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**DNA barcoding reveals multiple overlooked Australian species of the red algal order Rhodymeniales (Florideophyceae), with resurrection of *Halopeltis* J. Agardh and description of *Pseudohalopeltis* gen. nov.**

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**Abstract:** The DNA barcode (COI-5P) was used to investigate cryptic diversity among *Rhodymenia* spp. in southern Australia. Whereas eight species are currently recognized, we uncovered ca. 20 genetic species groups, phylogenetically assigned to four genera in two families. Procumbent specimens with molecular and anatomical signatures of the Fryeellaceae are assigned to *Pseudohalopeltis tasmanensis* gen. et sp. nov. Collections from Lord Howe Island recorded in the field as *Rhodymenia/Fauchea* sp. are assigned to the poorly known genus *Microphyllum* as *M. robustum* sp. nov. A cluster of species with distinct molecular and anatomical attributes is included in a resurrected *Halopeltis* J.G. Agardh, including: *H. australis* (J. Agardh) comb. nov. (type species); *H. austrina* (Womersley) comb. nov.; *H. cuneata* (Harvey) comb. nov. [including *Rhodymenia halymenioides* (J. Agardh) Womersley]; *H. gracilis* sp. nov.; *H. prostrata* sp. nov.; and *H. verrucosa* (Womersley) comb. nov. Four additional species of *Halopeltis* from Lord Howe Island (LH1, LH2), Tasmania (TAS) and Western Australia are not characterized further. For *Rhodymenia sensu stricto*, similar levels of cryptic diversity were noted. Samples tentatively field-identified as '*Rhodymenia sonderi*', but having affiliations to *Rhodymenia* rather than *Halopeltis*, are referred to *Rhodymenia novahollandica* sp. nov. Collections field-identified as *R. obtusa* are genetically distinct from that species and are assigned to *R. wilsonis* (Sonder) comb. nov. Two highly divergent species currently identified as *Rhodymenia leptophylla* (LH from Lord Howe Island; TAS from Tasmania), as well as two additional cryptic previously unnamed taxa from South Australia (SA) and Victoria (VIC), are not characterized further.

*Key words:* cryptic species, DNA barcode, *Halopeltis*, *Microphyllum*, *Pseudohalopeltis*, *Rhodymenia*.

## Introduction

The Rhodymeniales is a well defined (Bliding 1928; Kylin 1956; Sparling 1957; Lee 1978) order of red algae united by a distinct type of “procarpy” [a consistently close juxtaposition of the fertilized carpogonium (female gamete) and the auxiliary cell (the site of embryo development) that it diploidizes], auxiliary cells that are generally produced prior to or regardless of fertilization, and outward development of the carposporophyte (the diploid generation developing from the diploidized auxiliary cell and hemiparasitic on the gametophyte generation). Six families comprise the group, the Champiaceae, Faucheaceae, Lomentariaceae and Rhodymeniaceae (Saunders et al. 1999), plus the Frycellaceae and Hymenocladaceae recently segregated from the Rhodymeniaceae (Le Gall et al. 2008).

The Rhodymeniaceae has long been the largest family of the Rhodymeniales, defined largely on vegetative characters that include thalli that are either solidly constructed throughout or at least partially hollow, in which case the cavities lack peripheral linings of longitudinal narrow filaments (Bliding 1928; Sparling 1957; Ricker and Kraft 1979). More recently, reproductive characteristics have been increasingly emphasized, including the determination of whether the tetrasporangia are intercalary and/or terminal in nemathecial or non-nemathecial sori, carpogonial branches are either three- or (more usually) four-celled, and the interior surfaces of pericarps have or lack *tela arachnoidea* (persistent mesh-like networks of filaments) (Saunders et al. 1999, 2006; Dalen and Saunders 2007; Le Gall et al. 2008). Of particular importance is the recent downgrading of intercalary versus terminal tetrasporangia in defining taxa, with greater emphasis laid on whether or not tetrasporangia and their associated sterile

filaments (where present) are derived from existing cortical cells directly or arise adventitiously from precursor cortical cells (Saunders et al. 2006). As a concomitant to this distinction, molecular studies have indicated that a segregate family, the Fryeellaceae, is warranted for some species traditionally included in the Rhodymeniaceae that have either cruciate or tetrahedral tetrasporangia that develop directly from terminal cortical cells and for which adventitious cortical growth contributes to sterile filaments (paraphyses) amongst the developing sporangia (Le Gall et al. 2008), resulting in nemathecia rather than strictly sori.

In violation of the accepted pattern of tetrasporangial development in the genus *Rhodymenia*, four out of eight southern Australian species (*R. cuneata*, *R. halymenioides*, *R. sonderi* and *R. verrucosa*,) appear (e.g., Womersley 1996, figs 26F, 27H) to display terminal tetrasporangia in conjunction with adventitious sterile filaments similar to those noted for the Fryeellaceae (Le Gall et al. 2008) or Faucheaceae (Dalen and Saunders 2007). This deviation in reproductive attributes from the remaining members of the genus (and, indeed, the family) calls for critical re-evaluation of all the rhodymeniid species attributed to cool-temperate to subtropical Australian shores. Further, the most widely dispersed species of *Rhodymenia* in Australasia (Adams 1994, p. 230; Womersley 1996, p. 77; both as *R. australis*), *R. sonderi* P.C. Silva, encompasses a wide variety of forms throughout its range. As interpreted by Womersley (1996, p.77), this broadly defined entity occurs from low tide to 50-m depths and “varies considerably in width of branches depending on age, state of growth and degree of water movement.” These attributions of habit variability to phenotypic responses to environmental and life-phase factors are reasonable conclusions for an alpha-taxonomist to make, but with the development of

molecular-phylogenetic techniques the speculations now become testable hypotheses. Assessing conspecificity of these many morphs has been the major objective of the present project.

Molecular tools have been used successfully to elucidate phylogenetic relationships within many taxonomic groups. Establishing novel systems of classification that are based upon these relationships provides a more meaningful foundation from which to evaluate the true state of biological diversity within given regions. The use of these tools avoids problems such as putting emphases on misleading characteristics that have converged due to selective pressures, as well as overcoming problems inherent in the frequent lack of life-history details (Saunders and Hommersand 2004). At lower taxonomic levels, the relative morphological simplicity of macroalgae, exacerbated by convergent evolution, retention of ancestral features, and phenotypic plasticity, can lead to the designation of non-natural taxa due to underappreciated morphological differences or even completely cryptic anatomical distinguishing features (Saunders 2005; Le Gall and Saunders 2010). Molecular markers can detect diversity within such morphologically based “species”. They are an effective means of initial identification and establishment of genetically-based monophyly at all taxonomic levels. One such tool, the DNA barcode, has been successfully used to discriminate among cryptic species of red algae (e.g., Saunders 2005, 2008, 2009; Walker et al. 2009; Le Gall and Saunders 2010). The DNA barcode is a portion of the mitochondrial cytochrome-c oxidase subunit I (COI) gene that has been identified and championed as a standard for molecular species distinctions throughout all kingdoms and phyla of eukaryotic life (Hebert et al. 2003). Species identified by this tool can then be subjected to traditional morphological and anatomical

investigations in order to supplement the molecular results (molecular-assisted alpha taxonomy) and aid field-biologists in recognizing and correctly labeling the distinct entities (Saunders 2008). This combination of traditional and molecular approaches to species diagnosis and specimen identification enables researchers to distinguish between species-diagnostic characteristics and those that are either phenotypically plastic or have converged between species.

Although the DNA barcode is a useful tool for species identification, it is generally not a reliable aid to phylogenetic analyses on its own owing to the relatively short length of the region used in such procedures (ca. 660 base pairs; Saunders 2008). In order to facilitate meaningful phylogenetic investigations, additional sequence data must be generated. The nuclear ribosomal cistron has proven particularly useful for phylogenetic analyses (see Harper and Saunders 2001). A mix of conservative coding and variable non-coding regions allow this system to be applied to phylogenetic analyses over a wide spectrum of taxonomic levels, and the much longer genic regions [typically 2700 bp amplified for the large subunit ribosomal RNA gene (LSU) in red algae (Harper and Saunders 2001)] ensure adequate characters are available for resolution. Indeed, the LSU has been widely applied in phylogenetic investigations of red algae at many taxonomic levels (e.g., Freshwater et al. 1999; Harper and Saunders 2001; Withall and Saunders 2006).

It has been the goal of this study to use molecular tools to assess the taxonomic status of Australian entities currently included in *Rhodymenia*, and to identify cryptic taxa, which may account for the variation in anatomical states reported for some species. In this study, 137 collections unambiguously to tentatively field-identified as

*Rhodymenia* spp. in southern Australia (predominantly from Tasmania and Victoria, but also from South Australia, Western Australia, and Lord Howe Island off the coast of New South Wales) and related genera (such as *Epymenia* and *Rhodymeniocolax*) were collected for barcode analyses, as well as ca. 30 samples of species from allied Australian and extra-Australian genera to round out our barcode and phylogenetic analyses. Isolates were initially screened with the DNA barcode and assigned to genetic species groups in order to assess cryptic diversity within '*Rhodymenia*' spp. in Australia. Once 'genetic species' were defined, a representative(s) from each was included in LSU phylogenetic analyses to assess inclusion in or exclusion from the genus *Rhodymenia*. Particularly in the case of species with broad habit ranges and putatively anomalous reproductive characteristics, the goal has been to identify cryptic taxa and determine their true taxonomic affiliations.

## **Materials and Methods**

A total of 146 collections assignable on morphological/anatomical grounds to the genus *Rhodymenia* were obtained for purposes of DNA barcoding, including 137 samples from Australia (ca. 90 collected as *Rhodymenia sonderi sensu lato*) and nine from other regions (Table 1). Collections were pressed and dried on herbarium paper to be maintained as vouchers, with small portions of each dried in silica for DNA extraction. Dried portions were ground to a powder in liquid nitrogen and DNA was extracted according to Saunders (1993, 2008). Polymerase chain reaction (PCR) amplification of the DNA barcode was completed using oligonucleotide primers and methods as

published by Saunders (2005, 2008, 2009). LSU amplicons were obtained for a representative sample(s) of each genetic species group (as identified in the barcode analyses) following the protocol of Harper and Saunders (2001). PCR products were cleaned according to Saunders (1993). Sequencing reactions used the BigDye Terminator v3.1 Cycle Sequencing Kit following the manufacturer's recommendations (PE Applied Biosystems (ABI), Foster City, California) and samples were electrophoresed in an ABI 3100 Genetic Analyzer.

Sequences were edited with the Sequencher (Gene Codes Corporation) computer program, and the consensus sequences aligned in MacClade v4.08 (Maddison and Maddison 2003). Four separate alignments were created from the data.

All DNA barcode sequences (COI-5P) were compiled into a single alignment to be used for cluster analysis in order to assign collections to genetic species groups. Seven samples yielded contaminated COI sequences and were not included, while four published sequences were included for a final alignment of 143 samples and 664 positions (see Table 1). The 24 new LSU genes determined here were variously combined with published sequences (see Table 1) to generate three separate alignments. The first alignment included one or two species each from most genera of the Fryeellaceae and Rhodymeniaceae to resolve the phylogenetic affinities of the four major species complexes resolved in our barcode analyses (i.e., multiple closely related species within the genera detailed here, essentially redundant in considering higher taxonomic relationships, were excluded to reduce computational demands). This alignment included 21 taxa and 2755 positions (78 excluded as ambiguously aligned) and rooting was set between the two families (Le Gall et al. 2008).

A second alignment focused on *Halopeltis* spp., rooted on the sister genus *Halichrysis* (as established in the first LSU analyses), and was constructed so that more variable regions could be included in analyses (fewer ambiguously aligned sites among these more closely related taxa) to enhance resolution within this genus. The alignment included 12 taxa and 2695 positions (none excluded). Similarly, a third alignment (23 taxa, 2708 positions) was constructed for *Rhodymenia* spp. (including *Cordylecladia erecta*) with *Botryocladia leptopoda* and *Chrysomenia wrightii* included as outgroups (Le Gall et al. 2008).

For the barcode data, analyses were conducted in PAUP\* 4.0b10 (Swofford 2002) with distances corrected under a general time reversible model and neighbor joining was used to provide a visual display of COI-5P variation within and between species. The program Modeltest v.3.7 (Posada and Crandall 1998) was used for all three LSU alignments to determine the most appropriate model of nucleotide substitution. All tests returned the general time reversible model with invariant sites and gamma distribution (GTR+I+G) as the model that best fit the data. These models were incorporated into maximum likelihood (ML) analyses under heuristic searches (10 random additions) with tree-bisection reconnection branch swapping in PAUP 4.0b10. Robustness was assessed by completing ML analyses on 200 random bootstrap datasets for each of the three alignments.

For anatomical observations, sections were prepared from rehydrated material in a cryostat (CM1850, Leica, Heidelberg, Germany), stained with 1% aniline blue in 7% acetic acid, and subsequently mounted in 40-50% corn syrup. Observations were recorded on a Leica DFC480 digital camera mounted on a Leica DM5000B light microscope. Herbarium abbreviations follow the online Index Herbariorum

<http://sweetgum.nybg.org/ih/>, and standard author initials are from Brummitt and Powell (1992).

## Results and Discussion

### Molecular Observations

The DNA barcode was successfully sequenced for 139 of our 146 collections (Table 1; Fig. 1). It failed for a few collections of two species that were particularly infested with epiphytic animals (discussed below), DNA from the latter likely accounting for the contaminated amplicons. In these cases, the LSU D2/D3 region was used as a secondary marker to assign collections to genetic species groups (e.g., Saunders and Lehmkuhl 2005; see Table 1). Although not as sensitive for species discrimination among red algae as COI-5P (Saunders and McDevit unpublished data), this marker easily assigned these collections to one of two genera (*Microphyllum*, *Pseudohalopeltis*) that are thus far represented by only a single species in our analyses (thus finer resolution is not as critical as within the more speciose genera under study; Fig. 1).

There are currently eight species of *Rhodymenia* recognized in southern Australia (Womersley 1996), but DNA barcoding resolved ca. 20 genetic groups for our specimens field identified as *Rhodymenia* spp., with *Rhodymenia sonderi sensu lato* accounting for six of these and also ca. 50% of *Halopeltis verrucosa* (Womersley) comb. nov. isolates (Fig. 1). In more detailed phylogenetic analyses (Fig. 2), these genetic groups, rather than forming a single generic level cluster, were distributed among a minimum of four genus-level clades in two divergent families of the Rhodymeniales. The first cluster,

*Pseudohalopeltis tasmanensis* gen. et sp. nov., included 17 collections from Tasmania field identified as *Rhodymenia sonderi sensu lato* (Fig. 1; Table 1), but which nonetheless joined the Fryeellaceae (Fig. 2A). Divergence within this cluster ranged from 0-0.75%, slightly higher than noted for some previous red algal studies (see Saunders 2005, 2008), but consistent with intraspecific divergence in other accounts (Robba et al. 2006; Le Gall and Saunders 2010).

Collections GWS002046 and GWS002047 from Lord Howe were identical in COI sequence (Fig. 1) and associated with the genus *Cephalocystis* in our phylogenetic analyses (Fig. 2A). They, along with GWS002057, are assigned to the enigmatic genus *Microphyllum* as *M. robustum* sp. nov.

The next substantial cluster of taxa is assigned to the resurrected genus *Halopeltis* and includes three species typically included in *Rhodymenia*, as well as six overlooked species (Figs. 1 and 2B; Table 1), which resolved as sister to the genus *Halichrysis* rather than *Rhodymenia* in our phylogenetic analyses (Fig. 2A). First, a ‘*Rhodymenia sonderi*’ complex (= *Halopeltis australis* (J. Agardh) comb. nov.), including G0253 from Western Australia that was closely allied (1.5%) to GWS001279 and GWS001280, both from Western Australia, and GWS001570 from Victoria (the latter two only 0.045% divergent) (Fig. 1; Table 1), was resolved. A second major cluster included collections variously field-identified as *Rhodymenia cuneata* Harvey and *R. halymenioides* (J. Agardh) Womersley (Fig. 1; Table 1), which, with no COI-5P divergence, are synonymized and transferred to *Halopeltis* as *H. cuneata* (Harvey) comb. nov. (Figs. 1 and 2B). *Halopeltis verrucosa* included plants variously collected as *Rhodymenia verrucosa* Womersley, *Rhodymenia sonderi sensu lato* and *Rhodymenia* sp. This cluster, at 0-0.9% divergence,

clearly contained two closely allied subgroups that differed from one another at 0.45-0.9% divergence. The bulk of the collections form a Tasmanian subgroup and show divergence of 0-0.7% more typical for other red algal species. Victorian collections GWS002532, GWS002539 and GWS002541 have only 0-0.15% divergence, which is particularly interesting because the sequence putatively from the parasite *Halopeltis austrina* (Womersley) comb. nov. (GWS002531) growing on one of the mainland collections resolved solidly in this subgroup (Fig. 1; Table 1). This result is discussed below and is not without precedent in the literature (Le Gall and Saunders 2010). Fourteen collections simply recorded in the field as ‘procumbent *Rhodymenia sonderi*?’ form the next cluster of tightly (0-0.3%) allied individuals, which are described as *Halopeltis prostrata* sp. nov. (Fig. 1; Table 1). Finally, we have a series of lineages collected as unknown *Rhodymenia* sp. forming the following genetic groups: *Halopeltis* LH1 (GWS002041, Lord Howe Island, Australia); *Halopeltis* LH2 (GWS002061); *Halopeltis gracilis* sp. nov. (GWS002049, GWS002052, GWS002062); *Halopeltis* TAS (GWS002596); and *Halopeltis* WA (G0402 from Western Australia and originally confused with *Asteromenia*; see Saunders et al. 2006). Those genetic species represented by only a single collection were not characterized further, but highlight beguiling levels of cryptic diversity yet to be documented for Australian Rhodymeniaceae.

Within the genus *Rhodymenia sensu stricto* cryptic diversity was also uncovered (Fig. 1). The first cluster, *Rhodymenia novahollandica* sp. nov., is widely distributed in southern Australia and is commonly and incorrectly attributed to ‘*Rhodymenia sonderi*’ *sensu lato* (here restricted to *Halopeltis australis*) (Fig. 1; Table 1). As with *H. verrucosa* above, within-species divergence is uncharacteristically high (1.26-1.66%) with a

biogeographical split between Tasmanian (two at 0.15% divergence) and mainland Australia (0-0.6% divergence) collections. Collection GWS001959, referred to here as *Rhodymenia leptophylla* J. Agardh TAS (from Tasmania), is in need of further characterization and is sister in COI-5P analyses to a divergent cluster (0-0.6%) referable to *Rhodymenia prolificans* Zanardini (Fig. 1; relationships equivocal in LSU analyses, Fig. 2C), also from Tasmania, and the slightly more distant (1-1.2%) GWS001555, which was field identified as *Rhodymenia stenoglossa* J. Agardh from Victoria. These latter two species are thus closely related (Figs. 1 and 2C) and possibly represent a single species with the same Tasmania versus mainland biogeographical split noted for three other species here. *Rhodymenia obtusa sensu lato* resolved as three divergent clusters with the two closely allied (1.7-2.0%; uncharacteristically high and again with a biogeographic component) Australian entities [considered here as *R. wilsonis* (Sonder) comb. nov. TAS (0-0.32%), exclusively from Tasmania, and *R. wilsonis* VIC (0%) predominantly from Victoria (only GWS001496 is from Tasmania)] clearly distinct from our South African collection (type locality for *R. obtusa*) (Figs. 1 and 2C; Table 1). Of the remaining Australian *Rhodymenia* spp., we uncovered a new species from South Australia (*Rhodymenia* SA; DV006), *Rhodymenia* VIC (GWS002467) from Victoria, and *Rhodymenia leptophylla* LH (GWS002467) from Lord Howe Island (GWS001039) and nearby Balls Pyramid (GWS002043) (Fig. 1). Again, these species were not characterized further owing to the small number of collections, but point to significant cryptic diversity remaining for the genus *Rhodymenia* in Australian waters.

## Anatomical observations and taxonomic conclusions

### Fryeellaceae

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

Laminae dichotomae plerumque procumbentes interstitibus (muco impletis?) inter cellulas medullariis centrales. Tetrasporangia incepta per tumescientiam cellularum corticalium exteriorum utraque superficie laminae, cellulis aliis sporangia directe factis, aliis elongantibus et filamenta sterilia facientibus per divisiones vegetativas, his filamentis sterilibus suum diametrum originalem retinentibus (id est expansione tetrasporangiorum non plerumque compressa). Cystocarpia protuberantia ostiolata sine ‘tela arachnoidea’ aut alteris filamentis anastomosantibus. Fryeellaceis et Rhodymenialibus genetice affinis.

Blades generally procumbent, dichotomous, with (mucilage-filled?) spaces between central medullary cells. Tetrasporangial development initiated by swelling of outer cortical cells on both blade surfaces, some cells directly converting to sporangia, others elongating and undergoing vegetative division to form sterile filaments, these retaining their original girth (i.e., generally not compressed by the expanding tetrasporangia). Cystocarps protuberant, ostiolate, lacking a ‘tela arachnoidea’ or other anastomosing filaments. Genetic affinities with Fryeellaceae, Rhodymeniales.

TYPE SPECIES: *Pseudohalopeltis tasmanensis* G.W. Saunders, sp. nov.

ETYMOLOGY: Named for its superficial similarity to the rhodymeniacean genus *Halopeltis*.

*Pseudohalopeltis tasmanensis* G.W. Saunders, sp. nov. Figs. 3-16.

Thalli ad 10 cm longi, axibus 0.5-1 cm latis, stipitati (in collectionibus thallorum juniorum evidentibus). Sori tetrasporangiales juniores ovaes vel cordiformes, in maturitate ad circumferentiam apicum ramorum conformantes, superficiem praeter margines tegentes. Tetrasporangia 18-22 by 28-32  $\mu\text{m}$ .

Thalli to 10 cm long, axes 0.5-1 cm wide, stipitate (evident in younger collections).

Tetrasporangial sori oval to cordiform when young, maturing to follow the outline of branch tips, covering the surface except for the margins. Tetrasporangia 18-22 by 28-32  $\mu\text{m}$  in dimensions.

HOLOTYPE: *GWS & R. Withall*, 26 January 2004 (UNB – GWS001980) (Figs. 3, 7-12).

TYPE LOCALITY: Governor Island Reserve (-41.8701°, 148.3058°), Bicheno, Tasmania, Australia; depth 23 m.

HOLOTYPE BARCODE: HM033077.

ETYMOLOGY: Named for the island state of Tasmania and its southern and eastern waters from which the new species was collected.

DISTRIBUTION: Known thus far from Bicheno in the east, Devils Hole south of Eaglehawk Neck in the southeast, to Ninepin Point and Verona Sands Reef south of Hobart.

REPRESENTATIVE SPECIMENS: Listed in Table 1.

OBSERVATIONS: Plants were collected subtidally (6-30 m) on rock walls and flats growing amongst sponges and other invertebrates. Blades are procumbent reaching 10 cm, generally dichotomous with axes 0.5 to 1 cm (below dichotomies) broad, becoming narrower towards apices in older plants, branch ends narrowly rounded (Fig. 3), pointed (Fig. 4) or terminating in paddles following regenerative growth of apices (Fig. 5). The latter continue growth to replicate the bearing plants forming compound thalli (largely obscured by associated sponges). Apices of smaller plants can be broadly rounded and maintain the proximal width of the vegetative blade (Fig. 6). Basal systems in larger plants are difficult to distinguish, although terete stipes are evident in some collections (e.g., Fig. 4). In younger plants, a short, occasionally branched, stipe subtends the vegetative blades, this arising from a discoid holdfast (Fig. 6). Stolons were not evident. Tetrasporangial sori are broadly to narrowly oval to cordiform at the branch apices, maturing to follow the outline of the individual tips covering the entire frond except at the margins. Cystocarps are submarginal on female plants (Fig. 4, insert), while distinctly lighter tips characterize males, indicating the locations of spermatangial development (Fig. 6).

Blades in transverse section (Fig. 7) are 160-200  $\mu\text{m}$  wide and consist of a medulla of 2-3(5) layers of variably sized (22-60 by 30-90  $\mu\text{m}$ ) and shaped cells, slightly axially elongate (up to 100  $\mu\text{m}$  in longitudinal section). The inner cortex is a single layer of smaller cells, similar to medullary cells in appearance and contents, this supporting an incomplete outer cortex of 1-2 cell layers (Figs. 7 and 8). Cells on one surface are slightly larger and stain more intensely with aniline blue than those of the opposing surface, indicating a dorsiventral aspect to blades. The appearance of presumably mucilage-filled

spaces between medullary cells is evident in sections at mid-thallus (Fig. 7). In tetrasporophytes, outer cortical cells on both surfaces swell in regions of nemathecium development and some undergo adventitious divisions to initiate sterile filaments (Fig. 9). As the nemathecium develops, sporangial initials enlarge and undergo presumed meiotic divisions, while sterile-filament cells continue to elongate and divide, the branched filaments ultimately 2 or 3 cells in length (Figs. 10 and 11). Mature tetrasporangia are cruciate, 18-22 by 28-32  $\mu\text{m}$ . This mixture of few-celled sterile nemathecium filaments and sporangia developing directly from outer cortical cells is similar to that reported in the Fryellaceae (Le Gall et al. 2008), although the sparser concentration of sporangia in the nemathecium presumably exerts less pressure on the sterile filaments, which thus remain relatively uncompressed laterally compared to those of *Fryella*.

An additional feature, recorded here in the tetrasporangial holotype (but observed to varying degrees in all collections), is the presence of crystalline inclusions in cells of the medulla and inner cortex (Fig. 12).

Cystocarps are essentially spherical (940-960  $\mu\text{m}$  wide by 800-900  $\mu\text{m}$  high) and positioned submarginally in distal (commonly subterminal) regions of the thalli (Fig. 4, insert). Multiple gonimolobes at different developmental stages are borne on a fusion cell (Fig. 13), as is typical for the order. A layer of nutritive tissue at the base of the chamber is also present, as is a thick (ca. 200  $\mu\text{m}$ ) pericarp, which appears under low magnification to have a lining of stellate cells across the inner surface (Fig. 13). A closer inspection, however, reveals that it is composed of a solidly cellular tissue, the stellate appearance imparted by cytoplasmic strands within cells that extend to the pit connections and are perhaps an artifact of rehydration (Fig. 14). The pericarp is thus

solidly pseudoparenchymatous and composed of cells that are progressively smaller towards the thallus surface. An ostiole is present as detected in glancing sections (Fig. 15). Male gametophytes (e.g., Fig. 6) produce modified outer cortical cells (spermatangial mother cells) bearing spermatangia at varying stages of maturity (Fig. 16).  
 COMMENTS: This species displays many habit and anatomical features of the genus *Halopeltis* (see below), but it differs in critical details of tetrasporangial development. These differences constitute the primary distinguishing features between the families Fryeellaceae and Rhodymeniaceae (Le Gall et al. 2008), supporting the familial affinities of this taxon that were strongly implied in our phylogenetic analyses (Fig. 2A).

### **Rhodymeniaceae**

*Microphyllum robustum* G.W. Saunders, sp. nov. Figs 17-27.

Laminae ad basin cuneatae e stipite brevi ( $\leq 1$  cm) gracili ( $\leq 1$  mm) ramoso vel directe ex haptero parvo discoideo orientes, flabellatae distichae 4.0-4.5 cm altae e ramis subdichotome vel irregulariter divisio constantes, axibus in directione acropeta decrescentibus. Cystocarpia (sub)marginalia, raro in superficiebus laminarum disposita. Medulla uni- vel bistrata e cellulis comparate magnis plerumque isodiametricis (90-140  $\mu\text{m}$ ) angulatis parietibus modice crassis constans; cortex interior e cellulis minoribus 1-2-stratis cingentibus medullam constans, ad lacunas a cellulis medullariis relictas plerumque limitatus; cortex exterior incompletus 1(-2)-stratus e cellulis isodiametricis vel axialiter complanatis constans.

Blades basally cuneate from a short ( $\leq 1$  cm), slender ( $\leq 1$  mm) and branched stipe, or arising directly from a small discoid holdfast; axes expanding to flabellate, distichous blades, 4.0-4.5 cm in height, the blades subdichotomously to irregularly divided, the axes narrowing acropetally. Cystocarps positioned (sub)marginally, rarely on blade surfaces. Medulla 1-2 layered, composed of relatively large, generally isodiametric (90-140  $\mu\text{m}$ ) angular cells with moderately thick walls; inner cortex 1-2 layered, composed of smaller cells generally confined to gaps between adjacent medullary cells; outer cortex 1(2) layered, incompletely covering the frond surface, the cells isodiametric to slightly flattened.

HOLOTYPE: *GWS*, 1 February 2004 (UNB – GWS002047) (Figs. 17, 20-27).

TYPE LOCALITY: Balls Pyramid ( $-31.8079^\circ$ ,  $158.9852^\circ$ ), Lord Howe Island, Australia; depth 22 m.

HOLOTYPE BARCODE: HM033071.

ETYMOLOGY: Named for the robust nature of this species relative to the generitype.

DISTRIBUTION: Thus far reported only from the type locality.

REPRESENTATIVE SPECIMENS: Listed in Table 1.

OBSERVATIONS: Blades are basally cuneate and arise directly from a small discoid holdfast or from a short ( $\leq 1$  cm), slender ( $\leq 1$  mm) and branched stipe, then expand distally to flabellate, largely distichous axes 4.0-4.5 cm in length, the axes subdichotomously to irregularly branched and narrowing acropetally (Figs. 17-19).

Blades in transverse sections at mid-thallus are 170-250  $\mu\text{m}$  thick and composed of a 1-2 layered medulla of relatively large, generally isodiametric (90-140  $\mu\text{m}$ ) and angular cells

with moderately thick walls (Fig. 20). The medulla is surrounded by 1-2 layers of much smaller cells that are generally concentrated in the gaps between medullary cells. The outer cortex is incomplete and consists of 1(-2)-layers of isodiametric to axially flattened cells (Figs. 20-22). Cells of presumably the dorsal layer (Fig. 21) differ from those of the opposite layer (Fig. 22) in being arranged more compactly and composed of slightly smaller cells. Occasional inner cortical cells are densely stained and filled with refractive inclusions (Fig. 23) of unknown nature.

Carpogonial branches were not observed in detail, but one abortive branch appears to be three cells in length (Fig. 24). Cystocarps are situated (sub)marginally (Figs. 17-19), rarely on the broad surfaces, and are sessile and spherical in outline, 800-900  $\mu\text{m}$  in diameter (Fig. 25). The base of the cavity has a typically rhodymeniaceous cushion of nutritive filaments, and an ostiole is present (Fig. 25). The pericarp is 125-150  $\mu\text{m}$  thick and composed of 3-5 layers of inflated isodiametric cells (16-23  $\mu\text{m}$  in diam.) surrounded by a 1(-2)-celled outer cortical layer (Fig. 26). In rehydrated material, inner pericarp cells have thick walls with the cytoplasm concentrated centrally giving the impression of a stellate network of cells. Investments of reticulate inflated cells line the periphery of the pericarp chamber (Fig. 27), but a well-developed *tela arachnoidea* is absent.

Spermatangia and tetrasporangia were not observed.

COMMENTS: This species formed a novel lineage in our molecular analyses that was positioned close to *Cephalocystis* (Fig. 2A), with which genus it shares general familial traits (Millar et al. 1996). Although it is one of the few rhodymeniaceous genera not included in our analyses to date, *Microphyllum* has been chosen as a provisional home for the Lord Howe species as, besides being composed of similarly solidly

pseudoparenchymatous blades, the type species is also reported by Weber-van Bosse (1928) to display small star-shaped cells inside the pericarp (Fig. 27). The holotype collection of *Microphyllum borneense* Weber Bosse (L 0056026) was borrowed to confirm these features, the type sheet consisting of a few small, mostly simple blades (Fig. 28). Two of these appeared to terminate short stipes arising from a small discoid holdfast, whereas another blade appears to have proliferated smaller adventitious axes from a damaged(?) margin (Fig. 28). Owing to the paucity of the type collection, only a small piece including a single cystocarp was sectioned. Blades are thin (50-75  $\mu\text{m}$ ) in transverse section (Fig. 29) and consist of a 1-2 layered medulla of angular, axially-elongate cells covered by a 1-2-layered loose (partially incomplete) cortex of flattened cells. In addition, some cells subtending the outermost cortical layer are densely packed with refractive material (Fig. 29) and presumably account for Weber-van Bosse's (1928) report of clusters of refractive cells (the cells having a distinctly dissected appearance). Cystocarps are marginal and ostiolate, the chambers ca. 350-500  $\mu\text{m}$  in diameter. Basal nutritive tissue was observed in some sections, as well as 2-3 successively maturing gonimolobes typical of Rhodymeniaceae. The pericarp consists of 3-5 layers of compact inflated cells that become progressively smaller towards the surface (Fig. 30), whereas the cells become more loosely aggregated and stretched out into "star-shaped" profiles towards the chamber lining, as reported by Weber-van Bosse in the protologue. The number of similarities between *M. borneense* and the Lord Howe population seems compelling reason to place both in the same genus, the major species-level difference between the two being the larger dimensions overall of the fronds and medullary cells in *M. robustum*. There have been no further reliable records of the generitype by which to

evaluate its phenotypic plasticity, a claim that seems true even in light of Norris's (1991, p. 593, figs 24, 25) report of *M. cf. borneense* from South Africa. Norris describes and illustrates lobed, ear-shaped prostrate blades with dorsal cystocarps that, although anatomically similar to our collections and Weber-van Bosse's (1928), must surely represent a species distinct from both. We have thus chosen to regard the Lord Howe material, for which we have a good collection and molecular data, as new.

In the absence of tetrasporangial material, placement of *Microphyllum borneense* within the larger perspective of contemporary rhodymenialean systematics is difficult (Le Gall et al. 2008). Lacking terminal carposporangia, a well-developed *tela arachnoidea* or a lomentariaceous fusion cell, placement in the Champiaceae, Faucheaceae, and/or Lomentariaceae is largely ruled out. Inclusion in the Fryeellaceae, thalli typically with hollow portions or spaces in the medulla, seems unlikely. Thus the Hymenocladaceae and Rhodymeniaceae remain options, these taxa largely distinguished by molecular data (Le Gall et al. 2008), which are not available for *M. borneense*. If our determination that our new species, *M. robustum*, belongs in this genus is correct, then we can here add molecular data in support of placement in the Rhodymeniaceae. This conclusion is supported by the general vegetative and reproductive attributes discussed above, and which are most consistent with inclusion in this family. In summary, we note that vegetatively our new species is highly reminiscent of the type, but is more robust in terms of overall dimensions. Cystocarps are marginal and ostiolate in both species and the inner pericarp cells are inflated and produce a loose investment of star-shaped cells, a feature more developed in the generitype.

While investigating *Microphyllum robustum*, type material for *Rhodymenia setchellii* Weber Bosse was acquired from Leiden, details of vegetative anatomy recalling our species (Weber-van Bosse 1928). Morphologically, this species is distinct consisting essentially of once-dichotomous cuneate branches developing from the apices of similarly shaped blades (Fig. 31). The type is tetrasporangial, the nemathecium an expansive reticulate confluence over most of the blade surface. The material did not rehydrate well, but discernable vegetative details were as outlined by Weber-van Bosse. The medulla is composed of 1-3 layers of angular, essentially isodiametric, cells with relatively thick walls supporting a single layered inner cortex and an incomplete 1-2-layered outer cortex (Fig. 32). The cuticle is relatively thick (Fig. 33) and the tetrasporangial nemathecium is confined to a single surface (Fig. 32). Nemathecial development appears to involve adventitious growth yielding 2-3-celled sterile filaments that produce lateral tetrasporangia (Fig. 34) reminiscent of *Faucheaceae* (Dalen and Saunders 2007).

Weber-van Bosse considered that *R. setchellii* was better assigned to *Rhodymenia* than *Faucheia* owing to cystocarpic features, but subsequently indicated that she did not have cystocarpic material for her species. There is thus no strong justification for inclusion of this taxon in *Rhodymenia*, consistent with our anatomical observations above. Further, *Rhodymenia setchellii* lacks the anticlinal cell rows associated with the cortex of *Faucheia* spp. excluding this genus as a likely candidate (Dalen and Saunders 2007). The expansive reticulate nemathecium brings to mind *Agardhinula* (Schneider and Searles 1991), although it differs from that genus in details of vegetative anatomy and in the production of its tetrasporangia [we have observed tetrasporangial material of

*Agardhinula browneae* (J. Agardh) De Toni (private herb., C.W. Schneider) and find it to be more like members of the Fryeellaceae (Le Gall et al. 2008) than the Rhodymeniaceae with which it is normally associated (Kylin 1956)]. As indicated above, tetrasporangial development in *R. setchellii* appears more similar to the Faucheaceae (Dalen and Saunders 2007; Le Gall et al. 2008), although the sterile filaments are unusually short (more typical of Fryeellaceae), and it is to the Faucheaceae that this species is tentatively assigned. Among faucheacean genera, vegetative anatomy of *R. setchellii* is most like that observed in species of *Leptofauchea* (thin cortex), the thick cuticle in particular matching that of a poorly defined species from Western Australia [G0400 of Dalen and Saunders (2007)], as is the development of the tetrasporangial nemathecium on a single surface. Within this genus, the reticulate nemathecium of *R. setchellii* are most similar to *Leptofauchea chiloensis* Dalen et G.W. Saunders, but in the latter nemathecium remain discrete and do not form a reticulum. Although a possible member of the Faucheaceae, the taxonomic position of *R. setchellii* will only be unequivocally established with the collection and study of new samples (cystocarpic anatomy and/or molecular analyses). Regardless, it is clear that our new species from Lord Howe, *Microphyllum robustum*, is only superficially similar to *R. setchellii*, which is clearly neither assignable to the genus *Microphyllum* or the family Rhodymeniaceae.

#### *Halopeltis* J. Agardh 1854

NOMENCLATURAL NOTES: Agardh (1854) erected the genus *Halopeltis* ultimately on the basis *Rhodymenia australis* Sonder, which unfortunately has a convoluted nomenclatural history. Sonder (1845) included (as var. *constricta*) *Fucus constrictus* Turner (1809-

1811) in his description of *Rhodymenia australis*, rendering his name superfluous and thus illegitimate. In recognizing this, Silva (in Silva et al. 1996) proposed the substitute name *Rhodymenia sonderi* P.C. Silva unaware of Womersley's (1996, p. 77) proposal, published just three days earlier, that *R. foliifera* Harvey (1863) be regarded as a taxonomic synonym of *Rhodymenia australis* and thus an available name for this species. However, an earlier legitimate name is available for this taxon if it is transferred from *Rhodymenia*. In his transfer of *R. australis* to *Sphaerococcus* (as *S. australis*), Kützting (1849) excluded *F. constrictus* such that this binomial is not superfluous rendering 'australis' a legitimate epithet and available for this species in genera for which the binomial is not a later homonym. Unfortunately, *Sphaerococcus australis* Kützting is a later homonym of *S. australis* Harvey (1844) rendering this binomial illegitimate. However, in transferring *S. australis* Kützting to *Acropeltis*, J. Agardh (1852) established a legitimate name (*Acropeltis australis* J. Agardh) for what is presently called *Rhodymenia sonderi* P.C. Silva in the event this species is transferred from *Rhodymenia*. *Acropeltis australis* is thus a legitimate name on which Agardh (1852) based his genus *Halopeltis*. Unfortunately, Agardh never formally made the combination *Halopeltis australis* (effected here), but he did validly publish his genus (Agardh 1852, p. 110-111), which we resurrect for this speciose genus thus far known only from the Southern Hemisphere.

EMENDED DIAGNOSIS: Rhodymeniacean taxa with a medulla of large cells, typically two ordered rows near apices in some species, in irregular arrays in others, the cells separated by intervening spaces with small intercalating cells. Tetrasporangial sori initiated by the swelling of pre-existing (i.e., not adventitious) intercalary and terminal outer cortical

cells, some converting to sporangial production, others compressed between developing sporangia appearing as 1-2-celled sterile filaments, but the general impression is that most outer cortical cells will eventually convert to sporangial production. Tetrasporangial sori are confined to a single thallus surface in some species, produced predominantly on one surface in others, or developing equally on both surfaces, but with one side lagging in development relative to the other. Sori are initially circular to oval, but expand with age to become oblong to cordiform (where branch tips are dichotomous). Cystocarps are protuberant, spherical or occasionally hemispherical, weakly to strongly basally constricted, and ostiolate; pericarp chambers are lined to varying degrees with an anastomosing network of typically stellate cells. Spermatangial mother cells, where known, are typically columnar to obpyriform.

PHYLOGENETIC NOTES: Unexpectedly, a connection between *Halopeltis* and *Halichrysis*, rather than *Rhodymenia*, emerges when both molecular [Fig. 2A; see also the more comprehensive phylogenies of Le Gall et al. (2008)] and anatomical results (below) of the type species of both genera are taken into account. *Halopeltis* shares with *Halichrysis* distinctive aspects of vegetative anatomy, especially the medullary feature of intervening spaces with small intercalating cells between adjacent considerably larger cells (Saunders et al. 2006). The all-important tetrasporangial development is also similar in the two genera – in *Halichrysis* there is a direct conversion of terminal (at times intercalary) existing outer cortical cells across localized thallus regions on a single surface that results in sporangial initials, whereas in *Halopeltis* all outer cortical cells can so-differentiate, with some converting to sporangia but others compressed and appearing as sterile filaments, the sorus developing on one or both surfaces. Other differences include the

exclusively sessile and hemispherical nature of the cystocarps, absence of a network of anastomosing filaments lining the pericarp periphery, and presence of the ‘*réseau muqueux*’ in *Halichrysis* (Saunders et al. 2006). In contrast, *Halopeltis* generally has protuberant cystocarps that are basally constricted at the thallus surface, as well as typically an anastomosing network of stellate cells lining the pericarp chamber.

TYPE SPECIES: *Halopeltis australis* (J. Agardh) G.W. Saunders, comb. nov. Figs 35-38.

BASIONYM: *Acropeltis australis* J. Agardh 1852 (Sp. Gen. Ord. Alg. Vol. 2, part 2, Fasc. 2: 609-610).

LECTOTYPE: MEL 504193.

*Rhodymenia australis* Sonder 1845, nom. illeg.

TYPE LOCALITY: Western Australia.

*Rhodymenia sonderi* P.C. Silva in Silva et al. 1996, p. 370-371.

*Sphaerococcus australis* Kützinger 1849, p. 784, nom. illeg.

HETEROTYPIC SYNONYM: *Rhodymenia foliifera* Harvey 1863, p. XI.

REPRESENTATIVE SPECIMENS: Listed in Table 1.

REPRESENTATIVE BARCODE: HM033026 (G0253).

OBSERVATIONS: Many collections field-identified as ‘*Rhodymenia sonderi*’, as well as those so-named by colleagues, resolved as two independent lineages (Figs. 1 and 2) – one in *Rhodymenia* (*R. novahollandica*, discussed below), the other in *Halopeltis* (*H. australis*). Our collections of the latter have the characteristic ‘sonderi-morph’ habit and structure (Figs. 35 and 36) and are predominantly Western Australian in distribution, from which region the type collections of both *Rhodymenia australis* and *R. foliifera*

originate, the latter synonymized with the former by Womersley (1996). In describing *R. australis* and *R. foliifera* both Sonder (1845) and Harvey (1863), respectively, reported oval tetrasporangial sori, a feature consistent with Womersley's (1996) accounts of *R. australis* and which we have confirmed from images of the type collections in MEL and TCD, respectively. It is clear from Womersley's (1996; fig. 26C) descriptions and illustrations of spaces and intercalating cells in the medulla, cystocarps with constricted bases, mesh-like networks of stellate cells lining the inner pericarps, spermatangia on elongate outer cortical cells and tetrasporangial observations (Womersley 1996, fig. 26f), notably in being in oval 'nemathecioid' sori on one or both surfaces, that he was describing features consistent with *Halopeltis* as conceived here. Our collections match *R. australis* and *R. foliifera sensu* Womersley (1996) in attributes of the medulla, with larger cells separated by spaces with smaller intercalating cells (Fig. 37), and tetrasporangial development. Sori are initially oval, expanding to follow the outline of the thallus surface with maturity, and form adventitious bladelets from their margins and central regions, these themselves producing sori (we observed this to two orders on one branch of our collection G0253). We were fortunate to receive a single tetrasporangial branch tip from the lectotype for observation and it too had 'compound' sori as in G0253. In section, soral development starts with substantial enlarging of outer cortical cells with some converting to sporangial production, these commonly compressing other cortical cells imparting on them the appearance of sterile-filaments (Fig. 38). Soral development occurs on both surfaces with one lagging slightly behind the other. Mature tetrasporangia are cruciate, 18-25  $\mu\text{m}$  wide by (25-)32-42  $\mu\text{m}$  long (Fig. 38). The previous attributes are consistent with our observations of the lectotype. We have also observed a paratype of *R.*

*foliifera* (in MICH, Harvey 381.A) and found the tetrasporangial details to be as described here for *R. australis* (except the sorus examined was not ‘compound’), supporting Womersley’s proposal to subsume the former into the latter.

COMMENTS: In another chapter in the confused nomenclature of *Halopeltis australis*, Millar (in Millar and Prud’homme van Reine 2005) considered *Sphaerococcus caulescens* Kützing (1868) to be a synonym of *Rhodymenia sonderi sensu lato* and effected the combination *Rhodymenia caulescens* (Kützing) A. Millar. This name, however, is predated by *Acropeltis australis*, which, regardless of whether or not this proposed synonymization is correct, renders the latter the appropriate name for this species in the genus *Halopeltis*. Furthermore, considering our results here, sweeping synonymization of all ‘sonderi-like’ morphs should be rejected and synonymy of *S. caulescens* to our various genetic groups considered. Despite reportedly possessing general features consistent with the genus *Rhodymenia* (which need reassessment in light of our results), the New Caledonian provenance of *S. caulescens* and its stump-like primary stipes (Millar and Prud’homme van Reine 2005, fig. 9) are not consistent with any of the Australian taxa discussed here. The taxonomic status of *Sphaerococcus caulescens* requires further investigation.

*Halopeltis australis* as circumscribed here had uncharacteristically high levels of variation in the DNA barcode (Fig. 1; discussed below), which is consistent with, among other causes, possible incipient speciation. In any event, tetrasporangial details for G0253 match the lectotype of *Rhodymenia australis* Sonder and hence our genus-level taxonomic conclusions would not change even if additional species are eventually recognized in this complex.

## INCLUDED SPECIES:

*Halopeltis austrina* (Womersley) G.W. Saunders, comb. nov.

BASIONYM: *Rhodymeniocolax austrina* Womersley 1996 (The Marine Benthic Flora of Southern Australia. Rhodophyta. Part IIIB, Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales. Australian Biological Resources Study, Canberra, p. 86-89, figs 33, 34).

HOLOTYPE: *Watson & Womersley*, 16 January 1974 (AD – A44400).

TYPE LOCALITY: Crawfish Rock, Westernport Bay, Victoria, Australia; depth 8 m.

REPRESENTATIVE SPECIMEN: GWS002531 (see Table 1 for collection details).

REPRESENTATIVE BARCODE: HM033028.

COMMENTS: Although resolved in the same genetic species group as its host, *Halopeltis verrucosa* (Fig. 1), we consider the parasitic habit of *H. austrina* sufficient grounds for recognition as a distinct species. For a similar scenario in the Phylloporaceae see Le Gall and Saunders (2010).

*Halopeltis cuneata* (Harvey) G.W. Saunders, comb. nov.

BASIONYM: *Rhodymenia cuneata* Harvey 1859a (Algae. Part III. Flora Tasmaniae. In: The botany of the Antarctic voyage of H.M. discovery ships Erebus and Terror, in the years 1839-1843, under the command of Captain Sir James Clark Ross...Part III. Flora Tasmaniae. Monocotyledones and Acotyledones. (Hooker, J.D. Eds) Vol. II, Reeve, London. p. 319-320).

HOLOTYPE: TCD Herb. Harvey.

TYPE LOCALITY: East coast, Tasmania.

*Epymenia cuneata* (Harvey) J. Agardh 1892, p. 91.

HETEROTYPIC SYNONYM: *Rhodymenia halymenioides* (J. Agardh) Womersley 1996, p. 84.

REPRESENTATIVE SPECIMENS: Listed in Table 1.

REPRESENTATIVE BARCODE: HM033032 (GWS001521).

COMMENTS: We have viewed an image of the holotype of *H. cuneata* and found it to closely match the morphologies of three of our four recent collections from Tasmania, as well as the anatomical details given by Womersley (1996, p. 84-85, fig 32A-C). Our fourth collection, GWS001521, has the more flabellate and cuneate habit of *Rhodymenia halymenioides* (we did not examine the type collection in LD, but Womersley reported on it in his detailed account of this species), both species originating from the east coast of Tasmania. The fourth specimen also has proliferous *H. cuneata*-like blades from the frond apex and in morphological details there appear to be few differences between the two species, which Womersley (1996, p. 71) mainly separates on lacerate versus lobed fronds in *R. halymenioides* and *R. cuneata*, respectively, and the presence of tetrasporic surface proliferations in *R. halymenioides* (tetrasporangia being unknown in *R. cuneata*). Womersley also reported smaller medullary cells (50-90  $\mu\text{m}$  vs. 90-140  $\mu\text{m}$ ) in *R. halymenioides* than in *R. cuneata*. However, these dimensions do not accord with the scale on his cross-section photo of *R. halymenioides* (Womersley 1996, p. 84, fig. 31C), which depicts medullary cells of similar sizes to those in *H. cuneata* (consistent with our observations, not shown). It therefore appears that *H. cuneata* is simply a younger version of *R. halymenioides* and that these species should be synonymized. In line with our molecular results that ally this species to *Halopeltis*, Womersley (1996) noted spaces

with smaller intercalating cells among larger medullary cells, protuberant cystocarps that are constricted at the plant surface, and pericarp chambers lined by an anastomosing network of filaments in both *R. halymenioides* and *R. cuneata*. Womersley's tetrasporangial details (as outlined for *R. halymenioides*) are also in accord with those of *Halopeltis* rather than *Rhodymenia*.

*Halopeltis verrucosa* (Womersley) G.W. Saunders, comb. nov. Figs 39-49.

BASIONYM: *Rhodymenia verrucosa* Womersley 1996 (The Marine Benthic Flora of Southern Australia. Rhodophyta. Part IIIB, Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales. Australian Biological Resources Study, Canberra, p. 77-79, fig. 27).

HOLOTYPE: *Shepherd*, 17 February 1973 (AD – A43500).

TYPE LOCALITY: Gabo Island, Victoria, Australia; depth 18 m.

REPRESENTATIVE SPECIMENS: Listed in Table 1.

REPRESENTATIVE BARCODE: HM033068 (GWS001986).

OBSERVATIONS: The concept of *H. verrucosa* is here both broadened and modified from Womersley's (1996, p. 77, figs 27, 30C, as *Rhodymenia verrucosa*) original description. Whereas many of our collections are stipitate, erect (e.g., Fig. 39) and similar in overall morphology to the holotype (Womersley 1996, fig. 27A), we also uncovered deep-water (28-30 m) Tasmanian samples (e.g., Fig. 40) that are procumbent and similar to *Pseudohalopeltis tasmanensis* in habit (Figs. 3-6), as well as a shallower Tasmanian collection (10 m) with expanded flabellate branch apices (Fig. 41).

In line with Womersley's (1996) characterization of the species, our thalli are 3-14 cm high, complanate, and with one or a few fronds arising from a crustose base. Female fronds bear either verrucose (Fig. 42) and/or smooth (Fig. 43) cystocarps on younger branch regions, whereas apices on male gametophytes, reported here for the first time, are pale (Fig. 44). Tetrasporangial sori are oval to elongate and formed at the branch apices (Fig. 45). Distal longitudinal sections reveal fronds 150-200  $\mu\text{m}$  wide and composed of a medulla of essentially two regularly arranged rows of larger, axially elongate cells, 38-50  $\mu\text{m}$  wide by 55-90  $\mu\text{m}$  long, that are often separated by irregular gaps, as indicated by Womersley (1996, p. 77), but also by sparsely distributed smaller intercalating cells (Fig. 46). As did Womersley, we note globular (at times crystalline) inclusions in the medullary cells. The medulla is surrounded by 1-2 layers of progressively smaller inner cortical cells, and an outer cortex of 1-2 cell layers of small, deeply pigmented cells (Fig. 46). Cystocarps are as described by Womersley, notably in regard to the pericarps being lined by a mesh-like network of stellate cells (Fig. 47). Spermatangia, 2.5-3.0  $\mu\text{m}$  in dimension (Fig. 48), occur in expanded sori at the branch apices on both frond surfaces (Fig. 44). A notable feature is the columnar to obpyriform spermatangial mother cells, 2-3  $\mu\text{m}$  wide by 7-9  $\mu\text{m}$  tall (Fig. 48), that are commonly borne directly on inner cortical cells (possibly develop by direct conversion of existing outer cortical cells).

Our tetrasporangial observations differ from those of Womersley (1996). Sori are restricted to a single surface and are not the result of adventitious growth, but instead develop by the direct modification of existing outer cortical cells (Fig. 49) as noted for the genus. Adjacent cells are stretched, presenting a superficial resemblance to sterile

filaments, but most appear to be in various stages of tetrasporangial development [i.e., most outer cortical cells (intercalary and terminal) in the soral region appear to be converting to tetrasporangial development (as noted for the outermost cortical cells in *Halichrysis*; Saunders et al. 2006)]. Mature tetrasporangia are cruciate, 22-25  $\mu\text{m}$  wide by 30-35  $\mu\text{m}$  high (Fig. 49), slightly larger than was reported by Womersley (1996).

COMMENTS: Some morphologies of *Halopeltis verrucosa* are similar to those displayed by *Pseudohalopeltis tasmanensis*, and based on habit and a cursory consideration of anatomy the two would surely be judged closely allied, if not conspecific, as opposed to being members of separate families as is strongly indicated by our molecular trees (Fig. 2A; Le Gall et al. 2008). There are, however, key differences indicative of their respective family associations, one being the direct conversion of pre-existing cortical cells into tetrasporangial initials without a corresponding development of adventitious sterile filaments in *Halopeltis verrucosa*, as opposed to the production of such filaments in *Pseudohalopeltis tasmanensis* (see Saunders et al. 2006; Dalen and Saunders 2007; Le Gall et al. 2008). And whereas *Pseudohalopeltis* is apt to give the false impression of a filamentous network lining the inner pericarp (Figs. 13 and 14; discussed above), *H. verrucosa* truly has a mesh-like network of filaments at that location (Fig. 47). A third difference concerns the highly ordered central medulla of large cells that often abut gaps and contain globular (crystalline) inclusions (especially near branch apices of both species), but only *H. verrucosa* has the smaller intercalating cells that often come to fill the medullary-cell gaps (Fig. 46). Although Womersley did not mention this last attribute, this feature is clearly present in his cystocarpic holotype collection, although not as evident in his syntype tetrasporophyte (Womersley 1996, figs 27D and 27H,

respectively). Indeed, Womersley indicates adventitious growth in soral development for his syntype (although the family-level distinction now made in this regard would not have been considered by him at that time), and the tetrasporangial dimensions are slightly smaller, all of these features being more in line with *Pseudohalopeltis tasmanensis* rather than *H. verrucosa*. Womersley (1996, p. 79) apparently was not confident that all of his collections were representative of the same species, and it is possible that his description is based on a combination of these two (and possibly other) species. Arguing against the tetrasporangial syntype being *Pseudohalopeltis tasmanensis*, however, is the fact that this species forms tetrasporangia on both broad frond surfaces, an aspect of development about which Womersley makes no comment, although based on his figure (Womersley 1996; fig. 27H) it would appear that nemathecium are confined to a single surface in his syntype collection of *H. verrucosa*. This aspect of Womersley's collections requires further investigation, but it is clear that the syntype tetrasporangial material does not match observations for collections reported here and genetically linked to the gametophyte generation. In any event, the holotype is distinctive among rhodymeniacean taxa in its verrucose pericarps and closely matches our collections.

*Halopeltis prostrata* G.W. Saunders, sp. nov. Figs 50-58.

Laminae rubrae prostratae in aquis non profundis (< 6 m) in spongios et altera invertebrata immersae vel ex eis emersae; laminae typice stipitatae ubi proliferae e laminis senioribus, thallos complexos ramosos facientes; laminae individuae typice dichotomae. Rametti individui typice ad 10 cm, laminis prope apices 0.4-0.9 cm latis. Cystocarpia hemisphaerica vel ad superficiem thalli valde constricta, usque ad 1400 µm

(1.4 mm) lata, in parte superiore ad orificium ostiolis complanata, cellulis retis pericarpiorum typice rotundatis non extensis stellatisque. Tetrasporangia 25-35  $\mu\text{m}$  lata 35-45  $\mu\text{m}$  alta.

Blades prostrate, red, submerged in and emergent from sponges and other invertebrates in shallow (<6 m) water. Blades typically stipitate where proliferous from older blades, forming complex branched thalli, the individual blades typically dichotomous. Individual ramets typically to 10 cm in length, blades 0.4-0.9 cm wide near apices. Cystocarps hemispherical to highly constricted at the base; up to 1400  $\mu\text{m}$  (1.4 mm) wide; flattened at the ostiolate apex; cells of mesh-like network in the pericarp typically rounded, not stretched and stellate. Tetrasporangia 25-35  $\mu\text{m}$  wide by 35-45  $\mu\text{m}$  high.

HOLOTYPE: *GWS*, 16 September 2004 (UNB – GWS001592) (Figs 50, 57-58).

TYPE LOCALITY: Flinders Jetty (-38.4667°, 145.0167°), Victoria, Australia; depth 4 m on jetty piling.

HOLOTYPE BARCODE: HM033044.

ETYMOLOGY: Named for its consistently sprawled habit.

DISTRIBUTION: Presumably widely distributed in southeastern Australia, collected thus far from Kangaroo Island in the west, the mouth of Port Phillip Bay and adjoining waters of Victoria and southeastern Tasmania, found in the lowest intertidal to shallow (maximum ca. 6 m) subtidal (Table 1).

REPRESENTATIVE SPECIMENS: Listed in Table 1.

OBSERVATIONS: This species appears to be widely distributed in shallow waters of southeastern Australia (Table 1), typically growing on pier pilings (although some collections are epiphytic or epilithic) where it is only intermittently emergent from the various sponges and other invertebrates. When extracted from the invertebrate covering, prostrate red blades are revealed that varied from irregular thalli with some dichotomous tips (e.g., Figs. 50 and 51) to dichotomous plants more typical of a prostrate *Rhodymenia* (e.g., Fig. 52). Holdfasts were not discernable, but some blades are stipitate, these generally associated with the proliferation of blades from pre-existing blade margins, which appears to be the typical mode by which this species grows and spreads along the substratum. One collection (GWS002452) has robust stipes a few centimeters long and a few millimeters wide, but it is unclear if these are associated with this species (field notes indicate that DNA was taken from procumbent blades, which may have been epiphytic on the stipitate thallus). Ramets are typically less than 10 cm in length, but genets may be considerably larger as thalli continue their prostrate growth by proliferous branching and possibly also by fragmentation as older portions become buried. Blades range from 0.4-0.9 cm in breadth near the tips (Figs. 50-52). Apical portions in longitudinal section are 100-180  $\mu\text{m}$  wide (approaching 250  $\mu\text{m}$  in older portions of some sections) and composed of a medulla of 2-3 (or more), typically irregular (as in the generitype), layers of large cells (25-50  $\mu\text{m}$  wide by 60-130  $\mu\text{m}$  in length) (Fig. 53), these separated by spaces often containing smaller intercalating cells (Fig. 54) that are generally sparse, although locally common. Some are situated in the intervening spaces and borne on the larger medullary cells in a way typical of secretory cells in other rhodymeniaceous taxa (Fig. 54). The medulla is surrounded by an inner cortex of 1-2 layers of isodiametric cells

and an outer cortex of only 1-2 layers of smaller deeply pigmented cells (Fig. 53). In all regards the vegetative anatomy is typical of the genus. Cystocarps are produced on the terminal third of blades and ranged from highly (Fig. 55) to barely basally constricted, some appearing hemispherical, which is not typical of other species in *Halopeltis*.

Cystocarps ranged from 900-1400  $\mu\text{m}$  wide and were typically flattened at the ostiolate apex (Fig. 55). A mesh-like network of cells lined the chamber (Fig. 56), but the cells remained isodiametric in overall form, although still separated by spaces, not stretching to form the stellate cells of other species and with only occasional remnant filaments extending into the chamber.

Tetrasporangial sori are on both surfaces, but with one lagging substantially behind in development, and result from the swelling of outer cortical cells with some converting to tetrasporangial initials and others appearing compressed (Fig. 57). As with the other species in the genus, there is a sense that all of the outer cortical cells (including the few intercalary cells) within the sori are in various stages of tetrasporangial development, with compression of some cells giving the impression of sterile filaments. Mature tetrasporangia are cruciate, 25-35  $\mu\text{m}$  wide by 35-45  $\mu\text{m}$  in length (Fig. 58).

COMMENTS: Of the *Halopeltis* spp., *H. prostrata* was the most convergent in habit to *Pseudohalopeltis tasmanensis* (indeed they were all field identified as ‘procumbent *Rhodymenia sonderi*?’). All individuals are prostrate and can grow in thick mats with sponges and other benthic invertebrates, while some collections are epiphytic or epilithic. It is nonetheless distinct in regard to the anatomical details discussed above, has a broader distribution (*P. tasmanensis* has only been collected from southeastern

Tasmania), and occurs in shallower waters (<6 m vs 6 m but typically 15-30 m for *P. tasmanensis*).

*Halopeltis gracilis* G.W. Saunders, sp. nov. Figs 59-60.

Thalli procumbentes ramis angustis, 1.5-3.0 mm, laxe dichotomis; ramis proliferis vulgaribus, initiis ramorum nonnullis individuis aspectum papillatum donantibus.

Procumbent thalli with narrow, 1.5-3.0 mm, loosely dichotomous branches; proliferous branches common, initials imparting a papillate appearance to some individuals.

HOLOTYPE: *GWS*, 1 February 2004 (UNB – GWS002049) (Fig. 59).

TYPE LOCALITY: Balls Pyramid (-31.8079°, 158.9852°), Lord Howe Island, NSW, Australia; depth 22 m on rock wall.

HOLOTYPE BARCODE: HM033033.

ETYMOLOGY: Named for the narrow vegetative axes.

DISTRIBUTION: Thus far only known from the type locality.

REPRESENTATIVE SPECIMENS: GWS002051, GWS002052, GWS002062 (see Table 1 for collection details).

OBSERVATIONS: This procumbent species (Figs. 59 and 60) was collected on rock walls and reef flats from Balls Pyramid. Thalli are typically less than 10 cm in lateral spread and are loosely dichotomously branched. Proliferous branches obscure the overall pattern and start out as marginal proliferations that give specimens (e.g., GWS002052; Fig. 60, insert) a papillate appearance. The axes of this species are particularly narrow, being only

1.5-3.0 mm broad. Vegetative structure near branch apices is typical of the genus: thalli are 110-190  $\mu\text{m}$  thick with a central medulla of 2-4 layers of cells (slightly more than other species discussed) 37-45  $\mu\text{m}$  wide by 60-125  $\mu\text{m}$  long, these separated by spaces that can be occupied by smaller intercalating cells; the inner cortex is of 1-2 cell layers and the outer cortex is typically of a single (at times two) layer(s). None of the collections were demonstrably reproductive.

#### **Four additional overlooked/cryptic *Halopeltis* spp.**

In addition to the species formally investigated above, our barcode analyses uncovered single collections for four additional species of *Halopeltis*. *Halopeltis* LH1 (Fig. 61; GWS002041) was collected from the coral flats of Lord Howe Island and is procumbent in habit. *Halopeltis* LH2 (Fig. 62; GWS002061) was collected from Balls Pyramid and is even finer than *H. gracilis*, but differs from it in both COI (Fig. 1) and LSU sequence (Fig. 2B), thus clearly representing a distinct species. *Halopeltis* TAS (Fig. 63; GWS002596) was collected intertidally from southeastern Tasmania and is superficially the most *Rhodymenia*-like in being stipitate and in producing stolon-like laterals from its stipe. Finally, *Halopeltis* WA (G0402) was collected from Western Australia and accounts for an earlier, incorrect, report of *Asteromenia peltata* (W.R. Taylor) Huisman et A. Millar by Saunders et al. (1999) from those waters (see Saunders et al. 2006). This species is sister to *Halopeltis* spp. in our phylogenetic analyses (Fig. 2A-B) and may, upon further study, be considered as a separate genus allied to *Halopeltis*. In all four cases, more collections are necessary prior to describing formally these species, but they point to the species richness of this previously overlooked lineage in Australian waters.

Species of *Rhodymenia* in southern Australia

*Rhodymenia novahollandica* G.W. Saunders, sp. nov. Figs 64-73.

*Rhodymenia* erecta vel prostrata characteribus typicis generis; soris tetrasporangialibus junioribus ad apices ramorum distincte fasciatis, in maturitate cuneiformibus vel obovatis, postremo totos apices ramorum praeter margines tegentibus.

An erect to prostrate *Rhodymenia* with features typical of the genus. Tetrasporangial sori distinctly banded at branch apices when young, becoming cuneiform to obovate with maturation and ultimately covering both surfaces of branch tips except for the margins.

HOLOTYPE: *GWS*, 10 December 2002 (UNB – GWS001604) (Figs. 64, 67-72).

TYPE LOCALITY: Queenscliff Jetty (-38.2669°, 144.6678°), Port Phillip Heads, Victoria, Australia; from 4 m on jetty piling.

HOLOTYPE BARCODE: HM033117.

ETYMOLOGY: Named for the provenance of this new species.

DISTRIBUTION: Distributed widely throughout Victoria, but a collection from Western Australia and two from Tasmania indicate a wider distribution along southern Australian coasts.

REPRESENTATIVE SPECIMENS: Listed in Table 1.

OBSERVATIONS: This widely distributed *Rhodymenia* displays the ‘sonderi-morph’ (Figs. 64-66) and was the most common species (47 collections) uncovered during our survey

(Table 1). It undoubtedly accounts, albeit incorrectly, for most reports of *Halopeltis australis* (as *Rhodymenia sonderi* and *R. australis*) in these waters, and is the image that phycologists in southeastern Australia call to mind when recording that species.

Collections were made from rock and jetty pilings at depths of 1-10 m and included plants commonly, as with many previous species, associated with a variety of sessile invertebrate life (notably sponges). Thalli are typically rose to dark red, between 6-20 cm in height with axes 3-8 mm wide, stipitate, and roughly dichotomous but with proliferous branches common from damaged branch tips as well as from margins (Fig. 65). In all of these aspects this species is typical of the genus *Rhodymenia*. With regards to reproductive morphology, tetrasporangial sori are distinctly band-shaped when young (Fig. 67) becoming progressively cuneiform to obovate with maturation ultimately covering branch tips except for the margins. Cystocarps are distributed on the terminal third of blades, on both surfaces and the margins, and spermatangial sori form irregular light colored sori at branch apices. In section, blades are 180-220  $\mu\text{m}$  thick near the apices (Fig. 68). Whereas in some *Halopeltis* spp. vegetative anatomy of the medulla near branch apices is typically of two ordered rows of medullary cells separated by occasional spaces with small intercalating cells (of variable occurrence), this *Rhodymenia* has an irregular appearance to the medulla, both in terms of cell size (25-60  $\mu\text{m}$  high by 25-110  $\mu\text{m}$  in length in longitudinal section) and order, with the cells largely compact and consisting of 4-6 layers surrounded by an inner cortex of 1-2 cell layers and finally an outer cortex of 2-3 layers (Fig. 68). Tetrasporangial sori develop on both surfaces of the blades (Fig. 69) as in some species of *Halopeltis*, but the derivation, for the most part, of tetrasporangial initials from intercalary cortical cells at the transition between the inner

and outer cortical layers (Fig. 70) is distinct from that genus. Further, the outermost cortical cells, which swell and variously convert to sporangial production or appear as 'faux' sterile filaments in *Halopeltis*, remain largely undifferentiated in *R.*

*novahollandica* (Fig. 69). Thus, mature tetrasporangia are embedded in the cortex (Fig. 69), are cruciate in division and range from 20-25  $\mu\text{m}$  wide by 30-45  $\mu\text{m}$  in height (Fig. 71). Mature cystocarps are hemispherical to slightly constricted at their bases, 800-1200  $\mu\text{m}$  wide and prominently ostiolate. The pericarp is largely composed of compact cells (despite the stellate appearance of the cytoplasm), but a shallow anastomosing layer of cells line the pericarp chamber (Fig. 72) and occasional short filaments (possibly dislodged anastomosing filaments) extend from the pericarp wall into the cavity. Male structures are produced in subterminal sori on both blade surfaces and have squat spermatangial mother cells similar in dimensions (2.5-3.0  $\mu\text{m}$  wide by 4-5  $\mu\text{m}$  high) to the terminal ovoid spermatangia (Fig. 73).

COMMENTS: Aspects of tetrasporangial development, notably initiation of the sorus as a distinct transverse band, and conversion of predominantly intercalary cells at the inner-to-outer cortical-layer boundary without swelling or significant modification of the outer cortical cells, in combination with the predominantly solid thallus lacking smaller intercalating cells among larger cells of the medulla, squat spermatangial mother cells, as well as, to a lesser extent, the slight development of a distinct mesh-like network of filaments lining the cystocarp chamber are useful in delineating *Rhodymenia novahollandica* from *Halopeltis* spp. Interestingly, GWS001278, genetically identified as *R. novahollandica*, was our only collection of this species from Western Australia and it was similar in color and morphology (Fig. 66) to *Halopeltis australis* isolates (e.g., Fig.

36) collected on the same date and at the same location, but it had a vegetative anatomy consistent with inclusion in *Rhodymenia*, in agreement with the molecular data. With habits so overlapping or virtually identical across so large a longitudinal range, it is not surprising that the taxonomic assumption that all collections of the general “*sonderi/australis*” form belong to one and the same species by 19<sup>th</sup> Century phycologists like Sonder, Harvey, Kützing and J. Agardh, as well as Womersley in modern times, has not been challenged.

*Rhodymenia wilsonis* (Sonder) G.W. Saunders, comb. nov.

BASIONYM: *Epymenia wilsonis* Sonder 1854 (Plantae Muellerianae. Algae annis 1852 et 1853 collectae. Linnaea 26: 516).

HOLOTYPE: MEL 674904.

TYPE LOCALITY: Wilsons Promontory, Victoria, Australia.

HETEROTYPIC SYNONYM: *Epymenia membranacea* Harvey 1859b, pl. 89.

REPRESENTATIVE SPECIMENS: see Table 1.

REPRESENTATIVE BARCODE: HM033155 (GWS002528).

COMMENTS: Despite Womersley’s (1993, p. 79) synonymization of the two Australian species *Epymenia membranacea* Harvey and *E. wilsonis* Sonder with the South African *Rhodymenia obtusa* [see Womersley (1996) for a summary], our data unequivocally distinguish a collection of *R. obtusa* from the type region from two closely related (1.7-2.0% divergence in COI) genetic groups in Australia (Fig. 1). The Australian clusters correspond to a Tasmanian clade and a largely Victorian clade (Table 1; Fig. 1). The two described Australian species, with type localities of Georgetown, Tasmania and Wilsons

Promontory, Victoria for *E. membranacea* (Harvey 1859b) and *E. wilsonis* (Sonder 1854), respectively, may correspond to our two genetic groups, but there are no clear morphological differences. It is not unusual to find few, if any, morphological or anatomical features that enable closely (at times even distantly) related genetic species to be differentiated (Saunders 2008; Saunders 2009; Le Gall and Saunders 2010), and it is unlikely that detailed morphological and anatomical observations of the various type collections would reveal distinguishing characteristics between *Epymenia membranacea* and *E. wilsonis* at that level of observation. Other genetic evidence (discussed below), however, suggests that these two clusters should be considered as representing a single species. The older epithet *Epymenia wilsonis* Sonder (1854) in that event has priority over *E. membranacea* Harvey (1859b) and is thus reinstated and formally transferred to the genus *Rhodymenia*.

#### Other Australian species of *Rhodymenia*

In addition to the results detailed above, our work points to further cryptic diversity in this genus as was the case for *Halopeltis*. Two collections field-identified as *Rhodymenia leptophylla* from Lord Howe Island (LH) only distantly allied to our single collection attributed to this species from Tasmania (Fig. 1). As well, unidentified species with only single collections (Table 1) from South Australia (*Rhodymenia* SA) and Victoria (*Rhodymenia* VIC) have yet to be characterized (Fig. 1) pending additional collections. Neither is particularly close to any currently recognized species based on our various molecular analyses (Figs. 1 and 2C). A final result in need of further study is the very close alliance between our collections of *Rhodymenia prolificans* from Tasmania

(site of the type locality) and our only specimen attributed to *R. stenoglossa* (from Victoria, the type locality), which Womersley (1993, p. 71) regards as a rare species. These taxa resolved as two genetic groups in COI-5P analyses (Fig. 1), but with only 1.0-1.2% divergence in this marker – additional molecular and anatomical observations are needed to test further their status as distinct species (Saunders 2005). Finally, an unidentified species of *Rhodymenia* sent by colleagues in New Zealand (Table 1) failed to associate closely with any of our Australian species (Figs. 1 and 2C) and suggests, not surprisingly, that cryptic diversity within *Rhodymenia* is a widespread phenomenon in Australasia and most probably generally.

#### Intraspecific divergence

Four of our genetic species groups (possibly five pending evaluation of mainland *Rhodymenia stenoglossa* and Tasmanian *R. prolificans*) have uncharacteristically high within-species COI-5P variation (Fig. 1). *Halopeltis australis* G0253 from Western Australia was 1.4-1.5% divergent from the remaining collections (0-0.45% divergent). Saunders (2005) established that genetic groups with as little as 1% divergence in COI-5P might constitute distinct species. *Halopeltis australis* thus requires further study (genetic screen of more samples emphasizing Western Australia) and may actually represent a species complex (this will not impact on the taxonomic conclusions presented here except to add more species to *Halopeltis*). Saunders (2005, 2008) has also cautioned that in cases where COI sequences indicate close affinities for genetic groups (in our experience typically <4% for red algae), it is critical to check a nuclear marker to corroborate the COI-5P conclusions (e.g., Ross et al. 2003) and to assess for putative

hybridization between what were essentially incipient species (e.g., Lane et al. 2007). In this regard, the other three genetic species groups were interesting. *Halopeltis verrucosa* (within and between cluster divergence of 0-0.75% and 0.45-0.9%, respectively), *Rhodymenia novahollandica* (0-0.45% and 1.2-1.6%) and *Rhodymenia wilsonis* (0-0.45% and 1.6-2.2%) are all characterized largely by a biogeographical split between Tasmania and the mainland consistent with a recent vicariant speciation event (incipient speciation). As part of another study (Saunders and McDevit unpublished data), we have used ribosomal internal transcribed spacer (ITS) data to study the two *Rhodymenia* spp. with this biogeographical pattern and have uncovered evidence for single genetic groups in both cases indicating that the isolation that led to the incipient speciation (as recorded in the mitotypes) is no longer in effect, these incipient species now freely interbreeding. It is thus conservative at this time to recognize only a single species for both *Rhodymenia novahollandica* and *R. wilsonis*.

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## Figure Legends

**Fig. 1.** Phylogram (for assignment of collections to genetic species, not presented as a robust phylogeny) from COI-5P sequences for collections of *Rhodymenia* spp. and related taxa. \*\*\**Halopeltis austrina* resolved within *Halopeltis verrucosa* VIC.

**Fig. 2.** Maximum likelihood analyses of the LSU family-level (A; genera key to this study presented in bold type), *Halopeltis* (B) and *Rhodymenia* (C) alignments, respectively, with bootstrap support indicated at the appropriate nodes. All scale bars are 0.01 substitutions/site.

**Figs. 3-11.** Type and representative collections of *Pseudohalopeltis tasmanensis* gen. et sp. nov.

Figs. 3-6. Tetrasporic holotype collection (Fig. 3, GWS001980), and representative cystocarpic (Fig. 4, GWS001982; insert provides a close up view of cystocarp position), tetrasporic (Fig. 5, GWS001967), and male (Fig. 6, GWS002614) specimens, respectively. Scales = centimeter ruler. Figs 7-11. Holotype (GWS001980). Fig. 7.

Transverse section at mid thallus showing the basically bi-layered medulla with intervening spaces (arrows) and thin cortex. Scale bar = 25  $\mu$ m. Figs. 8-11.

Tetrasporangial development as it proceeds from an unmodified vegetative cortex (Fig. 8), through enlargement of outer cortical cells with some undergoing oblique division (arrow, Fig. 9) to initiate sterile filaments while others differentiate as putative tetrasporangial initials (arrowhead, Fig. 9), to inner cortical cells bearing developing tetrasporangia and elongate outer cortical cells bearing two to three adventitious cells

(arrow; Fig. 10) and finally mature cruciate tetrasporangia surrounded by largely uncompressed sterile filaments (Fig. 11). Scale bar (Fig. 8 scale applies to Figs. 8-11) = 15  $\mu\text{m}$ .

**Figs. 12-16.** Type and representative collections of *Pseudohalopeltis tasmanensis* gen. et sp. nov.

Fig. 12. Holotype (GWS001980) displaying inclusions (arrows) in medullary and inner cortical cells. Scale bar = 25  $\mu\text{m}$ . Fig. 13. Section through cystocarp (not in plane of ostiole) with synchronously maturing gonimolobes of carposporangia and a thick pericarp (GWS001982). Scale bar = 150  $\mu\text{m}$ . Fig. 14. Closer view of pericarp establishing its compact cellular nature (GWS001982). Scale bar = 12  $\mu\text{m}$ . Fig. 15. Glancing section revealing cells lining the channel of an ostiole (arrows) (GWS001982). Scale bar = 25  $\mu\text{m}$ . Fig. 16. An ovoid spermatangium (arrow) borne singly on a rectilinear mother cell (GWS002614). Scale bar = 10  $\mu\text{m}$ .

**Figs. 17-27.** *Microphyllum robustum* sp. nov.

Figs. 17-19. Habits of the cystocarpic holotype (Fig. 17, GWS002047) and representative specimens (Fig. 18, GWS002046; and Fig. 19, GWS002057). Scales = centimeter ruler.

Figs. 20-27. Internal anatomy of holotype. Fig. 20. Inflated cells of the bi-layered medulla and narrow cortex of a mid-thallus transverse section. Scale bar = 25  $\mu\text{m}$ . Figs. 21-22. Details of presumably dorsal and ventral cortical surfaces, respectively. Scale bars = 10  $\mu\text{m}$ . Fig. 23. Surface view (through incomplete outer cortical layer) of a darkly staining inner cortical cell containing many refractive (arrow) inclusions. Scale bar = 10

µm. Fig. 24. Putative abortive three-celled carpogonial branch (sc = supporting cells; numbers indicate cells 1-3 of branch). Scale bar = 5 µm. Fig. 25. Cross-section of an ostiolate (arrow) cystocarp from which the gonimoblast has been dislodged from its basal cushion of “nutritive” tissue (arrowheads). Scale bar = 100 µm. Fig. 26. Detail of the compact pericarp, composed of thick-walled inflated cells with compressed cytoplasm. Scale bar = 40 µm. Fig. 27. Reticulate filament of stellate cells extending from the pericarp into the chamber. Scale bar = 10 µm.

**Figs. 28-34.** Type collections of *Microphyllum borneense* Weber Bosse (L 0056026) (Figs 28-30) and *Rhodymenia setchellii* Weber Bosse (L 0056127) (Figs. 31-34).

Fig. 28. The holotype sheet for *M. borneense*. Arrow indicates holdfast from which two small blades arise. Scale = centimeter ruler. Fig. 29. Vegetative section taken from a submarginal thallus portion with a refractive subcortical cell (arrow). Scale bar = 25 µm. Fig 30. Pericarp emphasizing the reticulate nature of stellate cells lining the chamber. Scale bar = 25 µm. Fig. 31. Tetrasporic holotype of *Rhodymenia setchellii*. Scale = centimeter ruler. Fig. 32. Transverse section through poorly rehydrated type with largely immature tetrasporangial nemathecium on a single (upper in figure) surface (arrows). Scale bar = 50 µm. Fig. 33. The narrow, 1-2 layered cortex bounding a large inflated cell of the medulla and covered by a thick cuticle. Scale bar = 25 µm. Fig. 34. Nemathecial development. Tetrasporangial initial obliquely-basally pit-connected (arrow) to a sterile-filament cell borne on an outer cortical cell (oc), itself borne on an inner cortical cell (ic). Scale bar = 12 µm.

**Figs. 35-49.** *Halopeltis* spp.

Figs 35-38. *Halopeltis australis* (J. Agardh) comb. nov. Figs. 35-36. Collections from Western Australia (Fig. 35, GWS001279) and Victoria (Fig. 36, GWS001570). Scale = centimeter rule. Fig. 37. Transverse section at mid-thallus, larger cells of the medulla abutting gaps into which smaller cells (arrows) are intercalated (GWS001570). Scale bar = 50  $\mu\text{m}$ . Fig. 38. Section through tetrasporangial sorus detailing dislodged cruciate tetrasporangium (arrow) among elongated outer cortical cells and tetrasporangial initials (arrowheads) (G0253). Scale bar = 20  $\mu\text{m}$ . Figs. 39-49. *Halopeltis verrucosa* (Womersley) comb. nov. Figs. 39-41. Representative habits ranging from erect (Fig. 39, GWS001986) to prostrate (Fig. 40, GWS001966) thalli with branch widths equal to slightly narrowing acropetally, to more flabellate fronds with branches expanding distally (Fig. 41, GWS001508). Scale = centimeter rule. Fig. 42. Surface view of cystocarps with verrucose pericarps (GWS002541). Scale bar = 750  $\mu\text{m}$ . Fig. 43. Surface view of cystocarps with smooth pericarps; ositole (arrow) in focus (GWS001981). Scale bar = 750  $\mu\text{m}$ . Fig. 44. Surface view of pale spermatangial sori (arrows) (GWS001966). Scale bar = 750  $\mu\text{m}$ . Fig. 45. Surface view of darkened tetrasporangial sorus (arrows) (GWS001972). Scale bar = 750  $\mu\text{m}$ . Fig. 46. Longitudinal section of thallus near branch apices showing internal anatomy (GWS002541). Note smaller intercalating cells in gaps between larger medullary cells (arrow). Scale bar = 50  $\mu\text{m}$ . Fig. 47. Close-up of anastomosing filaments lining cystocarpic chamber to form a reticulate inner pericarp layer (GWS002541). Scale bar = 40  $\mu\text{m}$ . Fig. 48. Section of male sorus displaying elongate spermatangial mother cells subtending oval to spherical spermatangia (GWS001966). Scale bar = 15  $\mu\text{m}$ . Fig. 49. Section of tetrasporangial sorus with

modified outer cortical cells and mature tetrasporangia directly pit connected (arrows) to inner cortical cells (GWS001972). Scale bar = 25  $\mu\text{m}$ .

**Figs. 50-63.** *Halopeltis* spp.

Figs 50-58. *Halopeltis prostrata* sp. nov. Representative habits of the tetrasporic holotype (Fig. 50, GWS001592) and representative cystocarpic (Fig. 51, GWS002430) and tetrasporic (Fig. 52, GWS002451) paratypes. Scale = centimeter rule. Fig. 53. Vegetative longitudinal section near branch apices (GWS002430). Scale bar = 30  $\mu\text{m}$ . Fig. 54. Detail of small intercalating cells filling gaps between inflated medullary cells, one (arrow) budding from a medullary cell and having the habit of a secretory cell (GWS002430). Scale bar = 25  $\mu\text{m}$ . Fig. 55. Glancing section of a cystocarp, constricted at plant surface, from which the carposporophyte has been dislodged, the pericarp with an apical ostiole (GWS002430). Scale bar = 200  $\mu\text{m}$ . Fig. 56. The interior lining of a pericarp, the cells subspherical and compact, the cytoplasm not drawn out into stellate arms (GWS002430). Scale bar = 20  $\mu\text{m}$ . Fig. 57. Outer cortical cells swelling in the region of tetrasporangial development with initials pit-connected (two from one inner cortical cell; arrows) to inner cortical cells (GWS001592). Scale bar = 20  $\mu\text{m}$ . Fig. 58. Mature cruciately divided tetrasporangium surrounded by modified outer cortical cells (GWS001592). Scale bar = 20  $\mu\text{m}$ . Figs. 59 and 60. *Halopeltis gracilis* sp. nov., habits of holotype (GWS002049) and paratype (GWS002052) specimens, the irregularly extended axes of the latter (insert enlarged from region at base of arrow) bearing papillae. Scale = centimeter rule. Figs 61-63. Pressed habits of three additional species of *Halopeltis* discovered in the study but not analyzed further for lack of adequate collections: *Halopeltis* LH1 (Fig. 61; GWS002041);

*Halopeltis* LH2 (Fig 62; GWS002061); *Halopeltis* TAS (Fig. 63;GWS002596). Scale = centimeter rule.

**Figs. 64-73.** *Rhodymenia novahollandica* sp. nov.

Figs. 64 – 66. Habits of the tetrasporic holotype (Fig. 64; GWS001604), a cystocarpic isotype (Fig. 65; GWS001600) and vegetative (Fig. 66; GWS001278, from Western Australia) paratype. Scale = centimeter rule. Figs. 67-71, morphological details from the holotype (GWS001604). Fig. 67. Band-shaped tetrasporangial sorus near branch tip. Scale bar = 0.1 cm. Fig. 68. Long-section of a mature axis, the inflated medullary cells tightly abutting and surrounded by several layers of progressively smaller inner and outer cortical cells. Scale bar = 40  $\mu$ m. Fig. 69. Slightly modified cortical layers of tetrasporangial sori developing on both sides of a distal frond. Scale bar = 40  $\mu$ m. Fig. 70. Detail of an intercalary tetrasporangial initial basally attached (arrowhead) to an inner cortical cell and apically connected to one- or two-celled outer cortical cells or filaments (arrows). Scale bar = 20  $\mu$ m. Fig. 71. Mature cruciately divided tetrasporangium surrounded by cortical cells. Scale bar = 20  $\mu$ m. Fig. 72. Stellate cytoplasm in the compact pseudoparenchymatous cells of the inner pericarp lining with a slight anastomosing network lining the chamber (GWS001600). Scale bar = 40  $\mu$ m. Fig. 73. Section through a spermatangial sorus (GWS002447). Scale bar = 20  $\mu$ m.

Table 1. Collection data and DNA sequence source for specimens used in this study. GenBank numbers in bold text identify sequence data newly generated during this study. <sup>a</sup>Single strand sequence for this barcode record. <sup>b</sup>Full LSU identical to conspecific sequence, not included in analyses. <sup>c</sup>Collected as *Rhodymenia halymenioides* (J. Agardh) Womersley. ND = not determined; Cont. = contaminated amplicon; Partial = the D2/D3 region of the LSU was used as a secondary marker to link specimen to this genetic species.

Family & Name	Voucher	Collection Details	Barcode	LSU
Fryellaceae				
<i>Fryella gardneri</i> (Setchell) Kylin	G0335	San Juan I., North side of Turn I., WA, USA. T. Schaeffer 8.7.1995.	ND	EF033622
<i>Hymenocladopsis prolifera</i> (Reinsch) M.J. Wynne	CCMP455	Antarctica, from CCMP.	ND	EU624144

<i>Pseudohalopeltis tasmanensis</i> G.W. Saunders gen. et sp. nov.	GWS001481	Bicheno, Tas., Australia. GWS 26.11.2002.	<b>HM033080</b>	EU624145
	GWS001502	Devils Hole, Eaglehawk Neck, Tas., Australia. GWS 27.11.2002.	Cont.	Partial
	GWS001903	Nine Pin Point, Tas. Australia. GWS & R. Withall 23.1.2004.	<b>HM033079</b>	ND
	GWS001947	Verona Sands, Tas., Australia. GWS & R. Withall 24.1.2004.	<b>HM033078</b>	ND
	GWS001950	Verona Sands, Tas., Australia. GWS & R. Withall 24.1.2004.	<b>HM033076</b>	ND
	GWS001951	Verona Sands, Tas., Australia. GWS & R. Withall 24.1.2004.	<b>HM033074</b>	ND
	GWS001957	Verona Sands, Tas., Australia. GWS & R. Withall 24.1.2004.	<b>HM033075</b>	ND
	GWS001967	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033073</b>	ND
	GWS001970	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	Cont.	Partial
	GWS001971	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	Cont.	Partial
	GWS001978	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	Cont.	Partial
	GWS001979	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033082</b>	ND
	GWS001980	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033077<sup>a</sup></b>	ND

	GWS001982	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033083</b>	ND
	GWS001983	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033081</b>	ND
	GWS002609	Verona Sands, Tas., Australia. GWS 23.1.2005.	Cont.	Partial
	GWS002614	Verona Sands, Tas., Australia. GWS 23.1.2005.	Cont.	Partial
Rhodymeniaceae				
<i>Botryocladia leptopoda</i> (J. Agardh) Kylin	GWS001073	Lord Howe I., NSW, Australia. GWS 16.3.2001.	ND	DQ345756
<i>Cephalocystis furcellata</i> (J. Agardh) A. Millar, G.W. Saunders, I.M. Strachan et Kraft	G0133	Point Lonsdale Reef, Vic., Australia. GTK & GWS 30.3.1993.	ND	EF033621
<i>Chrysomenia ornata</i> (J. Agardh) Kylin	G0281	Jervis Bay, NSW, Australia. A. Millar & P. Richards 1.2.1995.	ND	DQ343670
<i>C. wrightii</i> (Harvey) Yamada	GWS000306	Muroran, Hokkaido, Japan. K. Kogame 23.7.1997.	ND	EU624146

<i>Coelarthrum opuntia</i> (Endlicher) Borgesen	G0303	Pt. Nepean, Port Phillip Bay, Vic., Australia. GWS & GTK 5.4.1995.	ND	DQ343671
<i>Cordylecladia erecta</i> (Greville) J. Agardh	G0206	New Quay, Co. Clare, Ireland. M.D. Guiry 11.9.1986.	ND	DQ343713
<i>Halichrysis concrescens</i> (J. Agardh) DeToni	GWS002090	Malabar Reef, Lord Howe I., NSW, Australia. GWS 3.2.2004.	ND	DQ343672
<i>H. corallinarius</i> D.L. Ballantine, G.W. Saunders et H. Ruiz	PR6268	La Parguera, Lajas, Puerto Rico. H. Ruiz 11.7.2004.	AY970628	DQ343674
<i>H. micans</i> (Hauptfleisch) P. Huvé et H. Huvé	GWS001065	Malabar Reef, Lord Howe I., NSW, Australia. GWS 14.3.2001.	EF101937	DQ343673
<i>Halopeltis australis</i> (J. Agardh) G.W. Saunders comb. nov.	G0253	Wilson Bay, Rottneest I., WA, Australia. J. Huisman 20.7.1994.	<b>HM033026</b>	EU624152
	GWS001279	Carnac I., WA, Australia. J. Huisman 12.12.2001.	<b>HM033024</b>	ND

	GWS001280	Carnac I., WA, Australia. J. Huisman 12.12.2001.	<b>HM033027</b>	ND
	GWS001570	Point Lonsdale Reef, Vic., Australia. GWS 7.12.2002.	<b>HM033025</b>	ND
<i>H. austrina</i> (Womersley) G.W. Saunders comb. nov.	GWS002531	Warrnambool, Vic., Australia. GWS 17.1.2005.	<b>HM033028</b>	ND
<i>H. cuneata</i> (Harvey) G.W. Saunders comb. nov.	GWS001504	Arch Rock, south of Hobart, Tas., Australia. GWS 28.11.2002.	<b>HM033031</b>	<b>HM033163<sup>b</sup></b>
	GWS001521 <sup>c</sup>	Arch Rock, south of Hobart, Tas., Australia. R. Withall 28.11.2002.	<b>HM033032<sup>a</sup></b>	<b>HM033164</b>
	GWS001953	Verona Sands, Tas., Australia. GWS & R. Withall 24.1.2004.	<b>HM033030</b>	ND
	GWS001954	Verona Sands, Tas., Australia. GWS & R. Withall 24.1.2004.	<b>HM033029</b>	ND
<i>H. gracilis</i> G.W. Saunders sp. nov.	GWS002049	Balls Pyramid, Lord Howe I., NSW, Australia. GWS 1.2.2004.	<b>HM033033</b>	<b>HM033165</b>
	GWS002052	Balls Pyramid, Lord Howe I., NSW, Australia. GWS 1.2.2004.	<b>HM033035<sup>a</sup></b>	ND

	GWS002062	Balls Pyramid, Lord Howe I., NSW, Australia. R. Withall 1.2.2004.	<b>HM033034<sup>a</sup></b>	ND
<i>Halopeltis</i> LH1	GWS002041	Lord Howe I., NSW, Australia. R. Withall 31.1.2004.	EF101938	DQ343678
<i>Halopeltis</i> LH2	GWS002061	Balls Pyramid, Lord Howe I., NSW, Australia. GWS 1.2.2004.	<b>HM033051</b>	<b>HM033168</b>
<i>H. prostrata</i> G.W. Saunders sp. nov.	GWS001592	Flinders Jetty, Vic., Australia. GWS 9.12.2002.	<b>HM033044</b>	<b>HM033166</b>
	GWS002428	Flinders Jetty, Vic., Australia. GWS 16.10.2004.	<b>HM033043</b>	ND
	GWS002429	Flinders Jetty, Vic., Australia. GWS 16.10.2004.	<b>HM033042</b>	ND
	GWS002430	Flinders Jetty, Vic., Australia. GWS 16.10.2004.	<b>HM033041<sup>a</sup></b>	ND
	GWS002431	Flinders Jetty, Vic., Australia. GWS 16.10.2004.	<b>HM033040<sup>a</sup></b>	ND
	GWS002432	Flinders Jetty, Vic., Australia. GWS 16.10.2004.	<b>HM033039<sup>a</sup></b>	ND
	GWS002433	Flinders Jetty, Vic., Australia. GWS 16.10.2004.	<b>HM033038<sup>a</sup></b>	ND
	GWS002434	Flinders Jetty, Vic., Australia. GWS 16.10.2004.	<b>HM033037<sup>a</sup></b>	ND
	GWS002451	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033036</b>	ND
	GWS002479	Williamstown, Port Phillip Bay, Vic., Australia. GWS 20.10.2004.	<b>HM033048<sup>a</sup></b>	ND

	GWS002542	Point Lonsdale Reef, Vic., Australia. GWS 19.1.2005.	<b>HM033047</b>	ND
	GWS002558	Cottage By the Sea Reef, Queenscliff, Vic., Australia. GWS 20.1.2005.	<b>HM033045</b>	ND
	GWS002612	Verona Sands, Tas., Australia. GWS 23.1.2005.	<b>HM033046<sup>a</sup></b>	ND
	KAD35	Pennington Bay, Kangaroo Island, NSW, Australia. K. Dixon & F. Gurgel 9.2.2008.	<b>HM033049</b>	ND
<i>Halopeltis</i> TAS	GWS002596	Blowhole, near Eaglehawk Neck, Tas., Australia. GWS 23.1.2005.	<b>HM033050</b>	<b>HM033167</b>
<i>H. verrucosa</i> (Womersley) G.W. Saunders comb. nov. TAS	GWS001480	Bicheno, Tas., Australia. GWS 26.11.2002.	<b>HM033066</b>	ND
	GWS001497	Devils Hole, Eaglehawk Neck, Tas., Australia. GWS 27.11.2002.	<b>HM033064</b>	ND
	GWS001501	Devils Hole, Eaglehawk Neck, Tas., Australia. GWS 27.11.2002.	<b>HM033062</b>	<b>HM033169</b>
	GWS001508	Arch Rock, south of Hobart, Tas., Australia. GWS 28.11.2002.	<b>HM033061</b>	ND
	GWS001912	Nine Pin Point, Tas. Australia. GWS & R. Withall 23.1.2004.	<b>HM033060</b>	ND

	GWS001958	Verona Sands, Tas., Australia. GWS & R. Withall 24.1.2004.	<b>HM033059</b>	ND
	GWS001960	Verona Sands, Tas., Australia. GWS & R. Withall 24.1.2004.	<b>HM033058<sup>a</sup></b>	ND
	GWS001966	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033057</b>	ND
	GWS001968	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033056</b>	ND
	GWS001972	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033055</b>	ND
	GWS001973	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033053</b>	ND
	GWS001974	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033054<sup>a</sup></b>	ND
	GWS001981	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033052</b>	ND
	GWS001984	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033070<sup>a</sup></b>	ND
	GWS001985	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033069<sup>a</sup></b>	ND
	GWS001986	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033068<sup>a</sup></b>	ND
<i>H. verrucosa</i> VIC	GWS002532	Warrnambool, Vic., Australia. GWS 17.1.2005.	<b>HM033067</b>	<b>HM033170<sup>b</sup></b>
	GWS002539	Point Lonsdale Reef, Vic., Australia. GWS 19.1.2005.	<b>HM033065</b>	ND
	GWS002541	Point Lonsdale Reef, Vic., Australia. GWS 19.1.2005.	<b>HM033063<sup>a</sup></b>	ND
<i>Halopeltis</i> WA	G0402	NE of White I., Easter Group, Abrolhos I., WA, Australia. GTK &	EF101939	DQ343679

		GWS 10.11.1995.		
<i>Irvinea ardreana</i> (Brodie et Guiry) Guiry	G0173	Sines, Portugal. M.D. Guiry & J.A. West.	ND	DQ343714
<i>Leptosomia rosea</i> (Harvey) Womersley	G0384	Seven Mile Beach, WA, Australia. GTK & GWS 13.11.1995.	ND	EU624147
<i>Maripelta rotata</i> (Dawson) Dawson	G0177	Cordell Bank, CA, USA. R. Schmeider & R. Moe.	ND	EU624148
<i>Microphyllum robustum</i> G.W. Saunders sp. nov.	GWS002046	Balls Pyramid, Lord Howe I., NSW, Australia. GWS 1.2.2004.	<b>HM033072</b>	Partial
	GWS002047	Balls Pyramid, Lord Howe I., NSW, Australia. GWS 1.2.2004.	<b>HM033071</b>	Partial
	GWS002057	Balls Pyramid, Lord Howe I., NSW, Australia. GWS 1.2.2004.	Cont.	<b>GU997654</b>
<i>Rhodymenia ardissoni</i> J. Feldmann	GWS001223	Petrokhori, Greece. GWS 22.8.2001.	ND	DQ343675
<i>R. californica</i> Kylin	GWS003239	Bamfield, Bradys Beach, BC, Canada. GWS 17.9.2005.	<b>HM033085</b>	ND
	JD009	Bamfield, Dixon I., BC, Canada. J. Dalen.	<b>HM033084</b>	<b>HM033171</b>

<i>R. delicatula</i> P.J.L. Dang	GWS001878	Woods Hole (MBL), MA, USA. GWS 15.10.2003.	ND	EU624149
<i>R. holmesii</i> Ardissonne	AR29696	Ste. Nonorine-des-Pertes, Calvados, Normandy, France. S. Gosset.	<b>HM033087</b>	ND
	GWS000260	Cap Gris-Nez, France. GWS 21.8.1997.	<b>HM033086</b>	<b>HM033172</b>
<i>R. intricata</i> (Okamura) Okamura	OK136	Iwaya, Awajishima, Kobe, Japan. J.H. Oak & Y-S. Keum 22.7.2000.	ND	EU624150
<i>R. leptophylla</i> J. Agardh LH	GWS001039	Roach I., Admiralty Group, Lord Howe I., NSW, Australia. GWS 12.3.2001.	<b>HM033148</b>	<b>HM033178</b>
	GWS002043	Balls Pyramid, Lord Howe I., NSW, Australia. GWS 1.2.2004.	<b>HM033147<sup>a</sup></b>	ND
<i>R. leptophylla</i> TAS	GWS001959	Verona Sands, Tas., Australia. GWS & R. Withall 24.1.2004.	<b>HM033088</b>	<b>HM033173</b>
<i>R. novahollandica</i> G.W. Saunders sp. nov. Mainland	GWS000925	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 3.12.2000.	<b>HM033135</b>	ND
	GWS000930	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 4.12.2000.	<b>HM033130</b>	ND
	GWS000950	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 10.12.2000.	<b>HM033128</b>	<b>HM033174</b>
	GWS001278	Carnac I., WA, Australia. J. Huisman 12.12.2001.	<b>HM033126<sup>a</sup></b>	ND

	GWS001567	Queenscliff, Port Phillip Heads, Vic., Australia. GTK 7.12.2002.	<b>HM033109</b>	ND
	GWS001575	Point Lonsdale Reef, Vic., Australia. GWS 7.12.2002.	<b>HM033124</b>	ND
	GWS001576	Point Lonsdale Reef, Vic., Australia. GWS 7.12.2002.	<b>HM033106</b>	ND
	GWS001577	Point Lonsdale Reef, Vic., Australia. GWS 7.12.2002.	<b>HM033122</b>	ND
	GWS001579	Point Lonsdale Reef, Vic., Australia. GWS 7.12.2002.	<b>HM033104</b>	ND
	GWS001600	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 10.12.2002.	<b>HM033102</b>	ND
	GWS001601	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 10.12.2002.	<b>HM033120</b>	ND
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	GWS001606	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 10.12.2002.	<b>HM033116</b>	ND
	GWS001607	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 10.12.2002.	<b>HM033115<sup>a</sup></b>	ND
	GWS001608	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 10.12.2002.	<b>HM033114</b>	ND
	GWS002380	Beach access west of Bay of Islands, Great Ocean Road, Vic.,	<b>HM033113<sup>a</sup></b>	ND

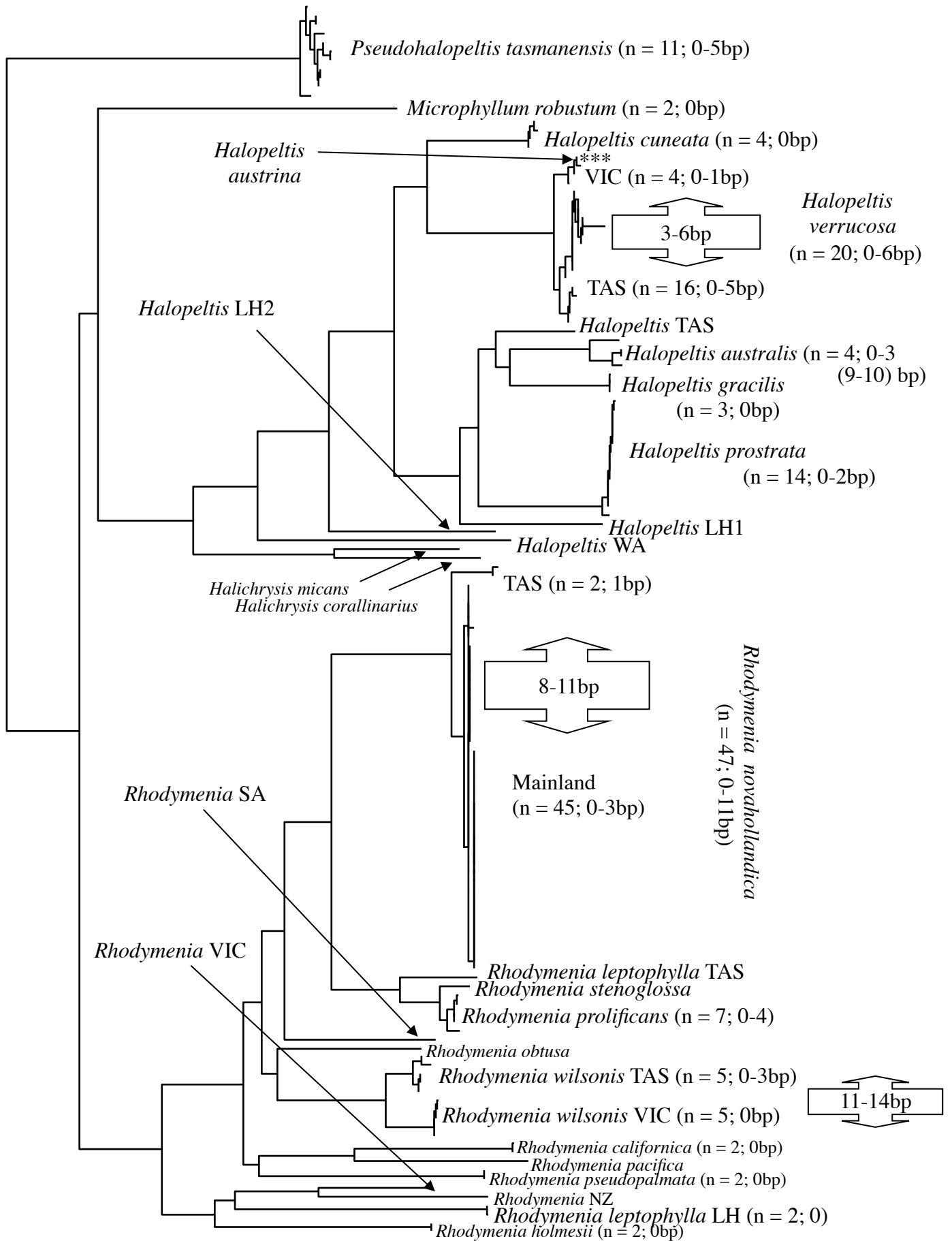
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	GWS002440	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033103<sup>a</sup></b>	ND
	GWS002441	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033101<sup>a</sup></b>	ND
	GWS002442	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033099<sup>a</sup></b>	ND
	GWS002444	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033097<sup>a</sup></b>	ND
	GWS002445	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033095<sup>a</sup></b>	ND
	GWS002446	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033093<sup>a</sup></b>	ND
	GWS002447	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033092</b>	ND
	GWS002448	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033091<sup>a</sup></b>	ND
	GWS002449	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033090<sup>a</sup></b>	ND

	GWS002450	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 17.10.2004.	<b>HM033089<sup>a</sup></b>	ND
	GWS002469	Breakwater, Portland, Vic., Australia. GWS 19.10.2004.	<b>HM033134<sup>a</sup></b>	ND
	GWS002470	Breakwater, Portland, Vic., Australia. GWS 19.10.2004.	<b>HM033133<sup>a</sup></b>	ND
	GWS002471	Breakwater, Portland, Vic., Australia. GWS 19.10.2004.	<b>HM033118</b>	ND
	GWS002472	Breakwater, Portland, Vic., Australia. GWS 19.10.2004.	<b>HM033132<sup>a</sup></b>	ND
	GWS002473	Breakwater, Portland, Vic., Australia. GWS 19.10.2004.	<b>HM033131<sup>a</sup></b>	ND
	GWS002536	Point Lonsdale Reef, Vic., Australia. GWS 19.1.2005.	<b>HM033129<sup>a</sup></b>	ND
	GWS002567	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 20.1.2005.	<b>HM033127<sup>a</sup></b>	ND
	GWS002568	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 20.1.2005.	<b>HM033125<sup>a</sup></b>	ND
	GWS002569	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 20.1.2005.	<b>HM033123<sup>a</sup></b>	ND
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	GWS002571	Queenscliff, Port Phillip Heads, Vic., Australia. GWS 20.1.2005.	<b>HM033119<sup>a</sup></b>	ND
<i>R. novahollandica</i> TAS	GWS001507	Arch Rock, south of Hobart, Tas., Australia. GWS 28.11.2002.	<b>HM033112</b>	ND
	GWS001905	Nine Pin Point, Tas. Australia. GWS & R. Withall 23.1.2004.	<b>HM033094</b>	ND
<i>Rhodymenia</i> NZ	GWS002130	Pahi, near Auckland, New Zealand. GWS 12.2.2004.	<b>HM033149<sup>a</sup></b>	<b>HM033179</b>

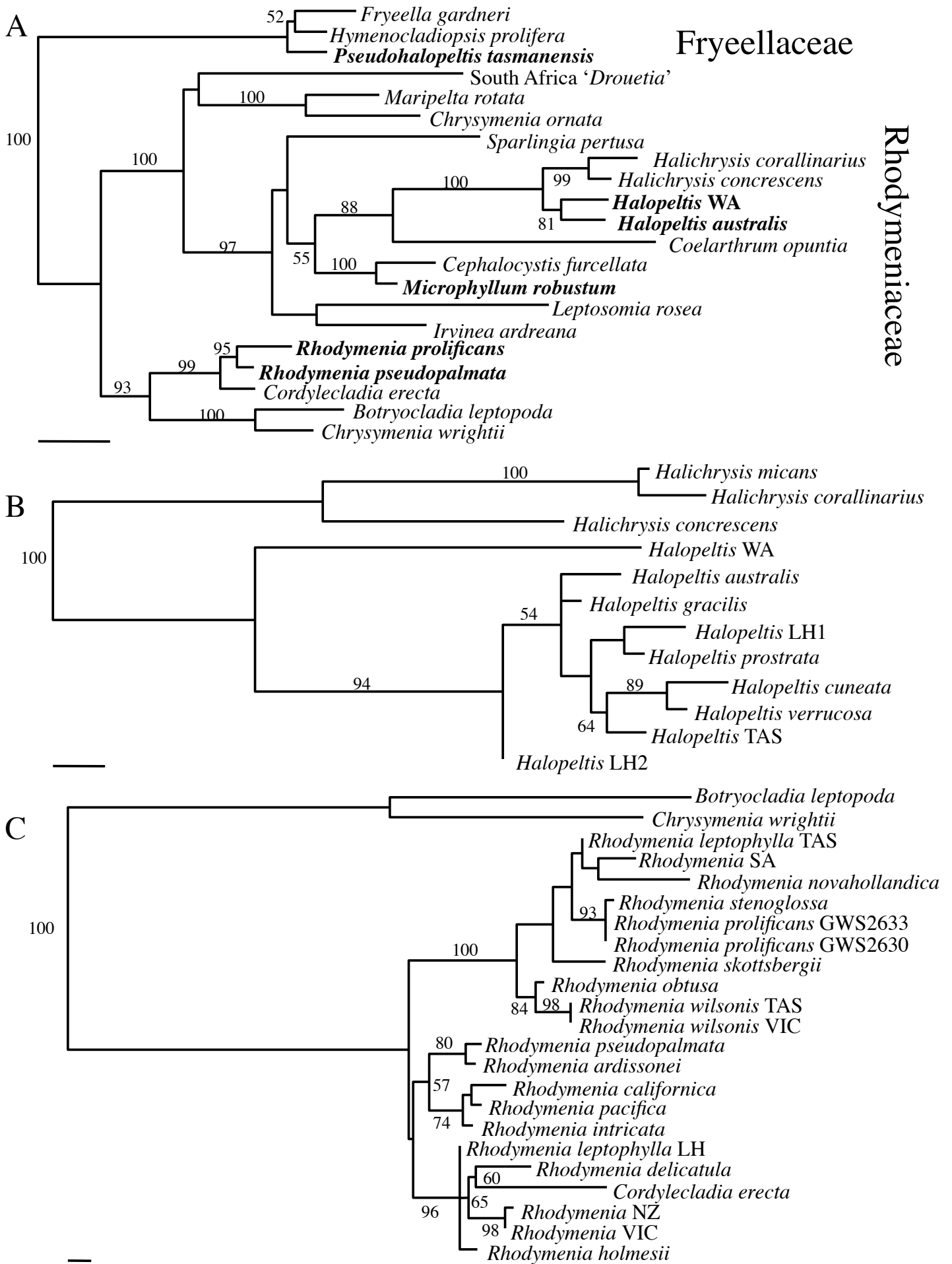
<i>R. obtusa</i> (Greville) Womersley	G0200	Grossebucht, Luderitz, Namibia. M.H. Hommersand 9.7.1993.	<b>HM033136</b>	<b>HM033175</b>
<i>R. pacifica</i> Kylin	GWS003221	Bamfield, Bradys Beach, BC, Canada. GWS 17.9.2005.	<b>HM033137</b>	ND
	JD008	Bamfield, Dixon I., BC, Canada. J. Dalen.	ND	<b>GU997652</b>
<i>R. prolificans</i> Zanardini	GWS002629	Bicheno, Tas., Australia. GWS 25.1.2005.	<b>HM033144</b>	ND
	GWS002630	Bicheno, Tas., Australia. GWS 25.1.2005.	<b>HM033143<sup>a</sup></b>	<b>HM033177</b>
	GWS002631	Bicheno, Tas., Australia. GWS 25.1.2005.	<b>HM033142</b>	ND
	GWS002633	Bicheno, Tas., Australia. GWS 25.1.2005.	<b>HM033141</b>	<b>HM033176</b>
	GWS002635	Bicheno, Tas., Australia. L. Le Gall 25.1.2005.	<b>HM033140</b>	ND
	GWS002593	Eaglehawk Neck, Tas., Australia. GWS 23.1.2005.	<b>HM033139</b>	ND
	GWS002594	Eaglehawk Neck, Tas., Australia. GWS 23.1.2005.	<b>HM033138</b>	ND
<i>R. pseudopalmata</i> (Lamouroux) P.C. Silva	GWS000261	Cap Gris-Nez, France. GWS 21.8.1997.	ND	<b>GU997653</b>
	RDW501	South Jetty, Port Arkansas, TX, USA. R. Withall 17.2.2007.	<b>HM033146</b>	ND
	RDW502	South Jetty, Port Arkansas, TX, USA. R. Withall 17.2.2007.	<b>HM033145</b>	ND

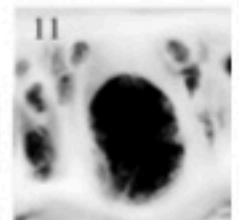
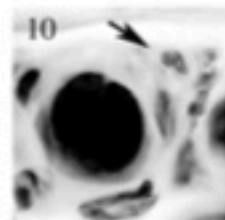
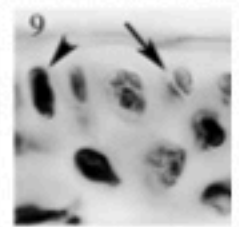
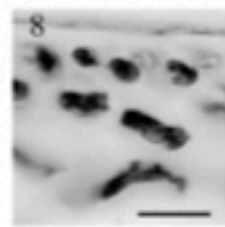
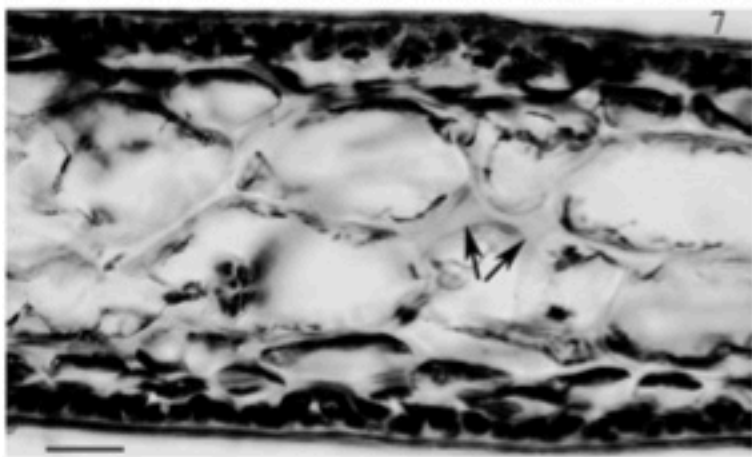
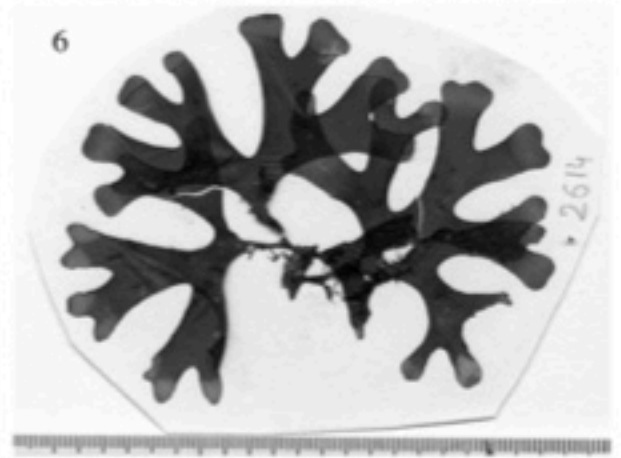
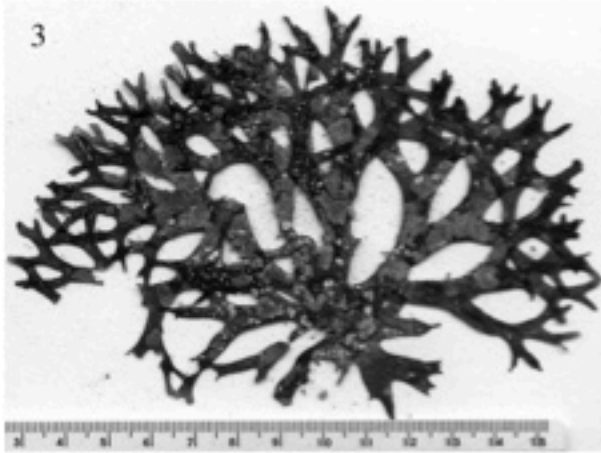
<i>Rhodymenia</i> SA	DV006	Smooth Pools, Eyre Peninsula, SA, Australia. GTK & K. Dixon 12.1.2005.	<b>HM033150</b>	<b>HM033180</b>
<i>R. skottsbergii</i> Dawson	GWS000747	Playa Grusea, near Ancud, Chiloe, Chile. GWS 21.11.1999.	ND	EU624151
<i>R. stenoglossa</i> J. Agardh	GWS001555	Warrnambool, Vic., Australia. GWS 3.12.2002.	<b>HM033152</b>	EU624153
<i>Rhodymenia</i> VIC	GWS002467	Portland, Vic., Australia. GWS 19.10.2004.	<b>HM033151</b>	<b>HM033181</b>
<i>R. wilsonis</i> (Sonder) G.W. Saunders comb. nov. TAS	GWS001517	Arch Rock, south of Hobart, Tas., Australia. C. Sanderson 28.11.2002.	<b>HM033160</b>	<b>HM033183</b>
	GWS001922	Tinderbox Reserve, South of Hobart, Tas., Australia. GWS & R. Withall 23.1.2004.	<b>HM033159<sup>a</sup></b>	ND
	GWS001969	Bicheno, Tas., Australia. GWS & R. Withall 26.1.2004.	<b>HM033158</b>	ND
	GWS002640	Bicheno, Tas., Australia. GWS 25.1.2005.	<b>HM033157<sup>a</sup></b>	ND
	GWS002641	Bicheno, Tas., Australia. GWS 25.1.2005.	<b>HM033156</b>	ND
<i>R. wilsonis</i> VIC	GWS001496	Devils Hole, Eaglehawk Neck, Tas., Australia. GWS 27.11.2002.	<b>HM033162</b>	ND
	GWS001556	Warrnambool, Vic., Australia. GWS 3.12.2002.	<b>HM033161</b>	ND

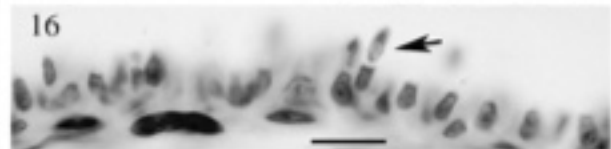
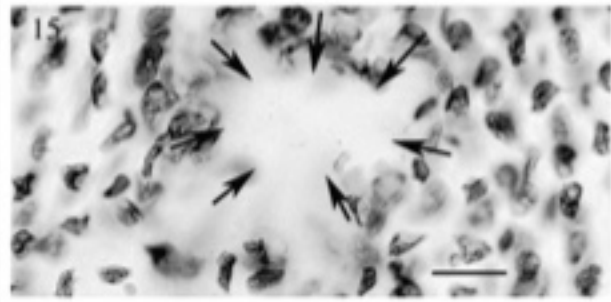
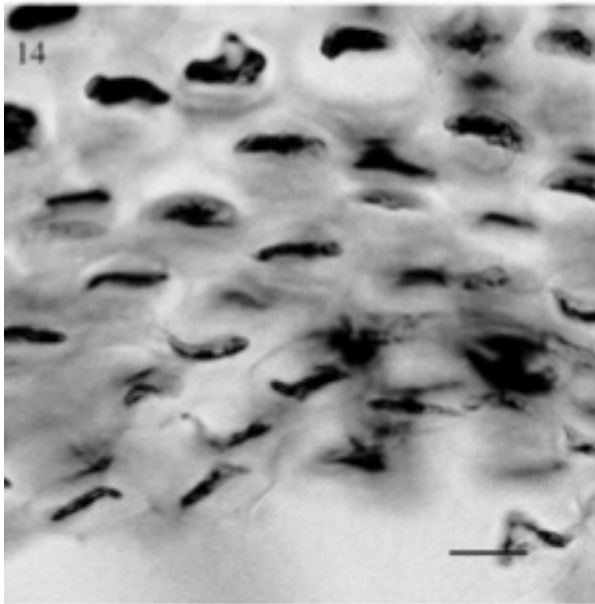
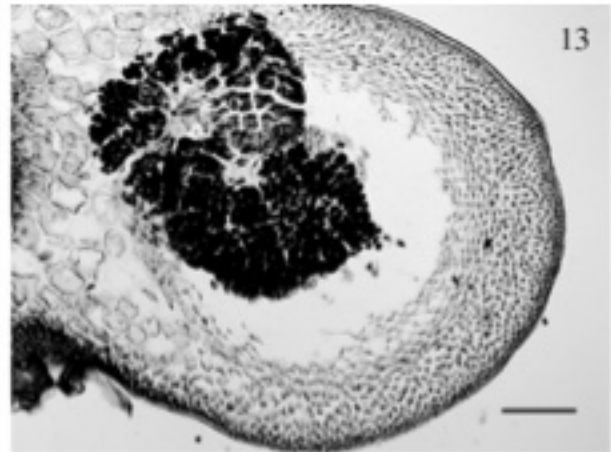
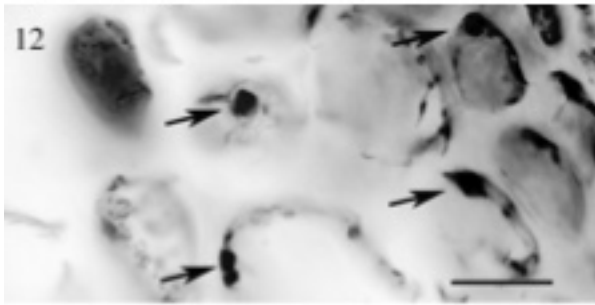
	GWS002528	Warrnambool, Vic., Australia. GWS 17.1.2005.	<b>HM033155<sup>a</sup></b>	ND
	GWS002529	Warrnambool, Vic., Australia. GWS 17.1.2005.	<b>HM033154</b>	ND
	GWS002530	Warrnambool, Vic., Australia. GWS 17.1.2005.	<b>HM033153</b>	<b>HM033182</b>
South Africa 'Drouetia'	KZNb2258	Sodwana, 5-mile Reef, Thombstone, South Africa. O. DeClerck, T. Schils, H. Verbruggen & E. Demeulenare 6.11.2003.	ND	DQ343676
<i>Sparlingia pertusa</i> (Postels et Ruprecht) G.W. Saunders, I.M. Strachan et Kraft	GWS000581	Bamfield, Dixon I., BC, Canada. GWS 6.5.1999.	ND	DQ343677

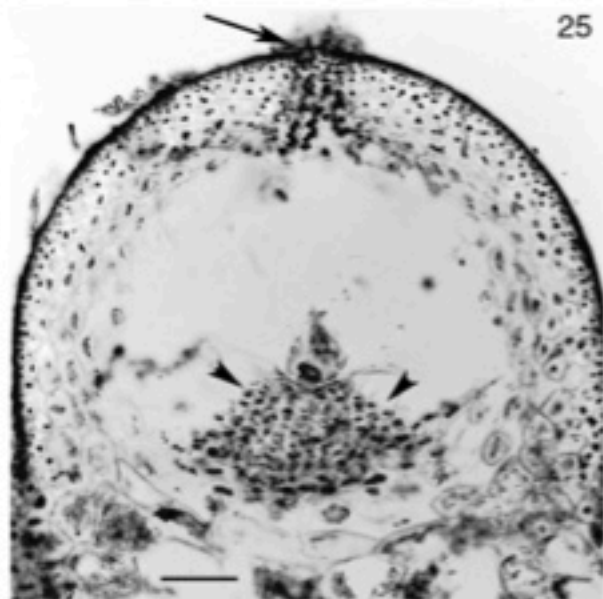
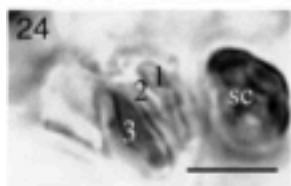
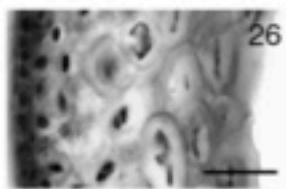
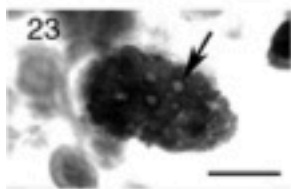
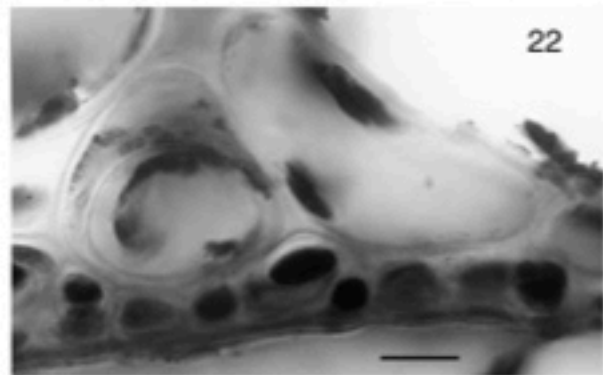
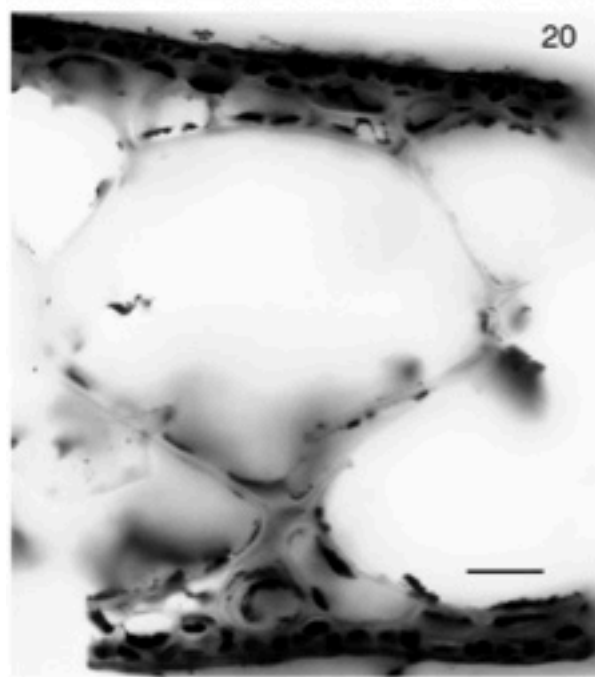
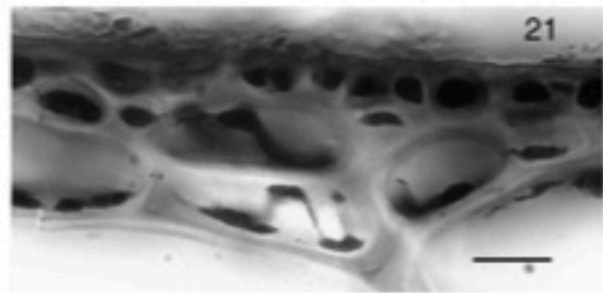
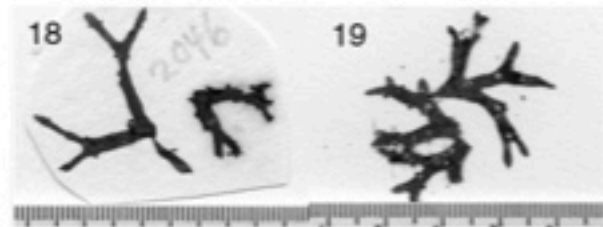


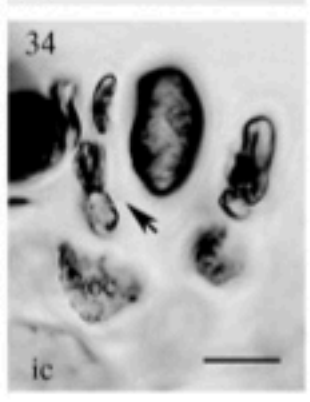
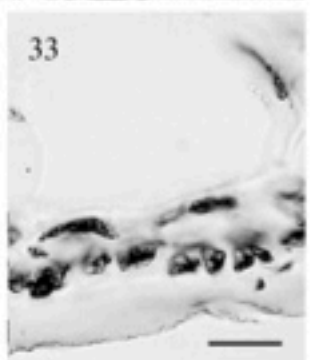
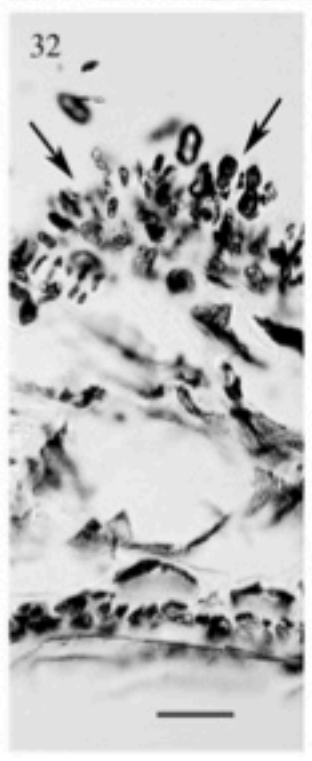
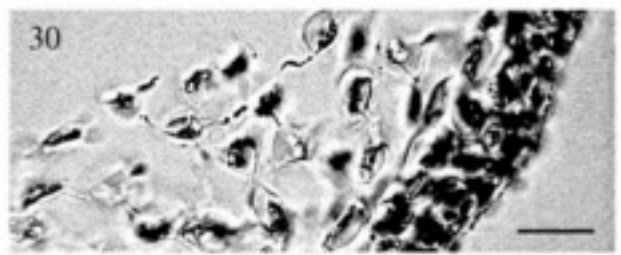
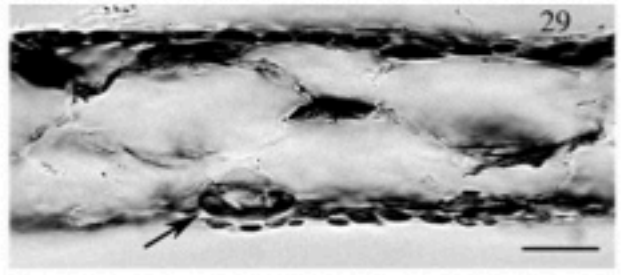
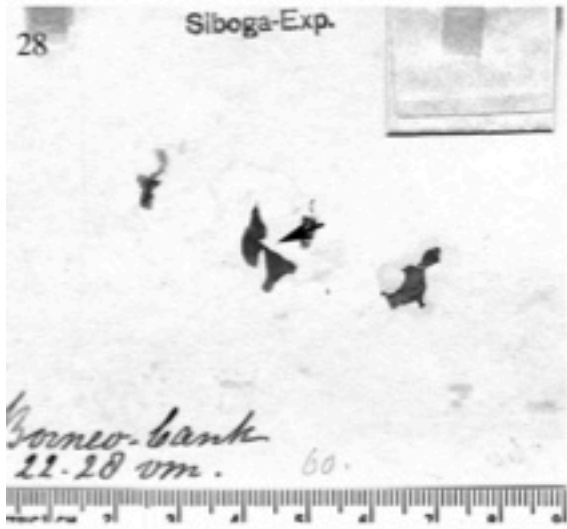
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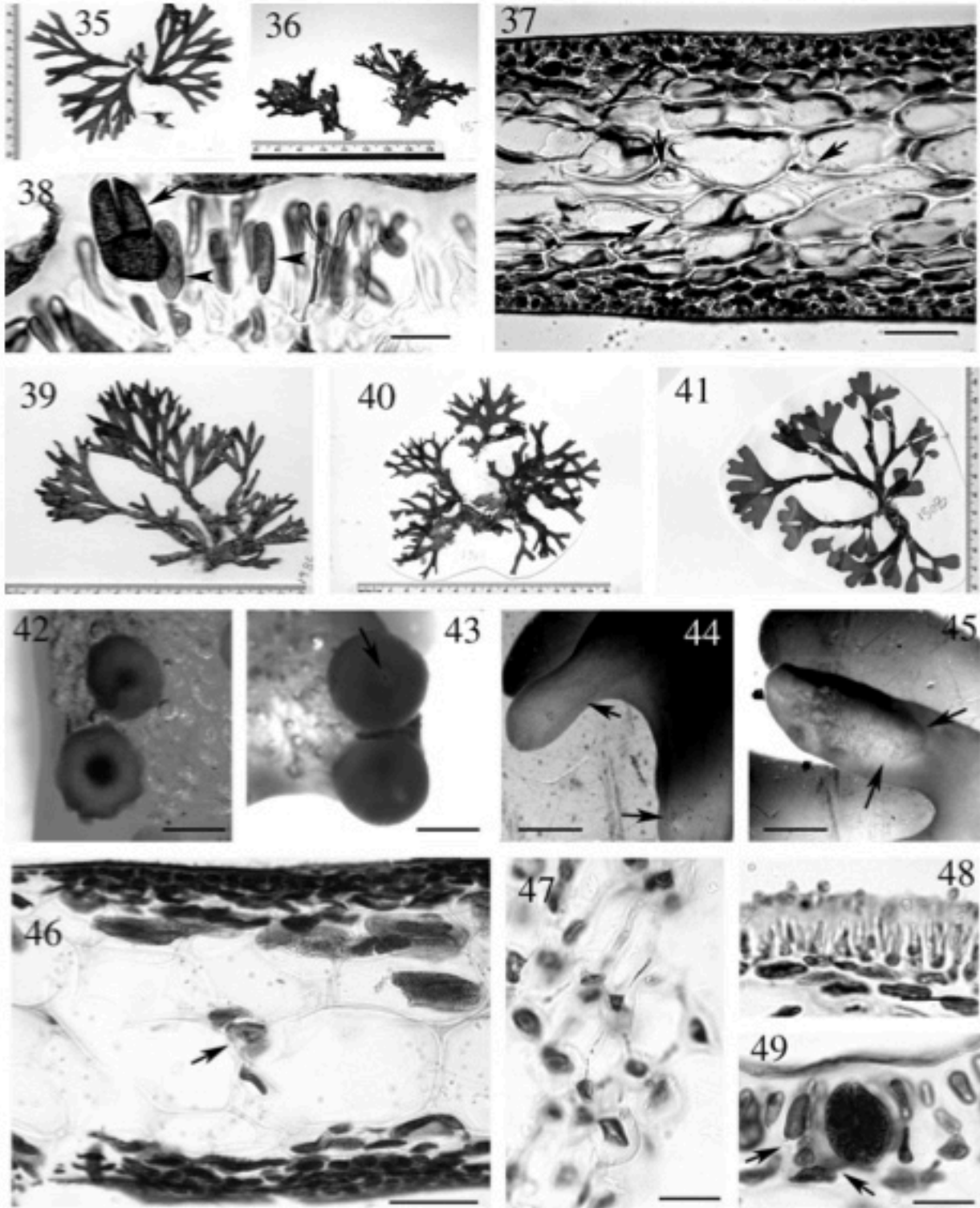


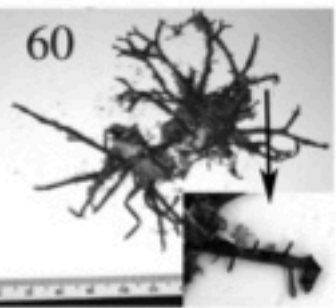
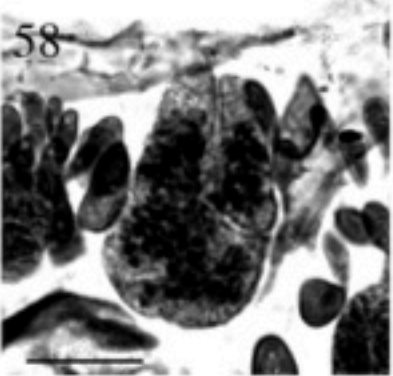
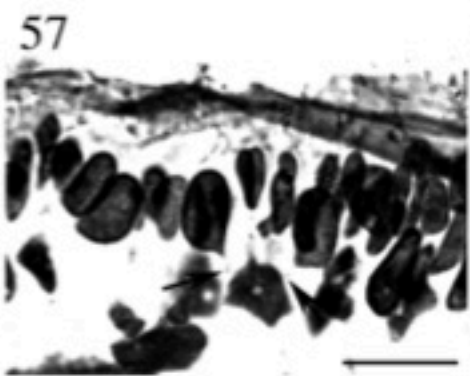
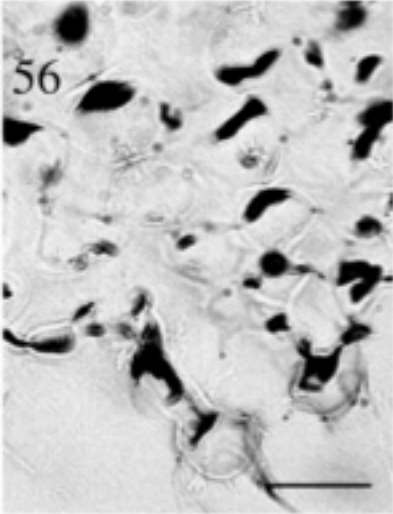
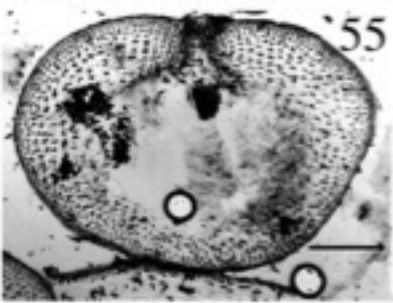
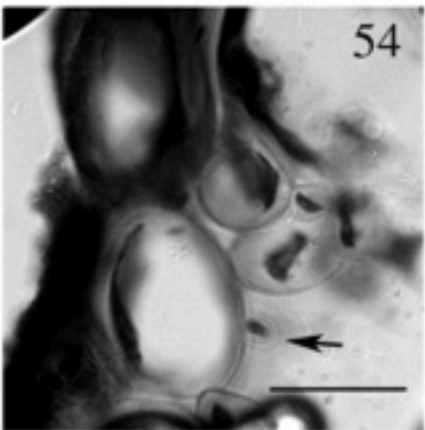
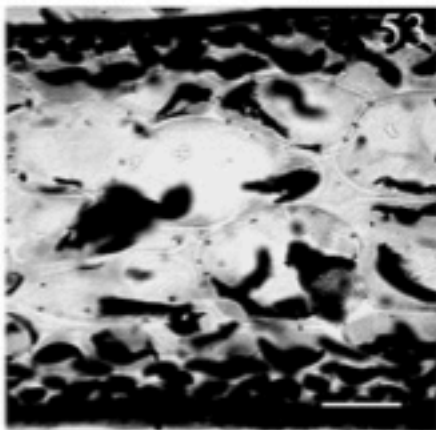
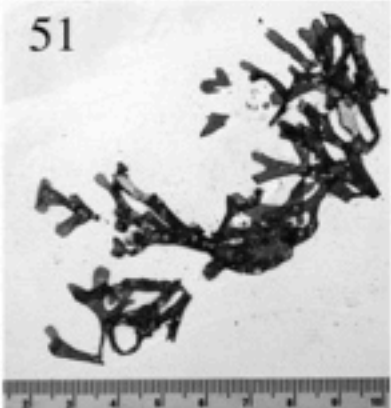
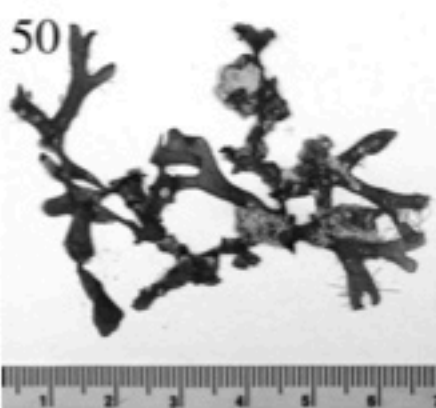


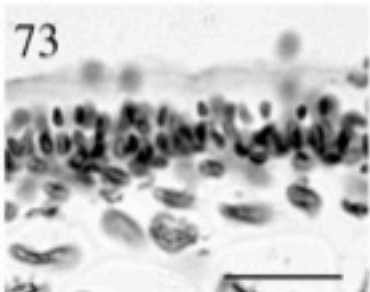
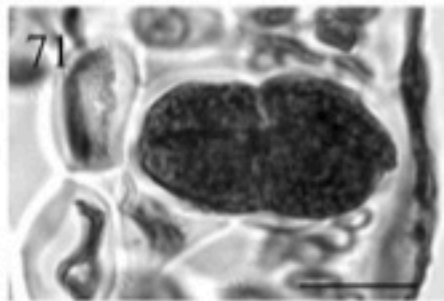
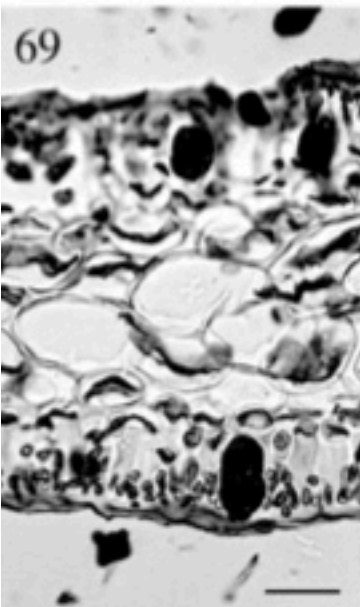
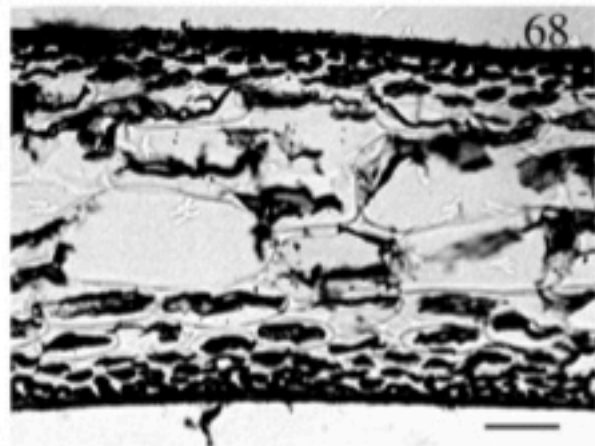
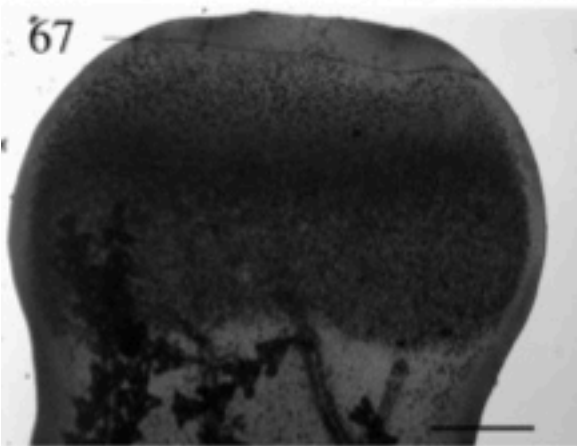
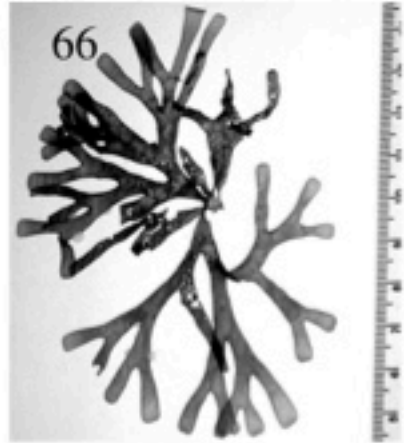














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**DNA barcoding reveals multiple overlooked Australian species of the red algal order Rhodymeniales (Florideophyceae), with resurrection of Halopeltis J. Agardh and description of Pseudohalopeltis gen. nov.**

**Saunders, Gary, W.; McDonald, Brian**

**2010**

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