Systematic studies of the antarctic species of the Phyllophoraceae (Gigartinales, Rhodophyta) based on *rbc*L sequence analysis

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Abstract

The taxonomic placement of four antarctic species of the marine red algal family Phyllophoraceae (Gigartinales) is assessed within a preliminary molecular phylogeny of the family based on direct sequence analysis of the chloroplast gene *rbc*L. Parsimony analysis of *rbc*L sequences indicates that *Gymnogongrus antarcticus* and *Gymnogongrus turquetii* cluster in a clade consisting predominantly of southern hemisphere species currently placed in *Gymnogongrus* and *Ahnfeltiopsis*, whereas *Phyllophora ahnfeltioides* and *Phyllophora antarctica* cluster in a separate clade that is widely divergent from the northern hemisphere *Phyllophora* clade. Results from molecular and morphological data challenge the current taxonomic concept that type of life history is a phylogenetically valid criterion for recognition of genera in the Phyllophoraceae.

Introduction

Few red algal families exhibit the wide range of life history types seen in the Phyllophoraceae, a carrageenan-producing family containing about 80–100 species worldwide that are currently classified into 9–10 genera (Maggs, 1990; Guiry & Garbary, 1990; Masuda, 1993). The Phyllophoraceae is closely related to the Gigartinaceae based both on morphological similarities (Guiry & Garbary, 1990), molecular criteria (Freshwater *et al.*, 1994; Hommersand *et al.*, 1994; Fredericq *et al.*, 1996) and biogeographical distribution patterns; however, both families differ extensively in terms of life history strategies. All members of the Gigartinaceae are characterized by an isomorphic alternation between free-living gametophyte and tetrasporophyte generations; generic concepts in this family are well defined, based on a suite of characters of cystocarp development and tetrasporangial organization (Hommersand *et al.*, 1993). In contrast, generic concepts in the Phyllophoraceae correspond predominantly to one of the various life history types (Maggs,

1990; Guiry & Garbary, 1990; Masuda, 1993), and cystocarp and tetrasporangial development is more uniform than in the Gigartinaceae (pers. obs.).

Recent generic revisions have resulted in the splitting of several genera from the terete genus *Gymnogongrus* Martius and the blade-like genus *Phyllophora* Greville. Retained in *Gymnogongrus* were species that lack both cystocarps and a free-living tetrasporophyte but possess external pustules in which tetrasporangial filaments grow parasitically on the thallus surface of the female gametophyte. These wart-like structures are variously called tetrasporoblasts or carpotetrasporophytes. The species of *Gymnogongrus* with internal cystocarps and a heteromorphic alternation of generations were transferred to the new genus *Anfeltiopsis* Silva *et* DeCew (Silva & DeCew, 1992; Masuda, 1993). Likewise, species of *Phyllophora* with cystocarps borne on pinnules, spermatangia organized in pits and an isomorphic alternation of generations were retained in that genus, whereas the species possessing tetrasporoblasts, *P. truncata* (Pallas) A. D. Zinova, was transferred to *Coccotylus* Kuetzing (Wynne & Heine,

1992), and the entity characterized by a heteromorphic alternation of generations, *P. traillii* Holmes *ex* Batters (Maggs, 1989), was placed in *Erythrodermis* Batters (Guiry & Garbary, 1990).

This study focuses on the taxonomic position of the antarctic species *Gymnogongrus antarcticus* Skottsberg (1953: 542), *Phyllophora ahnfeltioides* Skottsberg *in* Kylin *et* Skottsberg (1919: 9), *Phyllophora antarctica* A. *et* E. S. Gepp (1907: 12), and *Gymnogongrus turquetii* Hariot (1907: 6) . It is part of a continuing effort to generate a phylogenetic analysis of the Phyllophoraceae world-wide based on direct sequence analysis of the chloroplast gene *rbc*L and developmental morphology (Fredericq, in prep.).

Two genera of Phyllophoraceae, *Phyllophora* and *Gymnogongrus,* were listed by Papenfuss (1964) as occurring in the southern oceans. Papenfuss included four species of *Phyllophora*: *P. antarctica*, known only from the antarctic, *P. appendiculata* Skottsberg from the subantarctic, *P. ahnfeltioides*, occurring in both the antarctic and subantarctic zones, and *P. abyssalis* Skottsberg from the antarctic. *Phyllophora abyssalis* was viewed by Skottsberg (1953) and Ricker (1987) as a synonym of *P. antarctica*; however, recently collected subtidal specimens from King George I., South Shetland Is., that resemble Skottsberg's illustration (Skottsberg, 1953, Figure 8, 542) instead suggest that this species may be based on a proliferating specimen of *Hymenocladiopsis crustigena* Moe, a member of the Rhodymeniales (Fredericq & Ramírez, pers. obs.).

Papenfuss (1964) listed two antarctic species of *Gymnogongrus*, *G. antarcticus* and *G. turquetii*. Skottsberg (1953) implied that the type of *G. turquetii*, described from South Georgia (Skottsberg *in* Kylin & Skottsberg, 1919), is conspecific with that of *Phyllophora appendiculata*, in which case the name *turquetii* has priority. Moe (pers. comm.) confirmed this taxonomic decision, which is adopted here.

Materials and methods

*Rbc*L sequences from five entities representing four antarctic and 33 additional species of Phyllophoraceae world-wide were produced and assessed in this study. Two species, *Agardhiella subulata* (C. Agardh) Kraft *et* Wynne and *Solieria filiformis* (Kuetzing) Gabrielson, both belonging to the Solieriaceae, another carrageenan-containing family, were used as outgroups. (Using species belonging either to the Solieri-

aceae or to the more closely related family Gigartinaceae did not alter the general tree topology.)

The following species were examined in the molecular investigation and the *rbc*L sequences have been deposited with GenBank (Benson *et al.*, 1994) under accession numbers listed. The species names are those currently in use in the literature: *Agardhiella subulata* (U04176; see Fredericq *et al.*, 1995, for collection data); *Ahnfeltia svensonii* Taylor, Playa Las Cuatas, Zihuatanejo, Guerrero, Mexico, coll. M. Cordeiro-Marino, 28.x.93 (U22333); *Ahnfeltiopsis complicata* (Kuetz.) Silva *et* DeCew, Noordhoek, S. Africa, coll. R. B. Anderson, 27.i.94 (U21735); *Ahnfeltiopsis concinna* (J. Agardh) Silva *et* DeCew, Susaki, Shimoda-shi, Shizuoka Pref., Honshu, Japan, coll. T. Tanaka, 17.vi.85, US#030251 (U22301); *Ahnfeltiopsis devoniensis* (Greville) Silva *et* DeCew, Ile Verte, Roscoff, Brittanny, France, coll. J. Cabioch, 22.vi.93 (U21697); *Ahnfeltiopsis durvillaei* (Bory) Silva *et* DeCew, Isla Negra, Prov. San Antonio, Chile, coll. S. Fredericq & M. E. Ramírez, 26.i.94, #SF-1-26-94-2-3 (U21696); *Ahnfeltiopsis flabelliformis* (Harvey) Masuda, Muroran, Hokkaido, Japan, coll. S. Fredericq, 6.ix.93, #SF-9-6-93-1-8 (U27017); *Ahnfeltiopsis furcellata* (C. Agardh) Silva *et* DeCew, Mar Brava, Chiloë, Chile, coll. S. Fredericq, 23.ii.94, SF#2-23-94-2-1 (U21739); *Ahnfeltiopsis gigartinoides* (J. Agardh) Silva *et* DeCew, Pigeon Point, California, USA, coll. M. H. Hommersand, 21.xii.92 (U21740), *Ahnfeltiopsis glomerata* (J. Agardh) Silva *et* DeCew, Oudekraal, S. Africa, coll. R. B. Anderson, 5.i.94 (U21737); *Ahnfeltiopsis humilis* (Lindauer) Lewis *et* Womersley, Victoria, S. Australia, s.d., coll. M. D. Guiry, (U21737); *Ahnfeltiopsis leptophylla* (J. Agardh) Silva *et* De Cew, Pigeon Point, California, USA, coll. M. H. Hommersand, 21.xii.92 (U21742); *Ahnfeltiopsis linearis* (C. Agardh) Silva *et* DeCew, Pigeon Point, California, USA, coll. M. H. Hommersand, 21.xii.92 (U21741); *Ahnfeltiopsis paradoxa* (Suringar) Masuda, Tokawa Choshi, Chiba Pref., Japan, coll. S. Fredericq, 2.ix.93, #SF-9-2-93-1-5 (U21695); *Ahnfeltiopsis vermicularis* (C. Agardh) Silva *et* DeCew, Swakopmund, Namibia, coll. M. H. Hommersand, 7.vii.93 (U22300); *Coccotylus truncatus* (Pallas) Wynne *et* Heine, Strangford Narrows, Co. Down, N. Ireland, UK, coll. C. A. Maggs, 17.i.94 (U21845); *Erythrodermis traillii* (Holmes *ex* Batters) Guiry *et* Garbary, Strangford Narrows, Co. Down, N. Ireland, UK, coll. C. A. Maggs, 17.i.94 (U21852); *Gymnogongrus antarcticus*, Bahía Collins, King George I., South Shetland Is., Antarctic Peninsula, 10.ii.94, coll. S. Fredericq &

J. Rodríguez, 15 m depth, #SF-2-10-94-1-6 (U22334); *Gymnogongrus chiton* (Howe) Silva, Crissie Field, San Francisco, California, USA, coll. M. H. Hommersand, 23.xii.92 (U21748); *Gymnogongrus crenulatus* (Turner) J. Agardh, Ile verte, Roscoff, Brittanny, France, coll. M. H. Hommersand, 22.vi.93 (U22299); *Gymnogongrus dilatatus* (Turner) J. Agardh, drift, Swakopsmund, Namibia, coll. M. H. Hommersand, 5.vii.93 (U21750); *Gymnogongrus furcatus* (Hooker f. *et* Harvey) Kuetzing, Timary Port, New Zealand, coll. W. Nelson, 17.x.93 (U22335); *Gymnogongrus griffithsiae* (Turner) Martius, Fort Macon Jetty, North Carolina, USA, coll. M. H. Hommersand, 19.ix.93 (U22305); *Gymnogongrus johnstonii* (Setchell *et* Gardner) Dawson, Puerto Escondido, Papanoa, Guerrero, Mexico, coll. M. Cordeiro Marino, 26.x.93 (U21749); *Gymnogongrus torulosus* (Hooker f. *et* Harvey) Schmitz, Cable Bay, Doubtless Bay, New Zealand, coll. W. Nelson, 30.xi.93 (U22336); *Gymnogongrus turquetii*, Hermit I., Arthur Harbor, Anvers I., Antarctic Peninsula, coll. R. L. Moe, 20.i.88 (U27018) and Bahía Fildes, King George I., S. Shetland Is., Antarctic Peninsula, drift, coll. S. Fredericq & M. E. Ramírez, 13.ii.94 (U27019); *Mastocarpus stellatus* (Stackhouse) Guiry, Bally Castle, Co. Antrim, Ireland, Coll. C. A. Maggs, 20.i.92 (U29920); *Mastocarpus papillatus* (C. Ag.) Kuetzing, Dichato, Concepcíon, Chile, coll. M. E. Ramírez, 30.iii.93 (U21737); *Ozophora clevelandii* (Farlow) Abbott, Fort Point, San Francisco, California, USA, drift, coll. J. A. West, 12.iii.94 (U21851); *Petroglossum pacificum* Hollenberg, Isla Negra, Prov. San Antonio, Chile, coll. S. Fredericq & M. E. Ramírez, 26.1.94, #SF-1-26-94-2-9 (U22337); *Phyllophora ahnfeltioides*, Pta. Peñon, Bahía Fildes, King George I., South Shetland Is., Antarctic Peninsula, 14.ii.94, coll. S. Fredericq & J. Rodríguez, 17 m depth, #SF-2-14-94-1-10 (U22338); *Phyllophora antarctica*, McMurdo Sound, Antarctica, coll. L. Goff, xii.93 (U21694); *Phyllophora crispa* (Hudson) Dixon, Spiddall, Co. Galway, Ireland, coll. M. D. Guiry, 7.iii.93 (UO2990); *Phyllophora pseudoceranoides* (S. G. Gmelin) Newroth *et* A. R. A. Taylor, Spiddall, Co. Galway, Ireland, coll. M. D. Guiry, 7.iii.93 (U22307); *Schottera nicaeensis* (Lamouroux ex Duby) Guiry et Hollenberg, France, 2.viii.93 (U22309); *Solieria filiformis*, (U04185; see Frederick *et al.*, 1995, for collection data); *Stenogramme interrupta* (C. Agardh) Montagne, Horcón, Prov. Valparaíso, Chile, drift, coll. S. Fredericq & M. E. Ramírez, 27.i.94, #SF-1-27-94-1-6 (U22308); Pigeon Point, California, USA, coll. M. H. Hommersand, 21.xii.92 (U27020).

Specimens used in the morphological study were part of the same collection used for sequence analysis, except for *Phyllophora antarctica*, collected at Cape Royds, McMurdo Sound, Antarctica, 16.xii.76, coll. T. De Laca and at Cape Evans, McMurdo Sound, Antarctica, 16.xii.76, coll. T. De Laca, depth 20–25 m.

Methods of sample preparation, DNA extraction, and sequencing protocols were followed and the DNA sequences analysed as previously decribed (Freshwater *at al.*, 1994, Hommersand *et al.*, 1994) except that PCR settings were set at denaturation 4 min at 94 °C, annealing 45 sec at 50 °C and extension 1 min 30 sec at 72 °C, followed by 39 cycles denaturation for 1 min 30 sec at 94 °C, annealing 45 sec at 50 °F, and extension 2 min at 72 °C. Analysis of the data set was restricted to the last 1357 base pairs of the 1467 base-pair *rbc*L coding region. Sequences were manually aligned and analysed with the maximum parsimony method using the computer programs PAUP 3.1.1. (Swofford, 1993) and MacClade 3.0. (Maddison & Maddison, 1992) for phylogenetic reconstruction. Heuristic searches were done with 236 random sequence additions, STEEPEST DESCENT, MULPARS, and NNI (nearest-neighbor interchange). Trees found in these random searches were then used as starting points for further searches with MULPARS and TBR (tree bisection-reconnection) until swapping was complete. As a measure of internal support, decay indices (d1-d>5) representing the number of steps less parsimonious than minimal at which branches were no longer resolved were determined based on strict consensus analysis of cladograms found by relaxing parsimony sequentially, one step at a time, up to five steps, and also by bootstrap resampling analyses using 100 bootstrap replicates.

Results

Heuristic searches of *rbc*L sequence data from 40 taxa resulted in six equally most parsimonious trees of length 1507, consistency index = 0.442, and retention index = 0.577. Figure 1 shows one of the most parsimonious trees. Parsimony analysis indicated that *Gymnogongrus antarcticus* and *Gymnogongrus turquetii* cluster in a clade consisting predominantly of southern hemisphere species currently placed in *Gymnogongrus* and *Ahnfeltiopsis*, whereas *Phyllophora ahnfeltioides* and *P. antarctica* cluster in a separate clade that is
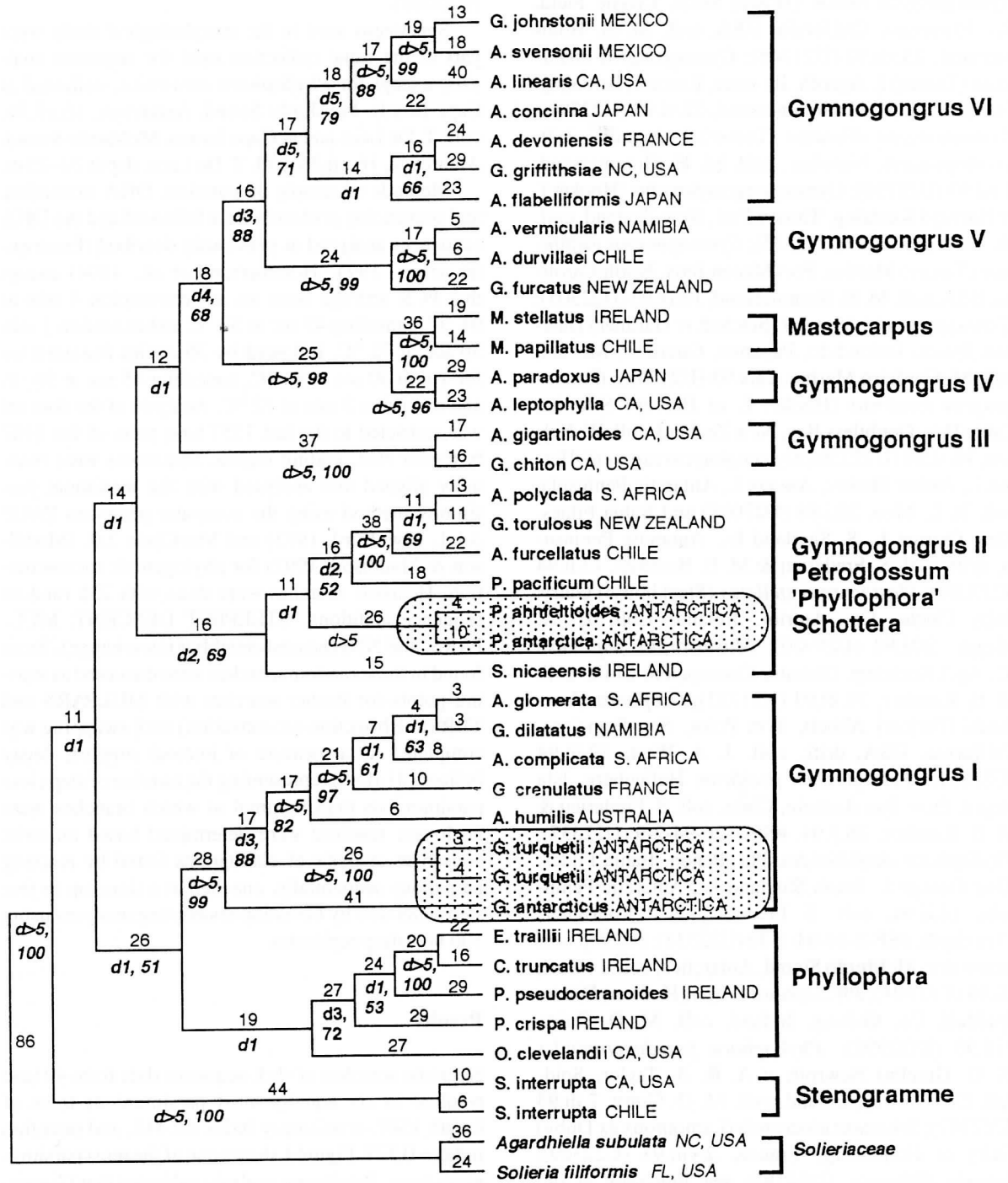
Figure 1. One of six equally most parsimonious trees of 38 taxa of Phyllophoraceae (L = 1507, CI = 0.442, RI = 0.577) resulting from *rbc*L sequence analysis. Branch length estimates are given above, and decay indices and bootstrap percentage values (100 replicates) below the internodal branches. The antarctic taxa are highlighted.

widely divergent from the northern hemisphere *Phyllophora* clade.

Six major clades of *Gymnogongrus/Ahnfeltiopsis* can be recognized: (1) 'Gymnogongrus I', a well-supported clade (d>5, 99% bootstrap value) that consists predominantly of southern hemisphere species from Australia, western South Africa and Namibia, in which the antarctic entities occupy a basal position, and with a single north-eastern Atlantic species, *G. crenulatus*; (2) 'Gymnogongrus II', a poorly supported southern hemisphere clade (d2, 69% bootstrap value) with species from Chile, New Zealand and South Africa, also including the antarctic *Phyllophora* species, as well as *Petroglossum* from Chile and *Schottera* from the eastern Atlantic; (3) 'Gymnogongrus III', a strongly supported northeastern Pacific clade (d>5, 100% bootstrap value) consisting of two Californian species; (4) 'Gymnogongrus IV', a strongly supported northern Pacific clade (d>5, 98% bootstrap value), consisting of the genus *Mastocarpus* and two species from California and Japan that are sister taxa to *Mastocarpus;* (5) 'Gymnogongrus V', a strongly supported southern hemisphere clade (d>5, 99% bootstrap value), consisting of species from New Zealand, Chile and Namibia, and (6) 'Gymnogongrus VI', a well-supported North Pacific/North Atlantic clade (d5, 71% bootstrap value), consisting of species from Pacific Mexico, California, Japan, eastern USA and Atlantic France. The other five most parsimonious trees did not differ in general topology, but differed in a few branch length estimates.

Gymnogongrus antarcticus is the only member of the antarctic Phyllophoraceae with cystocarps embedded in the female thallus. In *G. turquetii, P. ahnfeltioides* and *P. antarctica*, cystocarps are formed in secondarily formed pinnules. Spermatangia are formed in pairs by surface cortical cells in *G. turquetii, P. ahnfeltioides* and *P. antarctica* (pers. obs.).

Discussion

Species with tetrasporoblasts (found in the type of *Gymnogongrus, G. griffithsiae*, and in *G. chiton, G. dilatatus, Ahnfeliopsis complicata* and *Coccotylus truncatus*) do not group together in a single clade in the *rbc*L tree; instead they are scattered among several clades. Tetrasporoblastic entities may be genetically more closely related to taxa possessing cystocarps than to other tetrasporoblastic species; indeed, based on *rbc*L sequence analysis, tetrasporoblastic popula-

tions of both *A. complicata* from South Africa (Fredericq & R. Anderson, in prep.) and of *G. crenulatus* from Ireland were identical to specimens sequenced from otherwise similar populations bearing cystocarps. Tetrasporoblasts originate in the same manner as do cystocarps from auxiliary cells; tetrasporoblastic filaments are homologous to gonimoblast filaments, the gonimoblast cells, instead of producing carposporangia, transform into tetrasporangia after erupting above the thallus surface. Presence of tetrasporoblasts thus indicates that they correspond to a short cut in the life cycle, bypassing the free living tetrasporangial stage; as such, presence or absence of a tetrasporoblast cannot form the basis for recognition of different genera. More detailed morphological studies are needed before *Ahnfeltiopsis/Gymnogongrus* can be formally segregated into several genera.

Ricker (1987) noted that in *Gymnogongrus antarcticus* and *Phyllophora antarctica*, both without known sporophytes, small encrusting stages, which presumably are crustose tetrasporophytes, develop from the germination of carpospores; tetrasporophytes of *G. turquetii* (Lamb & Zimmermann, 1977) and *P. ahnfeltioides* have not been reported. Based on current generic concepts, *G. antarcticus* would be transferred to *Ahnfeltiopsis* (Silva *et* DeCew, 1992), and *P. antarctica* to *Erythrodermis* (Guiry & Garbary, 1990). The two antarctic species of *Phyllophora* were initially placed in this genus because cystocarps were borne on pinnules rather than embedded within the female thallus. However, *G. turquetii*, which clusters with *G. antarcticus*, also forms secondary cystocarp-bearing pinnules. The fact that such pinnules are also found in *Mastocarpus* Kuezing and in all members of the *Phyllophora* clade indicates that they are homoplasious in the Phyllophoraceae, hence downgrading their taxonomic importance at the generic level.

The various clades consisting of the *Gymnogongrus/Ahnfeltiopsis* taxa corroborate the distinctness of species-complexes based on preliminary morphological observations (Fredericq, in prep.). For example, species with cystocarps in clade 'Gymnogongrus I' are characterized by a simple cystocarp in which the overlying cortex is few-layered without carpostomes, and the young gonimoblast cells upon fusion with vegetative cells do not form fusion cells with one another. In contrast, entities belonging to 'Gymnogongrus II' possess a more complex cystocarp with a thick-layered cortex with prominent carpostomes, and gonimoblast cells form fusion cells.

The genus *Mastocarpus*, presently placed in the Petrocelidaceae, was reinstated to contain those species of *Gigartina* with a heteromorphic alternation of generations (Guiry *et al.*, 1984). The *Mastocarpus* clade, however, consistently forms a stongly supported ingroup within the Phyllophoraceae. Morphological features of vegetative and reproductive development also show *Mastocarpus* to reside within the Phyllophoraceae. The only character keeping the two families distinct is the number of cortical cells per cell file that transform into tetrasporangial initials in the crustose tetrasporophytes, one in *Mastocarpus* versus several in the Phyllophoraceae. If this trait is downplayed, *Mastocarpus* is a typical member of the Phyllophoraceae. Based on both the morphological and molecular data, *Mastocarpus* will formally be transferred to the Phyllophoraceae and the Petrocelidaceae synonymized (Fredericq *et al.*, in prep.). Due to the presence of spermatangia that are superficial rather than in pits, the two antarctic species placed in *Phyllophora*, *P. antarctica* and *P. ahnfeltioides*, do not belong in *Phyllophora*, a genus that now appears to be restricted to the northern hemisphere, and they will ultimately have to be placed in a new genus.

The phylogenetic hypothesis presented in Figure 1 sheds light on possible paleo-biogeographical scenarios that help explain current distributions. The Phyllophoraceae in essence show the same biogeographic distribution patterns as the Gigartinaceae, as revealed in *rbc*L tree topologies (see Hommersand *et al.*, 1994). Sibling relationships among S. Australian/New Zealand and South African species in Gymnogongrus I, II and V clades, with antarctic species occurring basally in two of the clades, with the antarctic species occurring basally in two of the clades, lend support to Hommersand's (1986) initial speculation that species that originated in eastern Gondwana (currently the southwest Pacific) may have reached southern Africa across ice-free passageways between east and west Antarctica during the Cenozoic, later reaching Europe by dispersal through the tropics (e.g. *G. crenulatus* in Gymnogongrus clade I). Taxa that instead are hypothesized to have evolved in western Gondwana should accordingly be distributed along the coasts of Pacific South and North America, with the ancestors of some of these Pacific entities subsequently reaching Europe and the northwestern Pacific via boreal distribution. This latter distribution is shown by the European species *A. devoniensis*, *G. griffithsieae* and the Japanese entities *A. flabelliformis* and *A. concinna*, which belong in the same clades as eastern Pacific (Chile, Mexico,

California) taxa. The fact that the tree topology clearly splits European species into two widely divergent clades may reflect the different biogeographical scenarios that eastern and western Gondwana have experienced.

Acknowledgments

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