relatively few radiating arms that are initiated from around the distal half of the enlarged central portion. We do not consider these cells as stellate or ganglionic because of their great diameters, light pigmentation, and the low numbers of short arms, which are unlike typical kallymeniacean stellate and ganglionic cells. Post-fertilization stages in *V. lacerata* are not well known and further studies are needed to establish whether this species is procarpic or not.

Verlaquea fimbriata G.W.Saunders, *sp. nov.* **Figs 79-85**

Description: Thalli small, up to 3-4 cm, composed of procumbent, entire to lobed blades with undulate/crenulate margins (Fig. 79) from which new blades or stolons arise, these variously anastomosing to other blades or forming secondary attachments



Figs 79-85. *Verlaquea fimbriata* G.W.Saunders, *sp. nov.* Images of the holotype (GWS037700). **79.** Living habit of the lobate thallus. **80.** Detail of marginal stolons. **81.** A densely staining central medullary cell (arrow) with two extremely fine arms connected to cells of the outermost opposite medullary layers. **82-83.** Narrow cells (arrows) initiated from the outer medulla (Fig. 82) that eventually link cells lining the opposite outer medulla (Fig. 83). **84.** Detail of the one- or two-layered inner and outer cortices and the thick overlying cuticle. **85.** Development of the marginal stolons by growth of filaments from the cortical cells. Scale bars: 79 = 0.5 cm; 80 = 0.5 mm; 81-83 = 25 µm; 84 = 10 µm; 85 = 50 µm.

to substratum (Fig. 80). Blades delicate, translucent, difficult to obtain sections from rehydrated tissue. Blade 100-130 μm wide in section (Fig. 81). Medulla composed of narrow central filaments 30-50 μm long by 2.5-4.0 μm tall, occasionally locally inflated to form larger central cells (up to 17 μm tall) bearing 2 thin-walled, inflated outer medullary cells, 30-70 μm long by 12-20 μm tall (Fig. 8) that issue rhizoidal cells and filaments (Fig. 82), these traversing the largely vacant medulla and secondarily connecting to outer medullary cells on the opposite side, eventually forming *Halymenia*-type struts (Fig. 83); inner cortex typically one- or (rarely) two-layered, the cells 12-20 μm long by 5-8 μm tall and internal to one or two layers of smaller isodiametric to elongate outer cortical cells 3-5 μm wide by 4-6 μm tall, the thallus covered on both surfaces by a thick (*ca* 20 μm) cuticle (Fig. 84). Stolons at the fimbriate margins formed by the production of filaments from the cortical layer (Fig. 85). Cells of inner and middle cortex occasionally with crystalline inclusions. Reproductive structures unknown.
Type collection: Coll. *G.W. Saunders & K. Dixon*, December 4, 2013, Cologne Gardens, south of Horsburgh Island, Cocos (Keeling) Islands, Australia, 12.08291°S, 96.83329°E, subtidal, 10 m on reef flat. Holotype, UNB [GWS037700, BOLD ABMMC18912-13 (Figs 79-85)]. Isotype, UNB [GWS037721].
Etymology: From the Latin *fimbria* meaning a marginal fringe in reference to the localized production of marginal projecting stolons.
Holotype DNA barcode: KX808042 (COI-5P).
Distribution: Only known from the type locality.
Remarks: The sister relationship of *Verlaquea fimbriata* to the type species *V. lacerata* is relatively deep in evolutionary terms when compared to species in other genera (Fig. 1), and separate genera may be justified. As the two species are largely consistent in morphology, this decision awaits documentation of reproductive structures for *V. fimbriata*.

Leiomenia Huisman & G.W.Saunders, *gen. nov.*

Description: Member of the Kallymeniaceae with solid or obligately perforate membranous blades, the medulla primarily of sparse filaments and lightly staining stellate cells with irregularly radiating arms. Supporting-cell systems mono- or polycarpogonial, bearing up to four carpogonial branches and 3-5 subsidiary cells. Post-fertilization fusion cell prominent, incorporating the supporting and subsidiary cells, producing numerous connecting filaments. Auxiliary cell systems with an auxiliary cell and 3-6 (-10) spherical subsidiary cells. Following fusion with a connecting filament, the auxiliary cell produces numerous gonimoblast filaments ultimately cutting off carposporangia. Cystocarps forming within the medulla, consisting of a dense mass of intermixed filaments and spherical to ovoid carposporangia. Spermatangia cut off from outer cortical cells. Tetrasporangia scattered in the outer cortex, cruciately divided.
Type species: *Leiomenia lacunata* Huisman & G.W.Saunders, *sp. nov.*
Etymology: From the Greek *leio* (smooth) and *hymen* (membrane), in reference to the texture of the blades.
Remarks: This new genus resolved as sister to *Verlaquea* in our phylogenetic analyses (Fig. 1). In *Leiomenia* we include three species, two newly described from the tropical Indian Ocean and *L. cribrosa* transferred from *Kallymenia*. The variation in supporting cell systems observed in these species (monocarpogonial in *L. cribrosa*, mono- or polycarpogonial in *L. lacunata*, and polycarpogonial in *L. imbricata*) would appear to confound one of the primary features previously used to distinguish species groups in *Kallymenia sensu lato*. However, the strong molecular support

for this clade indicates that the relatively small numbers of carpogonial branches in polycarpogonial *L. imbricata* (≤ 4), and the presence of both mono- and polycarpogonial systems (again with ≤ 4 carpogonial branches) observed in *L. lacunata*, represent minor variations within a natural group. The small number of carpogonial branches contrasts with the arrangement found in *Kallymenia sensu stricto*, where species often have greater than 10 carpogonial branches per supporting cell system. Trichogynes in *Kallymenia sensu stricto* are also typically coiled, at least basally, a feature not present in *Leiomenia*. From its sister genus *Verlaquea*, *Leiomenia* differs in producing a fusion cell following fertilization.

Leiomenia cribrosa* (Harvey) Huisman & G.W.Saunders, *comb. nov. **Fig. S4***

Basionym: *Kallymenia cribrosa* Harvey, *Transactions of the royal Irish academy* 22: 555 (1855).

Lectotype: Herb. Harvey, TCD 0011789 (Womersley & Norris, 1971, p. 5; Womersley, 1994, p. 233; Guiry & Guiry, 2016). Womersley & Norris (1971, p. 5) designated a Fremantle specimen 'Herb. Harvey TCD' as lectotype and noted that the specimen was labeled 'original'. The lectotype (TCD 0011789) bears this label and also the annotation 'TYPE (HBSW)' (=Womersley). A second specimen in TCD (TCD 0015030) from Harvey's Travelling Set (#274) is also from Fremantle ('Beach') and is labeled *Kallymenia cribrosa* in Harvey's hand. This is presumably the specimen Harvey had to hand when describing the species, which was done 'at sea' when Harvey only had access to his Travelling Set specimens (see Parnell *et al.,* 2010, p. 122).

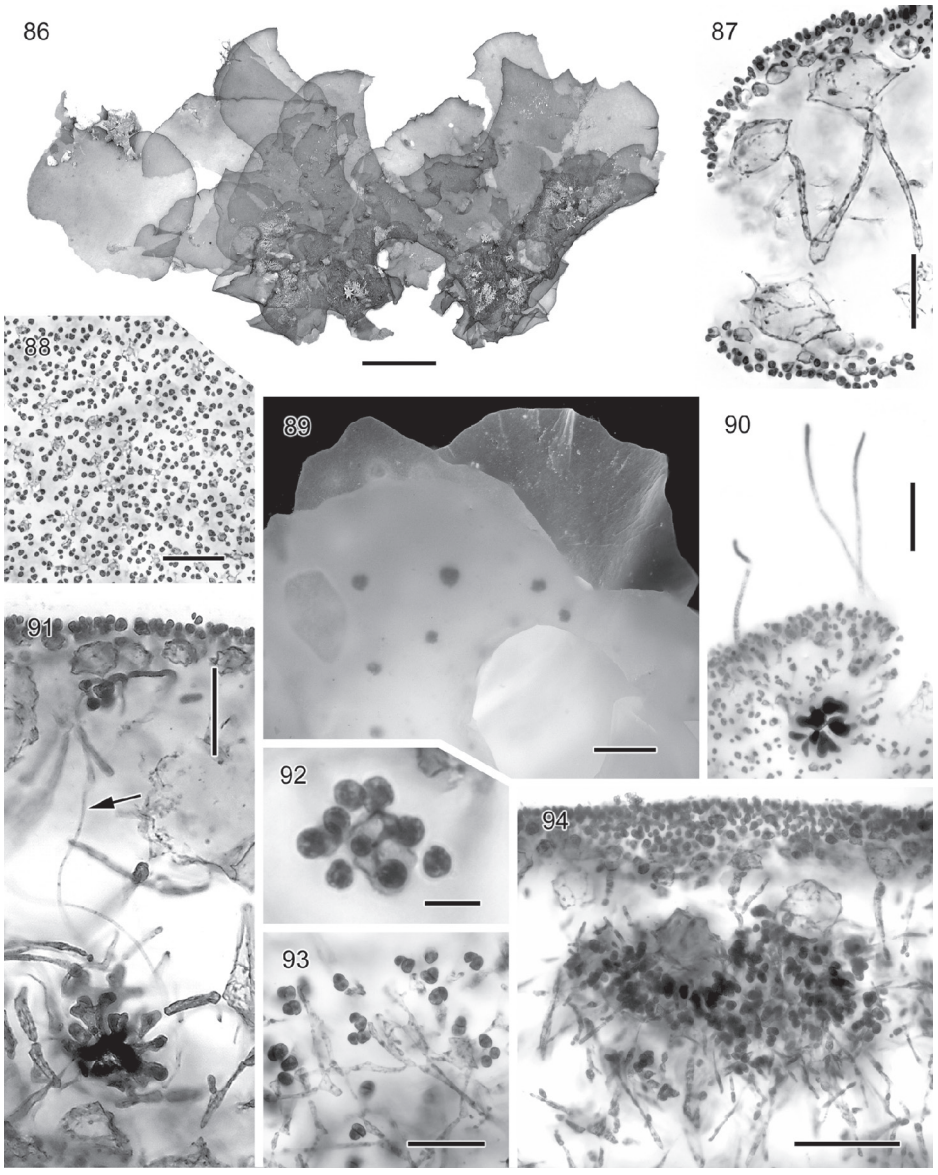
Representative DNA barcode: KX808058 (COI-5P).

Remarks: '*Kallymenia cribrosa*' appears twice in our molecular analyses (Fig. 1). Of these, GWS025287 (Table S1) was collected near the type locality (Fremantle, Western Australia) and is therefore accepted as representative of the species. The second entity, GWS000466, was collected at Vivonne Bay on Kangaroo Island, South Australia (Table S1) and requires taxonomic study, but is clearly assignable to *Leiomenia* (*L.* sp.2cribrosa; Fig. 1).

Leiomenia imbricata* Huisman & G.W.Saunders, *sp. nov. **Figs 86-94, S1***

Description: Thallus red (Fig. S1 cf. doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.2), sprawling, foliose, membranous, to 5 cm long, with numerous fleshy attachments to the substratum and between adjacent blades, the blades often imbricating (Fig. 86); fronds irregularly lobed (Fig. 89), without perforations, 270-350 µm thick, the margins smooth. Medulla loosely filamentous, the cells elongate, 5-20 µm diam., often transversely oriented and connecting large stellate inner cortical cells on the opposite sides of the frond (Fig. 87), the stellate cells 50-60 µm in diam. centrally, bearing numerous radiating arms, located in a single layer internal to 1-3 layers of progressively smaller cells, those of the surface layer deeply pigmented, rounded, 3-5 µm in diam. (Fig. 88). Supporting-cell systems polycarpogonial, causing slight swellings of the cortex (Fig. 90), the supporting cell bearing three or four three-celled carpogonial branches and three or four clavate or lobed subsidiary cells (Fig. 90). Basal and often hypogynous cells elongate and unequally laterally lobed, resulting in the pit-connections between cells of the carpogonial branch cells lying close to one another. Carpogonium attached near the proximal end of the hypogynous cell, with an elongate trichogyne. Auxiliary cell complexes with five or six (rarely up to ten) spherical subsidiary cells (Fig. 92). Following presumed fertilization, the cells of the carpogonial branches are assimilated into the supporting cell to form a

* See doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.2.

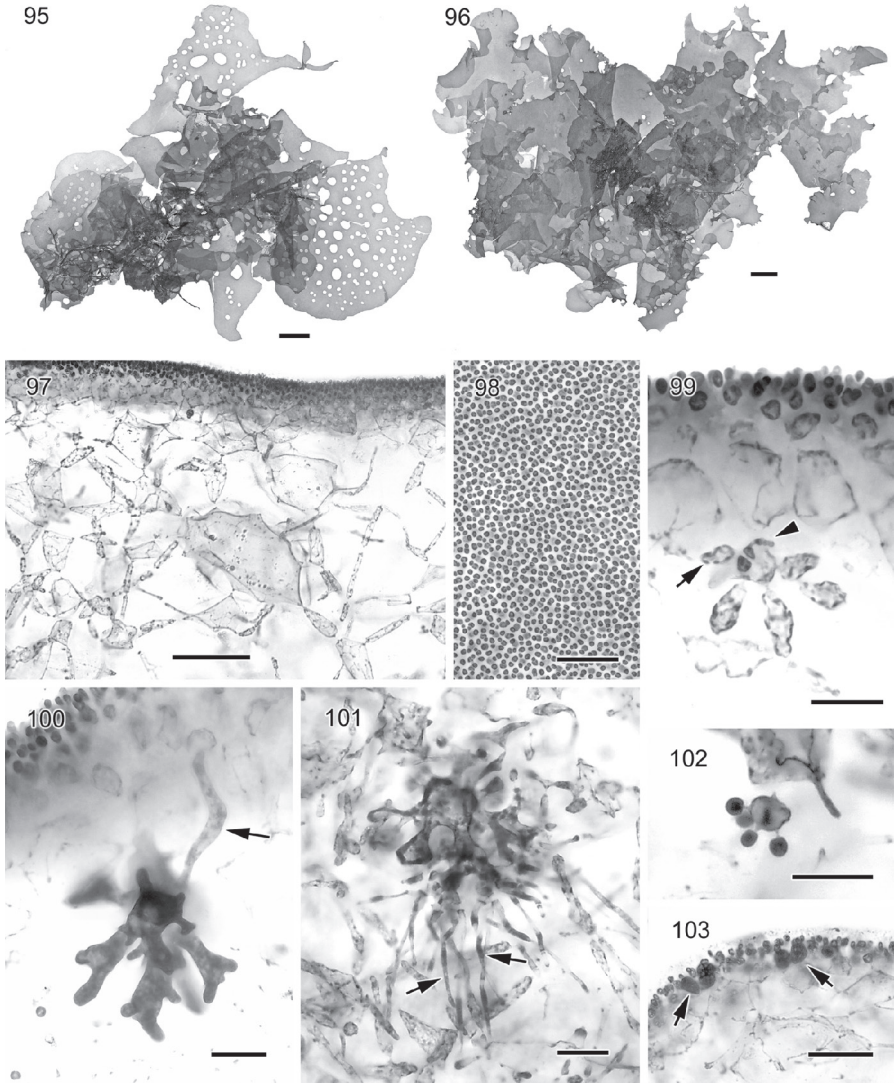


Figs 86-94. *Leiomenia imbricata* Huisman & G.W.Saunders, *sp. nov*. (holotype PERTH 08709297). **86.** The overlapping blades of the holotype specimen. **87.** Large inner-cortical cells of both blade surfaces linked across the mostly hollow medulla by narrow, transversely oriented cells. **88.** Wide gaps between clusters of outer cortical cells in surface view. **89.** Deeply immersed cystocarps at the margin of a wet-preserved frond. **90.** Darkly staining supporting-cell complex of lobed subsidiary cells and remnant trichogynes extending far beyond the cortex. **91.** A connecting filament (arrow) from the supporting-cell fusion structure traversing the medulla towards an auxiliary-cell complex. **92.** An auxiliary-cell complex of surrounding subsidiary one- and two-celled laterals. **93.** Carposporangia arising in clusters on diploidized cells in the early cystocarp. **94.** The complex admixture of carposporangia and sterile filaments and cells in the section of an immature cystocarp. Scale bars: 86 = 1 cm; 87, 88, 90, 91, 93 = 50 μm; 89 = 1 mm; 92 = 10 μm; 94 = 100 μm.

lobed fusion cell from which multiple connecting filaments are cut off, these coursing through the medulla (Fig. 91) to form a glancing connection with an auxiliary cell before formation of the gonimoblast. Origin of gonimoblast initial and further development of connecting filaments not observed. Cystocarps immersed in the thallus, causing no or only a slight swelling (Fig. 94); multiple gonimolobes of carposporangia borne on a weft of filaments. Carposporangia subspherical to ovoid, 10-15 µm in greatest dimension (Fig. 93). Other reproductive structures unknown.
Type collection: Coll. *J.M. Huisman*, October 5, 2013, Hibernia Reef, south east side on fore-reef slope, Western Australia, Australia, 11.97605°S, 123.38967°E, epilithic at 15 m depth. Holotype, PERTH [08709297, BOLD ABMMC19607-14, cystocarpic (Figs 86-94)].
Etymology: From the Latin *imbricatus* (imbricate) in reference to the frequently overlapping blades.
Holotype DNA barcode: KX808037 (COI-5P).
Additional specimens examined: See Table S1 (doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1).
Distribution: Known from the type locality (*ca* 42 km northeast of Ashmore Reef) and the Cocos (Keeling) Islands, Australia (Table S1).
Remarks: Several authors have tabulated the characteristics of the presently accepted species of *Kallymenia* (Abbott & McDermid, 2002; Vergés & Rodríguez-Prieto, 2006a, 2006b; Robuchon *et al.*, 2014; Vergés *et al.*, 2014), with none of them displaying the combination of features that distinguish *Leiomenia imbricata*, particularly its imbricating, sprawling habit, smooth, non-perforate blades, and polycarpogonial branch systems. Imbricating fronds with multiple holdfasts would appear to be restricted to tropical species such as *K. thompsonii* I.A.Abbott & McDermid and *K. sessilis* Okamura (both of which are perforate and monocarpogonial), whereas most cold-water species have upright, stipitate thalli. Of the tropical species with some similarities (although they are incompletely known reproductively), all differ from *L. imbricata* in some significant ways. The tropical Atlantic *K. limminghei* Montagne has a peltate thallus (Littler & Littler, 2000), and the Indonesian *K. requienii* var. *indica* Weber-van Bosse (1928) is only known from sterile material that could match any number of *Kallymenia* species *sensu lato*. *Kallymenia requienii var. requienii* is a Mediterranean species and, according to Rodríguez-Prieto & Vergés (2001, p. 487), its supposedly disjunct distribution suggests that Weber-van Bosse's variety is likely misattributed. *Leiomenia imbricata* does show some habit and structural similarities to *Kallymenia requienii* as illustrated by Rodríguez-Prieto & Vergés (2001, p. 488, figs 3-10), but the latter is apparently uniformly monocarpogonial, whereas *L. imbricata* is polycarpogonial. The autonomy of *L. imbricata* is further supported by our molecular analyses (CO1-5P, *rbc*L), which resolve it as an independent lineage (Fig. 1). Rather than making a highly provisional link of the Cocos and Hibernia Reef plants to the poorly known *K. requienii* var. *indica*, we prefer to name this as the new species *Leiomenia imbricata* based on a holotype characterized by diagnostic DNA sequence data.

Leiomenia lacunata* Huisman & G.W.Saunders, *sp. nov. **Figs 95-103, S2**

Description: Thallus foliose, sprawling, to 15 cm long, light pink to red-purple (Fig. S2, cf. doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.2), membranous, 200-300 µm thick, with few to numerous circular or oval perforations (Figs 95, 96), these mostly 1-3 mm diam. but some to 15 mm in width. Attachment by broad fusions to the substratum at multiple attachment points. Medulla filamentous (Fig. 97); cells elongate, 4-12 µm diam. Subcortical cells large, 50-70 µm in diam., spherical,



Figs 95-103. *Leiomenia lacunata* Huisman & G.W.Saunders, *sp. nov*. **95.** The profusely perforate pressed holotype specimen (PERTH 08709300). **96.** A rudimentarily perforate paratype specimen from Coral Bay, Western Australia (PERTH 08821364). **97.** The mixture of inflated and narrowly elongate medullary cells interior to the shallow cortex of a thallus in long-section (PERTH 08821364). **98.** The uniformly dense blade covering of the surface cortical layer (PERTH 08821364). **99.** Three-celled carpogonial branch, the basal cell (arrow) only slightly smaller than the one- and two-celled subsidiary laterals borne on the inner-cortical supporting cell. The trichogyne is indicated by the arrowhead (PERTH 08821356). **100.** Fusion of the dactyloid mature subsidiary and carpogonial-branch basal cells, the supporting cell and trichogyne (arrow) still visible (PERTH 08821356). **101.** The fusion product of the supporting-cell complex that is issuing multiple connecting filaments (arrows) toward the interior of the blade (PERTH 08709300). **102.** An auxiliary cell surrounded by four single-celled subsidiary laterals prior to diploidization (PERTH 08709300). **103.** Tetrasporangia (arrows) aligned with the surface of the outer cortex (PERTH 08821364). Scale bars: 95, 96 = 1 cm; 97 = 100 µm; 98, 103 = 50 µm; 99, 100, 101, 102 = 25 µm.

grading outwards to smaller cells, those of the outermost layer dark-pigmented and 5-9 µm in diam. (Fig. 98). Stellate cells prominent in the medulla of some, although not all, specimens. Supporting-cell systems mono- or polycarpogonial with 1-4 carpogonial branches and several clavate (Fig. 99) to lobed (Fig. 100) subsidiary cells. Following presumed fertilization, a large fusion cell is formed that cuts off numerous connecting filaments (Fig. 101). Auxiliary cells bearing 7-9 spherical subsidiary cells (Fig. 102). Diploidization of auxiliary cell not observed. Cystocarps 0.5-1.0 mm diam., immersed in the thallus, causing a slight swelling or none at all; multiple gonimolobes of carposporangia 14-20 µm diam. borne on a weft of filaments. Tetrasporangia scattered in the outer cortex, ellipsoidal or ovoid, 18-28 × 14-18 µm, cruciately or decussately divided (Fig. 103). Spermatangia unknown.
Type locality: Coll. *J.M. Huisman*, September 26, 2013, Ashmore Reef, northern channel, Australia, 12.21418°S, 123.02014°E, epilithic at 12 m depth. Holotype, PERTH [08709300, BOLD ABMMC19603-14, cystocarpic (Figs 95, 101, 102)].
Etymology: From the Latin *lacunata* (full of holes), in reference to the perforated thallus.
Holotype DNA barcode: KX808091 (COI-5P).
Additional specimens examined: Coral Bay, among *Acropora* tines at 2 m depth, June 26, 2014, *J.M. Huisman & Y.H. Koh* (PERTH 08821372); Coral Bay, among coral at 2 m depth, July 6, 2015, *J.M. Huisman* (PERTH 08821356); *Loc. cit.*, June 21, 2014, *J.M. Huisman* (PERTH 08821364); Coral Bay, 3-4 m, April 14, 1993, *J.M. Huisman* (MURU S109); Winderabandi, Ningaloo Reef, 2-3 m, August 16, 1995, *J.M. Huisman* (MURU NR5); Bundegi Reef, North West Cape, 4-5 m, April 27, 1996, *J.M. Huisman* (MURU NR214, 222). Hermite Island, Montebello Islands, epilithic at 6 m depth, July 11, 1992, *J.M. Huisman* (PERTH 07161743). (See Table S1 for addtional spcimens with molecular data.)
Distribution: Known from Ashmore Reef, Coral Bay, Ningaloo Reef and the Montebello Islands, Western Australia. Epilithic in the subtidal, often among coral tines.
Remarks: Of the known polycarpogonial, perforate species of *Kallymenia sensu lato*, *K. westii* Ganesan has a similar number of carpogonial branches [(1-) 2-4 (-8)] per system but differs from *L. lacunata* in the greater number of subsidiary cells (to 15) on the auxiliary cell (Ganesan, 1976, p. 170). The Coral Bay specimens were generally less perforated than those from Ashmore Reef, but were anatomically identical and matched the holotype in COI-5P or *rbc*L data (Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1).

Glaphyrymeniopsis Kraft & G.W.Saunders, *gen. nov.*

Description: Member of the Kallymeniaceae with orbicular, oliose blades; medulla uniform throughout, loosely filamentous, cells narrow or centrally inflated and stellate but not ganglioid; cortex shallow, 1-3-layered, the cells arising directly from medullary filaments. Nonprocarpic; supporting cells borne on peripheral medullary filaments, directed inwardly, bearing a single spherical subsidiary cell and a three-celled carpogonial branch, the basal cell being the same shape and size as the subsidiary cell, the hypogynous cell spherical but smaller, the carpogonium conical, inwardly directed with a reflexed trichogyne. Presumed fertilization followed by formation of a lateral projection of the supporting cell from which several septate connecting filaments arise; fusion cells lacking. Auxiliary-cell complex similar to that of the supporting cell, the auxiliary cell bearing two subsidiary cells, one occasionally dividing into two cells. Gonimoblast initial clavate, arising on the incoming connecting filament near but not at its point of fusion to the auxiliary cell, the connecting filament then growing on to effect further diploidizations. Fusion cell not formed; gonimoblast initials multiple, carposporangial filaments radiating from

a central mass of sterile gonimoblasts, forming peripheral clusters of carposporangia unmixed with vegetative tissue; carposporophytes at maturity globular, composed of a confluent mass of carposporangia. Tetrasporangia scattered, ovoid, decussate-cruciate, terminal on cortical mother cells.

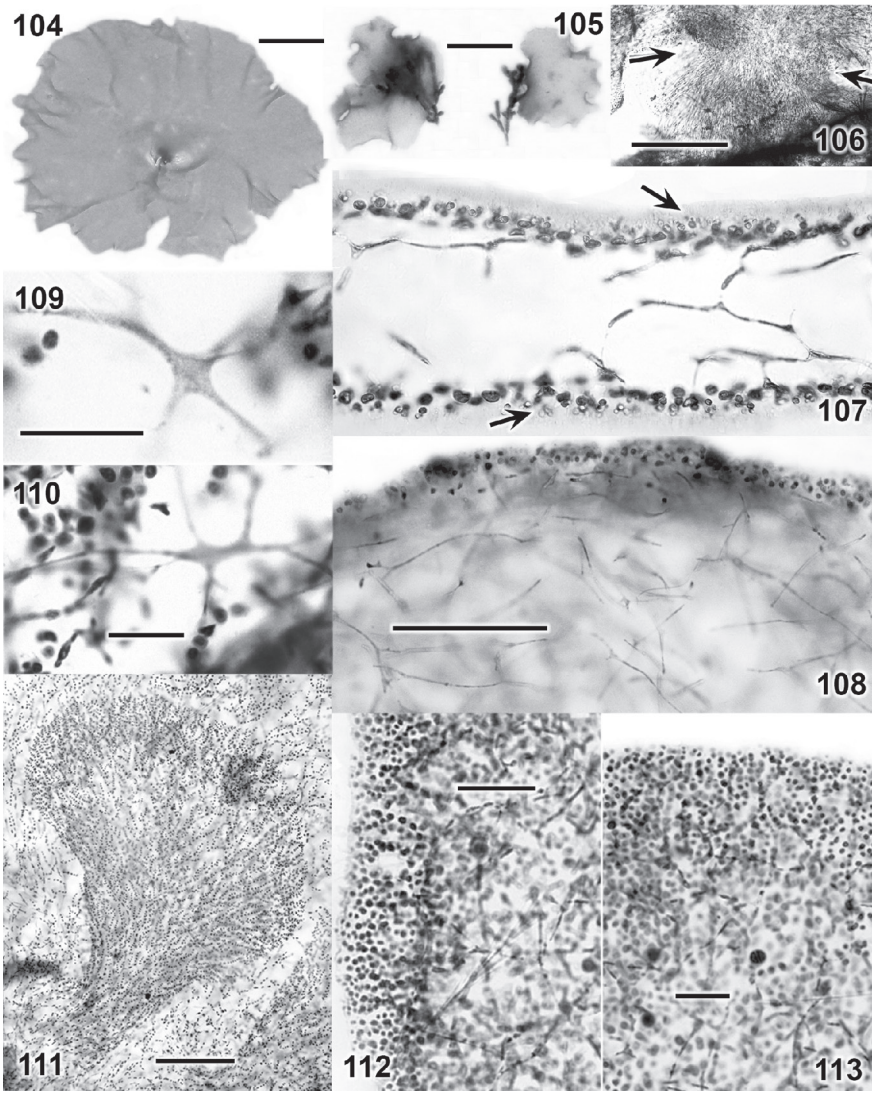
Etymology: Named for the resemblance of thalli to those of the monotypic genus *Glaphyrymenia* mainly in habit, vegetative and reproductive features, particularly the lack of a differentiated subcortex, the loosely filamentous medulla, subspherical subsidiary cells, and the single mass of consolidated carposporangia in mature cystocarps.

Type species: *Glaphyrymeniopsis mollis* Kraft & G.W.Saunders

Glaphyrymeniopsis mollis* Kraft & G.W.Saunders, *sp. nov. **Figs 104-126**

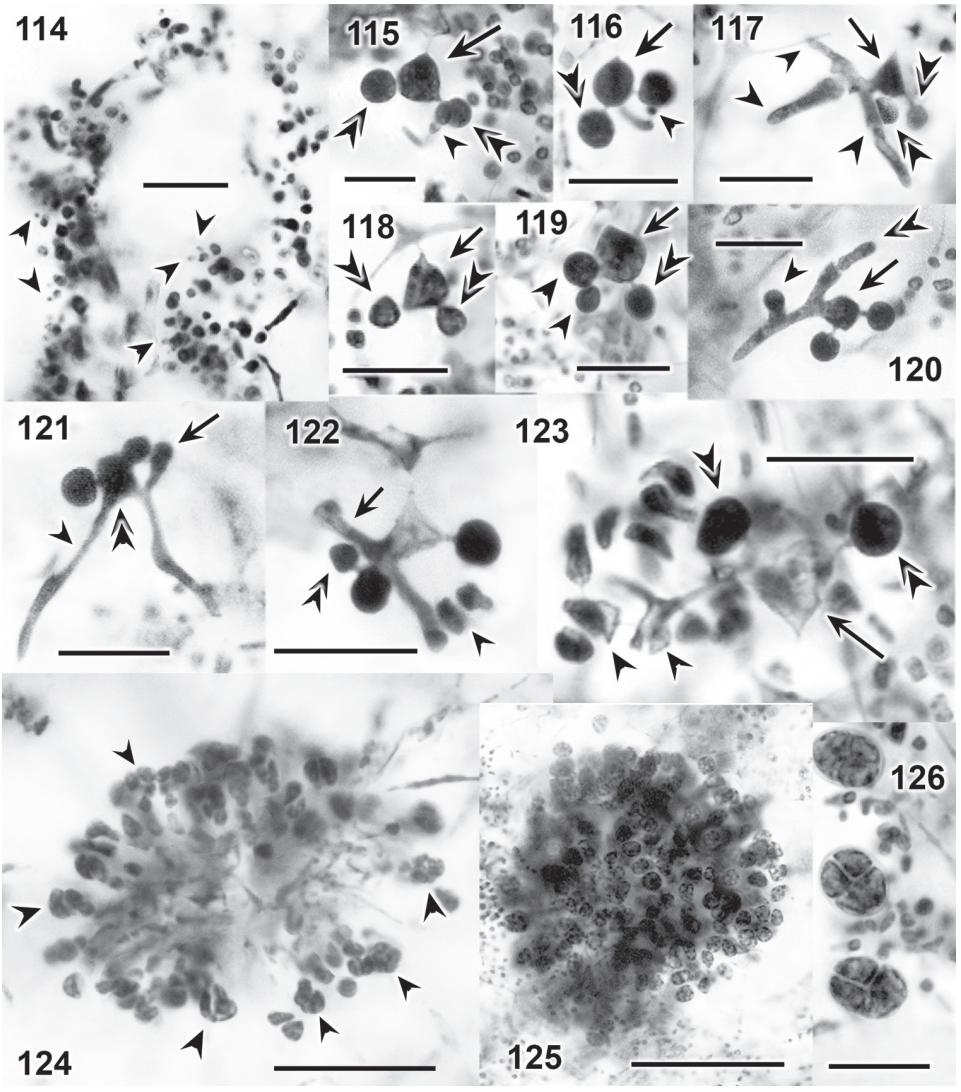
Description: Thalli growing on erect hydrozoans, the sole exception being a paratype specimen from Wheatsheaf Islet attached to *Halopeltis* sp. Blades are orbicular, slightly wider than long, soft in texture with smooth, pleated or undulate margins (Figs 104-105), the largest reaching a width of 2 cm but few exceeding 10 mm. Fronds non-stipitate, the medullary filaments passing through a basal constriction before fanning out into a dense weft of undifferentiated anchoring fibers (Fig. 106). Cross-sections < 100 μm wide distally, becoming thicker (Fig. 107) and reaching 250 μm proximally (Fig. 108), composed of widely spaced medullary filaments 2-3 μm in diam.; refractive and ganglionic cells absent, but central portions of cells often widening (up to 15 μm) at the sites of lateral filament development (Figs 109, 110). Cortex shallow, one to three layers deep, composed primarily of isodiametric cells 3-5 μm in diam. (Fig. 108) arising from medullary filaments without a differentiated subcortex. Cortical cells at margins of juvenile (Fig. 111) and growing (Fig. 112) blades forming a uniformly pigmented layer of moniliform chains, becoming compact and polystromatic in mature thalli (Fig. 113). Spermatangia 2-3 μm in diam., formed singly or in pairs from surface mother cells across blade surfaces (Fig. 114). Carpogonial branches three-celled, the basal cell similar in size and morphology to the single subsidiary cell produced on supporting cells (Figs 115, 116). Presumed fertilization resulting in a group of septate connecting filaments radiating from a lateral outgrowth of the supporting cell, the supporting cell and subsidiary cell not becoming incorporated into a fusion cell (Fig. 117). Auxiliary cells (Figs 118, 120) of similar shape, size (10-12 μm diam.) and position as supporting cells, bearing two subsidiary cells 6-8 μm in diam., of which one sometimes divides once (Figs 119, 120). Contact and fusion of connecting filaments to the auxiliary cell is lateral (Fig. 120), the connecting filament continuing on beyond the fusion point and septating (Fig. 120). Gonimoblast development beginning with a clavate perpendicular protrusion on the incoming connecting filament at varying distances from the auxiliary cell (Figs 120, 121), this dividing transversely (Fig. 122), then repeatedly as additional gonimoblast initials arise (Fig. 123), the subsidiary cells remaining unfused to the auxiliary cell (Fig. 123). Early carposporophyte development consisting of radial growth of gonimoblasts from a sterile center (Fig. 124), with tight clusters of incipient carposporangia forming at the periphery unmixed with surrounding gametophytic tissue (Fig. 124). Mature carposporophytes 100-220 μm in diam., globular, composed of a consolidated mass of spherical to ovoid carposporangia 7-15 μm in diam. (Fig. 125). Tetrasporangia ovoid, 20-25 μm in diam., scattered across broad surfaces of blades (Fig. 126).

Type collection: Coll. *G.W. Saunders, K. Dixon & R. Withall,* November 22, 2010, "Roach Wall", Roach Island, Admiralty Group, Lord Howe Island, New South Wales, Australia, 31.49822°S, 159.06557°E, subtidal 8 m on a fruticulose hydrozoan.



Figs 104-113. *Glaphyrymeniopsis mollis* Kraft & G.W.Saunders, *gen. et sp. nov*. **104.** Living habit of the tetrasporangial holotype specimen (GWS022990). **105.** Isotype specimens epizoic on a fruticulose hydrozoan (GWS023027). **106.** Thallus base (arrows), the medullary filaments continuous with the medulla distally and proximally fanning out into a lax holdfast pad (K-GEN-12719; Slide C). **107.** Longitudinal section of a male gametophyte showing the filamentous, mostly vacant medulla and numbers of minute surface spermatangia (arrows) (GWS023027). **108.** Portion of a mature frond showing abrupt transition of medullary filaments to the 2-3-layered small-celled cortex (K-GEN-12719; Slide G). **109.** Detail of the central region of a stellate medullary cell. (K-GEN-12719; Slide A). **110.** Medullary filament with expanded and elongated central region and radiating narrow arms. (K-GEN-12719; Slide A). **111.** A whole juvenile blade arising from the holdfast pad of a mature frond (K-GEN-12719; Slide A). **112.** Moniliform chains of cortical cells at the margin of a juvenile blade. (K-GEN-12719; Slide F). **113.** More tightly compacted margin of a mature tetrasporangial blade (K-GEN-16112; Slide J). Scale bars: 104 = 4 mm; 105 = 10 mm; 106 = 250 µm; 107, 112, 113 = 50 µm; 108, 111 = 100 µm; 109, 110 = 25 µm.

Holotype: UNB [GWS022990, BOLD OZSEA257-10, tetrasporangial (Fig. 104)]. Isotype UNB [GWS023027, spermatangial (Figs 105, 107)].
Etymology: Named for the extremely soft texture of the diminutive blades.
Holotype DNA barcode: KX808096 (COI-5P).
Additional specimens examined: Coll. *G.T. Kraft, G.W. Saunders & R. Withall*, February 1, 2004, Wheatsheaf Islet, Balls Pyramid, Lord Howe Island, 31.756451°S, 159.237771°E, subtidal 12-26 m on the hydrozoan *Aglaophenia* sp. attached to a vertical rock face. HO [K-GEN-12719, cystocarpic (Figs 106, 108-112, 114-126)]. Coll. *G.W. Saunders, G.T. Kraft & C.E. O'Brien*, March 13, 2001, "Ruperts Reef", Roach Island, Admiralty Group, Lord Howe Island, 31.497445°S, 159.065080°E, subtidal 12-23 m on hydrozoan. HO [K-GEN-11612, tetrasporangial (Figs 113, 126)].
Distribution: Known only from Lord Howe Island and Balls Pyramid, Australia.



Remarks: Although far smaller than the 10-60 cm-long blades of *Glaphyrymenia pustulosa* J.Agardh (Womersley, 1994), the new species shares many of its features, including frond outlines, soft texture, internal structure, and particularly the shapes of carpogonial-branch and subsidiary cells and the solid aggregates of carposporangia in mature cystocarps (Norris, 1961; Womersley & Norris, 1971). Significant anatomical differences between the two, however, support the generic separation that is indicated by the molecular results of our study (Fig. 2). Supporting cells are side branches of inner cortical cells in *Glaphyrymenia*, as opposed to being attached directly to cells of outer medullary filaments in *Glaphyrymeniopsis*, and can bear either one or two carpogonial branches (Norris, 1961; Womersley & Norris, 1971). Of greater significance is the formation of a fusion cell on presumed fertilization in *Glaphyrymenia* that incorporates the basal cell of the carpogonial branch and subsidiary cells (Norris, 1961), whereas there is no cell fusion in the post-fertilization of *Glaphyrymeniopsis*. Connecting filaments are non-septate in *Glaphyrymenia* but are septate in *Glaphyrymeniopsis*, in which genus they can grow on from an initial fusion with an auxiliary cell to presumably effect further diploidizations. In this genus as well, the gonimoblast initials cleave from a clavate perpendicular outgrowth of the connecting filament at a distinct remove from its point of fusion to the auxiliary cell rather than from the fusion product of the auxiliary cell, the terminating connecting filament and the subsidiary cells directly.

Glaphyrymenia J.Agardh

Type species: *Glaphyrymenia pustulosa* J.Agardh, 1885.
Remarks: The type and only formally named species of this genus has a distinctive vegetative anatomy and is reported from New Zealand and throughout southern Australia (Womersley, 1994). However, some records will require confirmation following our proposal of *Glaphyrymeniopsis mollis* (Fig. 2), which may account for attributions of "*Glaphyrymenia* cf. *pustulosa*" from mainland New South Wales

◀ Figs 114-126. *Glaphyrymeniopsis mollis* Kraft & G.W.Saunders, *gen. et sp. nov*. Reproductive features (K-GEN-12719). **114.** Single and pairs of minute spermatangia (arrowheads) on surface cortical mother cells (Slide C). **115-116.** Supporting cells (arrows) bearing a subsidiary cell and similarly sized basal cell (double arrowheads) of the three-celled carpogonial branch, which terminates in a conical carpogonium (arrowheads; Slide A). **117.** Diploidized supporting cell (arrow) that has issued a lateral protuberance that has initiated three connecting filaments (arrowheads). The basal and subsidiary cells (double arrowheads) remain unfused to the supporting cell (Slide A). **118.** An auxiliary cell (arrow) with two inwardly directed spherical subsidiary cells (double arrowheads) (Slide C). **119.** An auxiliary cell (arrow) with a one-celled (double arrowhead) and two-celled (arrowheads) subsidiary cells (Slide C). **120.** A gonimoblast primordium (arrowhead) arising on an incoming connecting filament that has fused laterally to an auxiliary cell (arrow) and continued on as a further septate connecting filament (double arrowhead) (Slide C). **121.** Further elongation of the goninoblast primordium (arrow) and continued growth of the connecting filament (arrowhead) from its site of fusion to the auxiliary cell (double arrowheads). **122.** The first two cells of the carposporophyte from the incoming connecting filament (arrowhead) at some remove from its fusion to the auxiliary cell and site of ongoing growth (arrow). One of the two subsidiary cells bears a single lateral cell (double arrowhead). **123.** Early development of gonimolobes (arrowheads) from an auxiliary cell (arrow) still bearing intact subsidiary cells (double arrowheads). **124.** Clusters of maturing carposporangia (arrowheads) terminating filaments radiating from the center of a developing carposporophyte. **125.** A mature cystocarp consisting of a consolidated surface covering of carposporangia and a complete lack of encircling medullary filaments. **126.** Decussate tetrasporangia in the outer cortex (Slide G). Scale bars: 114-123, 126 = 25 μm; 124 = 50 μm; 125 = 100 μm.

(Millar & Kraft, 1993). Records from Norfolk Island (Millar, 1999) require further study relative to the many unnamed kallymeniacean taxa uncovered for that flora, but may be in part accounted for by *Leiomenia* sp.1Nor (Fig. 1, Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1). We have also uncovered a second Australian species limited to a single cystocarpic collection from Western Australia that is in need of future characterization (*G.* sp.1WA; Fig. 2, Table S1).

Leniea R.L.Moe

Type species: *Leniea lubrica* R.L.Moe, 2009 (in Hommersand *et al.*).
Remarks: This genus was described in Hommersand *et al.* (2009) citing unpublished molecular data that were later published in D'Archino *et al.* (2016). In the latter report, this species was moderately resolved as sister to *Glaphyrymenia*, a result more solidly supported in analyses here (Fig. 2). We additionally add the novel Australian genus *Glaphyrymeniopsis* (above) and *Pugetia* (= *Leniea*) *kylinii* Baardseth from Tristan da Cunha (Baardseth, 1941) to this larger lineage, the last mentioned resolved as sister to *Leniea lubrica* (Fig. 2) and shares many features with this species.

Leniea kylinii (Baardseth) G.W.Saunders, *comb. nov.*

Basionym: *Pugetia kylinii* Baardseth, *Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937-1938* 9: 63-64, figs 29C; 31 (1941).
Lectotype: Regrettably type material could not be located in Oslo (Dr. K-H. Larsson, personal communication). Clarkston & Saunders (2012) observed the isotype specimen BM 000530325 (a vegetative collection from Inaccessible Island, Tristan da Cunha) and their observations are certainly consistent with the protologue and our contemporary collections. Because this collection was recently studied by one of the authors here, and was clearly in hand when Baardseth described this species, it is herein designated as the lectotype until the holotype is located in Oslo.
Representative DNA barcode: KX808051 (COI-5P).
Remarks: We have included *Leniea kylinii* for the first time in molecular analyses, which position this taxon as sister to *Leniea* rather than in *Pugetia* (Fig. 2). Observations of vegetative anatomy of an isotype collection prompted Clarkston & Saunders (2012) to question assignment of *L. kylinii* to *Pugetia*. In retrospect, their observations of vegetative details are more reminiscent of *Leniea* than *Pugetia*. *Leniea kylinii* also has carpogonial branch details (Baardseth, 1941) that are highly similar to those outlined for *Leniea* (Hommersand *et al.*, 2009) both typically monocarpogonial with the supporting cell bearing 1 (-2) subsidiary cell(s). The most significant difference is the reported procarpy for the former versus the nonprocarpy for the latter. *Leniea lubrica* reportedly has an auxiliary cell branch similar to the carpogonial branch. Our own observations revealed putative auxiliary cell branch systems in *L. kylinii*, which looked like developing carpogonial branches (supporting cell bearing a single subsidiary cell; data not shown) consistent with assignment of this species to *Leniea*.

Austropugetia R.L.Moe (?)

Type species: *Austropugetia crassa* R.L.Moe, 2009 (in Hommersand *et al.*).
Remarks: Material of CCMP719 was acquired from a culture originally isolated by R. Moe from Antarctica. Anatomically, it is roughly consistent with *Austropugetia crassa* (medullary cells are smaller, but this may reflect a culture artefact; data not

shown), a species collected on the same day that this culture was isolated (R. Moe personal communication). However, our sequence data fail to position this specimen anywhere near *rbc*L data considered representative of this species (Fig. 2) in D'Archino *et al.* (2016) and cited as unpublished data in Hommersand *et al.* (2009). Matters are further complicated because one unpublished *rbc*L sequence for *Nereoginkgo adiantifolia* Kylin matches our sequence for CCMP719, and these do not ally closely to other sequences of this species or those of *N. populifolia* R.L.Moe (unpublished *rbc*L data provided by P. Gabrielson). We are thus unable to resolve the genus-level assignment of this culture isolate. Considerably more genetic data from Antarctic specimens directly linked to vouchers are necessary to resolve this conundrum. For now we can report that CCMP719 is closely allied to three species currently, but incorrectly assigned to *Callophyllis*, viz., *C. atrosanguinea* (J.D.Hooker & Harvey) Hariot, *C. corollata* Baardseth (discussed below), and *C. macrostiolata* Arakaki, Alveal & Ramírez (Fig. 2).

'Callophyllis' incertae sedis 1

Remarks: This lineage includes three Southern Hemisphere species assigned to *Callophyllis* that may or may not form a genus with CCMP719. That decision awaits clarification of the issues outlined in the previous paragraph. *Callophyllis atrosanguinea* and *C. macrostiolata* were recently included in molecular analyses by Arakaki *et al.* (2011), but as that study was virtually restricted to species of *Callophyllis sensu lato* (except for *Judithia delicatissima* (R.E.Norris) D'Archino & S.-M.Lin and the outgroup *K. reniformis*), their true phylogenetic affinities were not uncovered. *Callophyllis corollata* Baardseth was synonymized with *C. variegata* (Bory) Kützing by Ricker (1987), but our data (based on eight barcoded collections from Tristan da Cunha; Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1) clearly resolved these two taxa in strongly divergent lineages (Fig. 2).

Rhizopogonia Kylin

Type species: *Rhizopogonia asperata* (Harvey) Kylin, 1934.
Remarks: *Rhizopogonia* was described by Kylin (1934) for the New Zealand endemic species *Callophyllis asperata* Harvey. D'Archino *et al.* (2011) included this species in phylogenetic analyses and their results, consistent with those here (Fig. 2), support *Rhizopogonia* as an independent genus. *Rhizopogonia asperata* resolved on a long branch weakly sister to a lineage including Kallymeniaceae sp.2LH (below), as well as species of the genera *Metacallophyllis*, *Pugetia* and *Salishia*.

Kallymeniaceae sp.2LH

Remarks: Kallymeniaceae sp.2LH consists of a single collection from Lord Howe Island and may be the basis for the record of *Pugetia* from New South Wales in Millar & Kraft (1993). We refrain from naming this genus-level lineage until more material is collected for anatomical observations.

Salishia Clarkston & G.W.Saunders

Type species: *Salishia firma* (Kylin) Clarkston & G.W.Saunders, 2012.
Remarks: Harper & Saunders (2002) were the first to include a cohort of species variously assigned to *Callophyllis* or *Pugetia* in molecular analyses. They argued

that *Callophyllis* and *Pugetia* were distinct genera and that *Pugetia chilensis* (J.Agardh) Kylin and *P. firma* Kylin were best maintained in the latter genus and more closely, albeit deeply, allied to the type *P. fragilissima* Kylin than they were to the type of *Callophyllis* (Harper & Saunders, 2002). Nonetheless, reproductive differences between *P. fragilissima* relative to *P. chilensis* and *P. firma,* as outlined in Norris (1957), foreshadowed the need for further taxonomic study. Clarkston & Saunders (2012) completed a detailed monograph of the genus *Pugetia,* considering the 13 species that had been assigned to the genus (many of which had been subsequently transferred to other kallymeniacean genera, primarily *Callophyllis*). They managed to include four of the previous species, plus the new species *P. cryptica* Clarkston & G.W.Saunders, in their phylogenetic analyses and resolved two discrete lineages separated by *Callophyllis* (=*Metacallophyllis*) *laciniata* (Hudson) Kützing (Clarkston & Saunders, 2012). Our present analyses (Fig. 2) agree with their study in recognizing *Salishia* for *S. chilensis*, *S. firma*, and *S. sanguinea* as distinct from the genus *Pugetia*.

Metacallophyllis A.Vergés & L.Le Gall, *gen. nov.*

Description: Member of the Kallymeniaceae with dichotomous to subdichotomous blades; medulla compact, with large, ovoid, hyaline cells surrounded by small pigmented cells arranged in filaments, stellate cells absent. Monocarpogonial, supporting cell lobed and usually bearing several lobed subsidiary cells, carpogonial branch three-celled; fusion cell lobed; procarpic. Tetrasporangia growing among cortical cells. Carposporophyte ostiolate.
Etymology: Named for its similarity in gross morphology with most species of the genus *Callophyllis*.
Type and only species: *Metacallophyllis laciniata* (Hudson) A.Vergés & L.Le Gall, *comb. nov.*

Metacallophyllis laciniata (Hudson) A.Vergés & L.Le Gall, *comb. nov.*

Basionym: *Fucus laciniatus* Hudson, *Flora anglica*: 475 (1762).
Lectotype: A Hudson specimen located in the BM is provisionally assigned as the lectotype (Irvine, 1983).
Representative DNA barcode: JF903294 (COI-5P).
Remarks: Our molecular analyses clearly separate *Metacallophyllis laciniata* from *Callophyllis* and resolve it as the sister genus of *Salishia* (Fig. 2). Both Northeast Atlantic and Mediterranean specimens hitherto sequenced for COI-5P belong to the same genetic group (Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1).

Pugetia Kylin

Type species: *Pugetia fragilissima* Kylin, 1925.
Representative DNA barcode: HM915628 (COI-5P).
Remarks: As indicated above, Clarkston & Saunders' (2012) detailed monograph of *Pugetia* resulted in the transfer of three of its former species to their new genus *Salishia*. They additionally examined type material of *P. latiloba* (W.R.Taylor) R.E.Norris (Galápagos Islands), *P. kylinii* (Tristan da Cunha), *P. japonica* Kylin (Japan), *P. delicatissima* R.E.Norris (New Zealand), *P. porphyroidea* (F.Schmitz ex Holmes) R.E.Norris (South Africa) and *P. harveyana* (South Africa), none of which were considered unambiguously assignable to *Pugetia*. If all are ultimately removed, *Pugetia* may become a genus restricted to the northeastern Pacific, although further

study is needed. We have here transferred *P. kylinii* to *Leniea* and *P. harveyana* to *Polycoelia* building on recognition of the genus *Judithia* for *P. delicatissima* by D'Archino *et al.* (2016) and the genus *Salishia* in Clarkston & Saunders (2012) (Figs 1, 2). The remaining *Pugetia* species from the Galápagos Islands, Japan, and South Africa require similar contemporary studies.

Ectophora J.Agardh

Type species: *Ectophora depressa* J.Agardh, 1876.
Remarks: The status of *Ectophora* as a genus distinct from *Callophyllis* was widely regarded as doubtful until molecular data supported its recognition (D'Archino *et al.*, 2011, and references therein). Our analyses agree with the work of D'Archino *et al.* (2011) and resolved a monophyletic lineage for the type and the only other species, *E. marginata* D'Archino & W.A.Nelson (Fig. 2).

Austrophyllis Womersley & R.E.Norris (?)

Type species: *Austrophyllis alcicornis* (J.Agardh) Womersley & R.E.Norris, 1971.
Remarks: This genus was established for two nonprocarpic Australian species that otherwise would have been assigned to the procarpic genus *Callophyllis* (Womersley & Norris, 1971). Unfortunately, we have only three genetically verified collections of *Austrophyllis*, one of which is loosely assignable to the type (a robust specimen if correctly identified), but which differs by five substitutions in the relatively conservative LSU from the second genetic group simply recorded as *A.* sp.1Aus (Fig. 2, Table S1). The latter is represented by two specimens that differ by only one substitution in their COI-5P, indicating that they may belong to a single genetic species, but *rbc*L-3P for these two specimens is identical over 800 bp relative to the full *rbc*L for *A. alcicornis,* which is consistent with incomplete lineage-sorting or hybridization for these two genetic species. None of our collections is a good habit match to the second morpho-species, *A. harveyana* (J.Agardh) Womersley & R.E.Norris. Our putative specimen of *A. alcicornis* is cystocarpic, which allowed us to confirm that this lineage is at least anatomically consistent with *Austrophyllis* as defined by Womersley & Norris (1971). Considerable further research is needed to establish the status of this enigmatic genus.

Stauromenia D'Archino & W.A.Nelson

Type species: *Stauromenia australis* D'Archino & W.A.Nelson, 2012 (in D'Archino *et al.*).

Stauromenia lacerata (Womersley & R.E.Norris) G.W.Saunders, *comb. nov.*

Basionym: *Thamnophyllis lacerata* Womersley & R.E. Norris, *Australian journal of botany,* Suppl. 2: 25-27, figs 48-52, 94-96 (1971).
Holotype: AD A35159 (Womersley, 1994, p. 249; Guiry & Guiry, 2016).
Representative DNA barcode: HM915923 (COI-5P).
Remarks: As foreshadowed by D'Archino *et al.* (2012, p. 459), *Thamnophyllis lacerata* has key features in common with *Stauromenia australis* D'Archino & W.A. Nelson. Among the features they share are strongly refractive medullary cells, monocarpogonial supporting cells, and one- to three-celled subsidiary cells/filaments on their auxiliary cells (Womersley & Norris, 1971; Womersley, 1994; D'Archino *et al.*, 2012). In these features the previous species differ from both the type of

Thamnophyllis, *T. pocockiae*, and *T. discigera* (Norris, 1964). The tell-tale anatomical links are strongly supported by our phylogenetic analyses (Fig. 2). *Thamnophyllis* thus appears to be a genus restricted to southern Africa that consists of the two species listed previously and a third, unbranched species, also collected from southern Africa (*T.* sp.1SAfr; Fig. 1, Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1), that is in need of formal description.

We have identified a second Australian species of *Stauromenia* that is closely allied to *S. lacerata* (*S.* sp.1Aus; Fig. 2) from the Houtman Abrolhos Islands, Western Australia, which is yet to be formally named (Table S1).

'Callophyllis' incertae sedis 2 & 3 and *Callophyllis* Kützing *'sensu stricto'*

Type species: *Callophyllis variegata* (Bory) Kützing, 1843.
Remarks: From this point forward the phylogenetic analyses present a poorly resolved speciose cluster of entities presently or provisionally assigned to *Callophyllis* and its close allies. Many of the sequences included in our tree were harvested from GenBank where they are simply entered as "sp.", and many, we suspect, lack vouchers. From our own data we present a significant number of informal species to which many genetically verified collections have been assigned and for which vouchers are available for future study (e.g. *C.* sp.1rangiferina; Fig. 2, Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1). Only a few of the genetic species allow some cautious confidence in the assigned names (e.g. Clarkston & Saunders, 2013), but even a few of these have been subsequently modified (Filloramo *et al.*, 2017). In all of our best-sampled floras (viz. Australia; the Northwest and Northeast Pacific), numerous overlooked species have been uncovered that require further study. For example, in Australia we have uncovered *ca* 12 genetic groups, but only the names *C. cervicornis* Sonder and *C. nana* A.Millar are assigned with any degree of confidence (Fig. 2, Table S1, doi/10.7872/crya/v38.iss2.2017.Suppl.Mat.1).

Resolution of *Callophyllis sensu lato* is outside the scope of the current study, but this is certain to be a major focus of attention in future studies. This work has already begun well with establishment of the genera *Judithia* and *Wendya*, both recently described from New Zealand by D'Archino *et al.* (2016) and both resolving deeply within *Callophyllis sensu lato*. We recognize these genera pending better phylogenetic resolution in that portion of the tree, although both *Judithia* and *Wendya* have aspects of reproductive anatomy that would on their own support genera distinct from *Callophyllis.* The conflicting sequence data associated with *Austropugetia* need to be resolved, as do better characterizations of morphological and molecular features of the entities in GenBank that resolve deeply in the *Callophyllis* lineage which, like that previously true of the *Kallymenia* clusters, will likely require division into monophyletic genera (Fig. 2).

Judithia D'Archino & S.-M.Lin

Type species: *Judithia delicatissima* (R.E.Norris) D'Archino & S.-M.Lin, 2016 (in D'Archino *et al.*).
Remarks: Despite anatomical differences in vegetative construction (D'Archino *et al.*, 2011), the reportedly cosmopolitan, Chilean-based type species *Callophyllis variegata* (Bory) Kützing as previously credited to New Zealand (Chapman & Parkinson, 1974; Adams, 1994, p. 218, pl. 75) resolved solidly as sister to *Judithia delicatissima* (Fig. 2). *Callophyllis variegata* is thus not represented in the New Zealand flora. Sister to to the previous two species, although with no support, was

Thamnophyllis laingii (J.Agardh) R.E.Norris (Fig. 2). Not remotely related to the type of *Thamnophyllis* (Fig. 1), *T. laingii* needs to be removed to at least an interim placement in *Judithia.*

Judithia laingii* (J.Agardh) G.W.Saunders, *comb. nov.

Basionym: *Dactylymenia laingii* J.Agardh, *Lunds Universitets Års-Skrift, Andra Afdelningen, Kongl. Fysiografiska Sällskapets i Lund Handlingar* 35(4): 54 (1899).
Type: LD, Herb. Agardh 24736 (Chapman & Parkinson, 1974, p. 231).
Remarks: An alliance of *Thamnophyllis laingii*, *"Callophyllis variegata* NZ", and *Judithia delicatissima* was missed in the combined analyses of D'Archino *et al.* (2016, fig. 2), in which *T. laingii* formed a seemingly unequivocal association with *T.* (= *Stauromenia*) *lacerata*. Regrettably their result must be erroneous as neither of the genes used in that study, LSU or *rbc*L, support that association [Fig. 2, and single-gene analyses here; and D'Archino *et al.* (2016, fig. 1)]. *Judithia laingii* joins *"Callophyllis variegata* NZ", which was reported to have features similar to *Thamnophyllis sensu lato* (D'Archino *et al.*, 2011, p. 249), and *Judithia delicatissima*. This association is at present weakly supported in our analyses and requires more study, but our interim taxonomic assignment seems preferable to leaving *J. laingii* in the distantly related genus *Thamnophyllis* (Fig. 1).

***Wendya* D'Archino & S.-M. Lin**

Type species: *Wendya incisa* D'Archino & S.-M. Lin., 2016 (in D'Archino *et al.*)
Remarks: Established for an overlooked species masked within the broader concept of *Pugetia delicatissima sensu lato* in New Zealand, *Wendya incisa* was established on the basis of clear anatomical and molecular differences from the former species (D'Archino *et al.*, 2016). In our analyses, this genus resolved as a solitary lineage positioned with no support between *Judithia* and what has loosely been designated *Callophyllis sensu stricto* here (Fig. 2).

CONCLUSIONS

Genera of the Kallymeniaceae have been traditionally distinguished by such features as frond habit (foliose, lacerate, branched), frond texture, presence or absence of a midrib and veins, degree of filamentous composition and compactness of the medulla, presence or absence of ganglionic and/or stellate cells in the medulla, trophic mode (completely photoautotrophic vs totally or mostly parasitic), diploidization processes (either procarpic or nonprocarpic), monocarpogonial vs polycarpogonial supporting cells, location and configuration of supporting cell and (when present) auxiliary cell systems, details of gonimoblast initiation and elaboration, degree of mixing of carposporangial and sterile filaments in carposporophytes, and presence or absence of an ostiolate or non-ostiolate pericarp. Whereas some of these features ultimately will prove useful at the generic level, others, such as whether or not blades are branched or foliose, simply lack utility. Ultimately our aim has not been to clarify fully which morpho-features will best resolve the various genera, but to put the molecularly defined species into taxonomically consistent natural groupings in order to point directions for future research. We break with long-standing morpho-taxonomic practices whereby species

were often forced to fit rather uncomfortably into systematic constructs of reportedly cosmopolitan genera such as *Callophyllis, Kallymenia* and *Pugetia*, all of which are actually much smaller taxa than previously thought and for the latter two, at least for now, largely restricted to the Northern Hemisphere.

Our study radically changes the understanding of generic diversity of the Kallymeniaceae at a global level. D'Archino *et al.* (2016) noted that New Zealand was the center of genus-level diversity for the family in the Southern Hemisphere, its flora including representatives of ten genera along coasts of a very limited and geographically isolated landmass. We have now reduced that number to nine with removal of *Thamnophyllis*, although at the same time raising the number of kallymeniacean genus-level lineages (one yet to be named) in Australia from eight (Womersley, 1994) to 18, with the even smaller landmass of Tasmania remarkably hosting 11. Numbers in both the Australian and New Zealand floras are likely to climb markedly, and we would extend to Australia the prediction of D'Archino *et al.* (2011) that some of the New Zealand species currently assigned to "*Callophyllis* will ultimately prove to belong to other genera". Considerable study thus remains to be conducted on this rich and diverse family, and this undoubtedly throughout its geographical and habitat ranges.

Acknowledgments. All of the collectors in Table S1 are thanked for their contributions to this project. Special thanks to Sue Scott and the Darwin Expedition for collections from Tristan da Cunha, and Kyatt Dixon and J. Ferreira Costa for collections from South Africa, which have allowed us to resolve a number of key outstanding taxonomic issues. Olivier De Clerck generously loaned key South African vouchers. Special thanks are extended to Tanya Moore, Dan McDevit and Kyatt Dixon for their molecular support at UNB (the University of New Brunswick) and to Delphine Gey for her support at MNHN. Craig Schneider provided guidance with Latin nomenclature, and along with Christine Maggs is thanked for thorough review of this lengthy manuscript. Paul Gabrielson is thanked for sharing unpublished sequence data and Richard Moe for discussions on culture CCMP719. Work completed at the Saunders laboratory at UNB, Canada, was supported by the Canadian Barcode of Life Network from Genome Canada through the Ontario Genomics Institute, the Natural Sciences and Engineering Research Council of Canada, as well as other sponsors listed at www.BOLNET.ca, with infrastructure support from the Canada Foundation for Innovation and New Brunswick Innovation Foundation. Molecular data generated for L. Le Gall at the Service de Systématique Moléculaire du Muséum National d'Histoire Naturelle (CNRS – UMS 2700) was funded by the ATM "Taxonomie moléculaire: DNA Barcode et gestion durable des collections". Sequencing was performed by the Genoscope through the projects entitled 'Speed ID" and "Bibliotheque du Vivant". A. Vergés is grateful for the Synthesis award received in 2009 and 2015 that supported the revision of *Kallymenia* specimens located at BM and PC. J. Huisman thanks the Australian Biological Resources Study (ABRS) for support and the Western Australian Museum for the invitation to participate in the Ashmore Reef survey (with financial support from Woodside Energy). G. Kraft acknowledges the logistic support of the Tasmanian Herbarium through its Director, Dr. Gintaras Kantvilas, and Chief Administrative Officer, Ms. Kim Hill. Information and scans of type material were provided through the courtesy of Ulf Arup at LD.

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