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PHYLOGENETIC RELATIONSHIPS WITHIN THE TRIBE JANIEAE (CORALLINALES, RHODOPHYTA) BASED ON MOLECULAR AND MORPHOLOGICAL DATA: A REAPPRAISAL OF *JANIA*[1]

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Generic boundaries among the genera *Cheilosporum*, *Haliptilon*, and *Jania*—currently referred to the tribe Janieae (Corallinaceae, Corallinales, Rhodophyta)—were reassessed. Phylogenetic relationships among 42 corallinoidean taxa were determined based on 26 anatomical characters and nuclear SSU rDNA sequence data for 11 species (with two duplicate plants) referred to the tribe Corallineae and 15 species referred to the tribe Janieae (two species of *Cheilosporum*, seven of *Haliptilon*, and six of *Jania*, with five duplicate plants). Results from our approach were consistent with the hypothesis that the tribe Janieae is monophyletic. Our data indicate, however, that *Jania* and *Haliptilon* as currently delimited are not monophyletic, and that *Cheilosporum* should not be recognized as an independent genus within the Janieae. Our data resolved two well-supported biogeographic clades for the included Janieae, an Indian-Pacific clade and a temperate North Atlantic clade. Among anatomical characters, reproductive structures reflected the evolution of the Janieae. Based on our results, three genera, *Cheilosporum*, *Haliptilon*, and *Jania*, should be merged into a single genus, with *Jania* having nomenclatural priority. We therefore propose new combinations where necessary of some species previously included in *Cheilosporum* and *Haliptilon*.

Key index words: **Corallinales; *Jania;* Janieae; morphology; nuclear SSU rDNA; phylogeny; Rhodophyta; systematics**

Abbreviations: **bp, base pair; GTR, general time reversible; TBR, tree bisection reconnection**

All members of the subfamily Corallinoideae (Aresch.) Foslie are constructed of uncalcified genicula and calcified intergenicula and form branched fronds. The Corallinoideae is characterized by genicula consisting of a single uncorticated and uncalcified tier of medullary cells and lateral cellular fusions. Although genicula arose independently in separate lineages of coralline algae, the character is symplesiomorphic within the Corallinoideae (Bailey and Chapman 1998). The genera of the Corallinoideae are referred to two tribes, the Corallineae and the Janieae, which are delimited on the basis of a number of morphological and reproductive features (Johansen and Silva 1978, Johansen 1981, Garbary and Johansen 1982). The Janieae is distinguished from the Corallineae by reproductive characteristics, such as thick, compact carposporophytic fusion cells bearing marginal carposporangial filaments, male conceptacles with narrow chambers and short canals, and a relatively small number of sporangia in each tetrasporangial conceptacle. The tribe currently includes *Jania* J. V. Lamour., *Cheilosporum* (Decne.) Zanardini, and *Haliptilon* (Decne.) Lindl.,

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while the Corallineae includes all remaining genera of Corallinoideae.

The type genus of the Janieae, *Jania* J.V. Lamour., which presently includes >30 taxa, is the most diverse genus of the Corallinoideae. Lamouroux (1812) separated the genus from *Corallina* mainly on the basis of dichotomous branching. It is currently characterized as having a dichotomously branched thallus with terete to compressed, wedge-shaped, or distally lobed intergenicula bearing axial conceptacles (Lamouroux 1812, Johansen 1969, 1981, Irvine and Johansen 1994, Johansen and Womersley 1994).

Decaisne (1842) established several sections among geniculate coralline genera based on characters, such as branching pattern and conceptacle positioning, of which the section *Cheilosporum* was included in the genus *Amphiroa,* and the section *Haliptilon* (as ''groupe'' *Haliptylon*) in the genus *Jania.* Subsequently, Zanardini (1844) proposed the elevation of the section *Cheilosporum* Decne. to generic rank, and the entity has since generally been recognized at this rank. *Cheilosporum,* currently including about 10 entities, is characterized by dichotomous branching and strongly projected intergenicular lobes, within which the marginal conceptacles are embedded (Johansen 1981, Srimanobhas et al. 1990). Lindley (1846) proposed the elevation of Decaisne's ''groupe'' *Haliptylon* to generic rank and corrected the spelling to *Haliptilon* (Johansen and Silva 1978). This genus is characterized by dichotomous primary branching, with secondary branches often pinnately and/or dichotomously arranged with terete to subterete intergenicula bearing axial conceptacles (Johansen 1981, Johansen and Womersley 1986, Irvine and Johansen 1994). Johansen and Womersley (1986) examined hundreds of collections, including 14 type specimens from southern Australia, and concluded that only one species, *Haliptilon roseum* (Lam.) Garbary et H. W. Johans., occurs in the area. They described three morphological forms (ecotypes) under *H. roseum* based on the vegetative features. Because a holotype had not been selected by Lindley (1846), a lectotype—labeled as *Corallina cuvieri* by Lamouroux and now located at the herbarium of the Université de Caen—*Haliptilon cuvieri* (J. V. Lamour.) H. W. Johans. et P. C. Silva was selected by Johansen and Silva (1978, p. 417). *Haliptilon cuvieri* was placed in synonymy with *H. roseum* by Johansen and Womersley (1986); *H. roseum* is thus currently the correct name for the generitype. Thus, only three species of *Haliptilon*—*H. cubense, H. roseum,* and *H. squamatum*—are now recognized worldwide, mainly because of the perceived great morphological variability of *H. roseum* (Johansen and Womersley 1986).

Cheilosporum, Haliptilon, and *Jania* have been distinguished from each other mainly by branching pattern. Almost all species of *Jania* are considered to be dichotomously branched, while species of *Haliptilon* are regarded as being primarily dichotomously branched and secondarily pinnately branched (Johansen and Womersley 1986). Indeed, some *Haliptilon* specimens superficially resemble species of *Corallina* sensu stricto because of their pinnate branching. *Cheilosporum* has long been treated as a genus phylogenetically distinct from *Haliptilon* and *Jania* on the basis of marginal rather than axial conceptacles and sagittate intergenicular lobes.

Although taxomomic boundaries among the three genera of the Janieae are clear in most parts of the world, the genera are so closely related that particular species are frequently very difficult to assign to one genus or the other using traditional criteria. For example, the European entity currently known as *J. rubens* var. *corniculata* (L.) J. V. Lamour. (Irvine and Johansen 1994) has pinnate branches (Hamel and Lemoine 1953, plate IV, fig. 1, as *Corallina elegans*; http://www.algaebase.org) that may be interpreted as vestigial determinate branches (Johansen and Silva 1978, Johansen and Womersley 1986). Furthermore, in Western Australia, *J. pulchella* (Harv.) Johansen et Womersley (1994) has sagittate and flattened intergenicula in the lower part of the frond (''cheilosporoid segment'' in Womersley and Johansen 1996, fig. 140B; Huisman 2000, p. 53, as *J. affinis* Harv.), whereas the upper intergenicula are terete (''janioid segment'' in Womersley and Johansen 1996). Tetrasporangial and spermatangial conceptacles in this species are apical, as typically seen in *Jania.* Harvey (1855) referred this species to *Cheilosporum* on the basis of its sagittate intergenicula.

However, recent molecular phylogenetic studies of the subfamilies of the Corallinales have supported the tribe Janieae as a natural taxon; the genus *Jania* was not so clearly supported by Bailey and Chapman (1998, fig. 1) and Bailey et al. (2004, fig. 1). These authors analyzed the type species of all three genera, including *J. verrucosa* (as *J. crassa*), but due to an insufficiency of molecular data, they could not reach a conclusion as to the monophyly of *Jania.*

The aims of the present study were to establish the phylogenetic relationships among genera of Janieae based on nuclear SSU rDNA sequences and anatomical data and to reassess generic boundaries within the tribe based on traditional anatomical characters.

MATERIALS AND METHODS

SSU rDNA sequence data. Collection information for taxa investigated is provided in Table S1 (see the supplementary material). The morphology of taxa examined in this study is also presented (Fig. 1). To determine nuclear SSU rDNA sequences, samples were processed, and genomic DNA extracted using a protocol modified from Strach-Crain et al. (1997); the DNA was purified with Wizard® DNA Clean-Up System (Promega Corp., Madison, WI, USA). The SSU rDNA was PCR-amplified from total genomic DNA using the primer combinations of Saunders and Kraft (1994, 1996). The High Pure™ PCR Product Purification Kit (Roche Diagnostics,

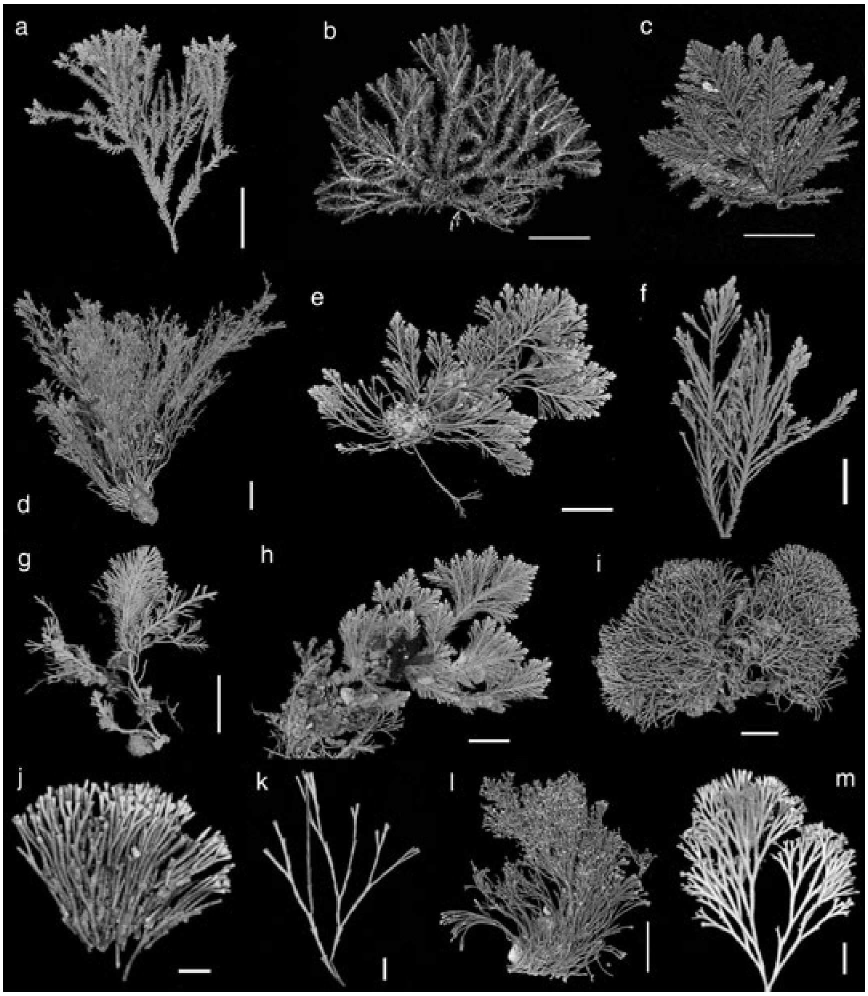

FIG. 1. Gross morphology of the specimens examined. (a) *Cheilosporum cultratum* (South Africa, CH947). Scale bar, 10 mm. (b) *Haliptilon roseum* (form A, southern Australia, OK245). Scale bar, 10 mm. (c) *Haliptilon roseum* (form B, southern Australia, OK242). Scale bar, 10 mm. (d) *Haliptilon roseum* (''*H. gracilis*'' sensu Johansen 1971a; California, CH750). Scale bar, 10 mm. (e) *Haliptilon roseum* (sensu De Clerck et al. 2005; South Africa, CH971). Scale bar, 5 mm. (f) *Haliptilon squamatum* (Ireland, CH985). Scale bar, 5 mm. (g) *Haliptilon* sp. 1 (Korea, KC144). Scale bar, 5 mm. (h) *Haliptilon* sp. 2 (South Africa, CH935). Scale bar, 5 mm. (i) *Jania adhaerens* (South Africa, CH932). Scale bar, 5 mm. (j) *Jania rubens* (Ireland, CH1000). Scale bar, 1 mm. (k) *Jania rubens* (Ireland, CH1002). Scale bar, 2 mm. (l) *Jania verrucosa* (South Africa, CH972). Scale bar, 10 mm. (m) *Jania ungulata* (Korea, KC061). Scale bar, 1 mm.

Indianapolis, IN, USA) was used to clean PCR products, which were sequenced using the BigDye^{TM} Terminator Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems [ABI], Foster City, CA, USA). Sequence data were collected with the ABI 3730 DNA Analyzer and edited with the SeqEd DNA sequence editor (ABI) software package. Sequences were aligned relative to one another using the SeqPup program (Gilbert 1995).

The final alignment for SSU consisted of 42 taxa, including 10 previously published red algal SSU sequences (Table S1). The 5′ and 3′ PCR primer regions (G01 and G07, Saunders and Kraft 1994) as well as ambiguously aligned regions were excluded, yielding 1729 sites for phylogenetic inference.

Maximum likelihood, distance, and parsimony analyses were completed in PAUP* 4.0b10 (Swofford 2002). For maximum likelihood and distance analyses, we used Modeltest 3.06 (Posada and Crandall 1998) to determine the best model for our data. The best model was a general time-reversible (GTR) model with a gamma correction for among-site variation (Γ) and invariant sites (I). Distance analyses were completed with neighbor joining (Saitou and Nei 1987) and were subjected to 1000 rounds of bootstrap resampling (Felsenstein 1985). Maximum likelihood and parsimony analyses (unweighted, gaps treated as missing data) were completed under a heuristic search (5 and 100 random additions, respectively) with tree-bisection-reconnection (TBR) branch swapping in effect. To estimate the robustness of internal nodes, bootstrap resampling was completed for the parsimony analysis (1000 replicates; random additions set to 10).

The SSU data were also used to generate trees using MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001). The GTR+Γ+I model was used, and 5,000,000 generations were run with four chains and sampling every 100 generations (burn-in subsequently identified at 60,300 generations). In all analyses, unrooted trees were calculated, and the ingroup taxa subsequently rooted with *Arthrocardia filicula* (see Table S1 for taxonomic authors) as designated outgroup (Bailey and Chapman 1998, Bailey et al. 2004).

Anatomical data. To assess phylogeny based on anatomical features and to consider the probable evolution of these same characters in light of our molecular trees, 26 features (Table 1) were coded in unordered, multistate format for 23 taxa (Table 2). Twenty-three taxa were included in parsimony analyses of anatomical data only. Of these, 20 were the same as those from which the previous molecular data were obtained (molecular data could not be obtained for *H. roseum* [''form C''], *J. pulchella,* and *J. rubens* var. *corniculata*).

Parsimony analyses were completed (random sequence addition, 100 replicates, gaps treated as missing data) using a heuristic search, steepest descent, and TBR branching swapping of PAUP with all changes equally weighted. Anatomical character states were mapped on the resulting tree(s) using PAUP. Parsimony analyses were subjected to 1000 rounds of bootstrap resampling (random additions set to 10). Unrooted

TABLE 1. Characters used in cladistic analyses of anatomical data.

Vegetative structures

1. Main axis branching: pinnately (0), dichotomously (1), pinnately/dichotomously (2)
2. Ultimate branching: pinnately/dichotomously (0), dichotomously (1), pinnately (2)
3. Strongly projecting (sagittate) intergenicular lobes: absent (0), present (1)
4. Intergenicula wedge shaped: absent (0), present (1)
5. Intergenicula shape: terete to compressed (0), terete through the frond (1)
6. Epithallial surface structure: *Corallina* type (0), *Jania* type (1)
7. Destiny of crustose base after first formation: extensive (0), reduced (1)
8. Tendril-like stolons in lower part of fronds: absent (0), present (1)
9. Height of intergenicular medullary cells: short (50–90 μm) (0), long (80–170 μm) (1)
10. Endophytic crustose coralline *Choreonema thurettii*: absent (0), present (1)

Female reproductive structures

11. Carposporophytic fusion cells: thin (<12 μm) and expanded (90–300 μm broad) (0), thick (up to 35 μm) and compact (40–130 μm broad) (1)
12. Carposporangial filaments arising: from upper surface/margins (0), margins (1)
13. Surmounting branches on carposporangial conceptacles: present (0), absent (1)
14. Number of supporting cells per procarpic conceptacle: >200 (0), <200 (1)
15. Origin of carposporangial conceptacle primordia: medullary tissue (0), medullary/cortical tissue (1), cortical tissue (2)

Male reproductive structures

16. Spermatangial conceptacle chamber: broad (350–450 μm) (0), narrow (90–250 μm) (1)
17. Spermatangial conceptacle canal: long (200–500 μm or more) (0), short (30–120 μm) (1)
18. Origin of spermatangial conceptacle primordia: medullary tissue(0), medullary/cortical tissue (1), cortical tissue (2)

Tetrasporangial structures

19. Number of tetrasporangia per conceptacle: >30 (0), <15 (1)
20. Number of tetrasporangial initials per conceptacle: >200 (0), <200 (1)
21. Paraphyses interspersed among tetrasporangia: present (0), absent (1)
22. Tetraspores: relatively small with thin mucilaginous coating (0), relatively large with thick mucilaginous coating (1)
23. Surmounting branches on tetrasporangial conceptacles: present (0), absent (1)
24. Pores of mature conceptacles: eccentric (0), centric (1)
25. Origin of tetrasporangial conceptacle primordia: medullary tissue(0), medullary/cortical tissue (1), cortical tissue (2)
26. Spore germination rate: slow (0), rapid (1)

trees were calculated, and the ingroup taxa subsequently rooted with *Arthrocardia flabellata* as the outgroup (Bailey and Chapman 1998, Bailey et al. 2004).

Cladistic analysis of combined molecular and anatomical data. The anatomical data were appended to the SSU data matrix. The combined matrix included 29 taxa (including duplicates in some taxa and excluding *Jania pulchella*, *H. roseum* [''form C''], and *J. rubens* var. *corniculata*, for which molecular data were not obtained). Combined parsimony analyses were performed (random sequence addition 100 replicates, gaps treated as missing data) using a heuristic search, steepest decent, and TBR branching swapping of PAUP with all changes equally weighted. Parsimony analyses were subjected to 1000 rounds of bootstrap resampling (random additions set to 10).

RESULTS

Thirty-two SSU sequences were newly determined for this study. No ambiguities were observed in the SSU data. Sequence data have been deposited in GenBank (Table S1).

Phylogeny based on SSU rDNA sequence data. A tree was generated by Bayesian inference with posterior probabilities and bootstrap results from the distance and maximum-parsimony analyses appended (Fig. 2) for the SSU data. The tribe Janieae was monophyletic with strong support (100% posterior probabilities and bootstrap support in all analyses) in this tree. Our analyses resolved two distinct clades among the included Janieae: (i) temperate North Atlantic entities, including *Haliptilon squamatum* and *J. rubens* from Ireland; and (ii) Indian-Pacific members, containing *Cheilosporum* spp. (South Africa and Australia), *H. roseum* sensu lato (South Africa, Australia, and California, USA), *Haliptilon* sp. 1 (Korea), *Haliptilon* sp. 2 (South Africa), *J. adhaerens* (South Africa), *Jania* sp. 1 (Australia), *J. ungulata* (Korea), and *J. verrucosa* (South Africa and California, USA). Monophyly of the genera *Haliptilon* and *Jania* was not supported.

The distance tree differed from the Bayesian result in the relative positioning of *Bossiella* spp. and *Calliarthron* spp. among the Corallineae, and *H. roseum* (as ''*H. gracilis*'') and *Haliptilon* sp. 1 among the Indian-Pacific members.

Unweighted parsimony generated four trees (length = 316, consistency index [CI] = 0.677, retention index [RI] = 0.911). A strict consensus of 359 equally parsimonious solutions differed from the Bayesian tree in the relative positioning of *J. adhaerens*, *Jania* sp. 1, and *J. ungulata* among the Indian-Pacific members. There was no support for any of these relationships.

Phylogeny based on anatomical data. Unweighted parsimony of the anatomical characters generated three trees (length = 37, CI = 0.838, RI = 0.944). The result of parsimony analysis of morphological characters coincides with the molecular results in that *Jania* and *Haliptilon* were polyphyletic. One of the trees is selected for presentation, with distribution of character-state changes appended (Fig. 3).

For the analysis, the Janieae was monophyletic with strong support (100% bootstrap support) and rooted to a common ancestor within the tribe Corallineae. The tribe Janieae was defined by 14 characters (five vegetative and nine reproductive) among 26 anatomical characters: five synapomorphic vege-

TABLE 2. Data matrix of anatomical characters and references for the species included in the cladistic analysis.

	Characters																										
Taxa	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	20	1	2	3	4	5	6	Reference[a]
Corallineae																											
Arthrocardia carinata	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2[d], 9[b], 10[c], 11[d], 21
A. flabellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1, 2[c], 6, 9[b], 10[c], 11[e], 21
Bossiella orbigniana subsp. *orbigniana*	1	1	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	2	0	0	0	0	1	1	2	0	7, 8[c], 9[b], 11
Corallina elongata	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5[c], 9[b], 10[c], 11, 16
*C. officinalis**	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	5, 9[b], 10[c], 11
Marginisporum declinatum	0	2	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	1	1	1	0	3[f], 9[b], 10[c]
Janieae																											
*Cheilosporum sagittatum**	1	1	1	0	0	?	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	0	1	9[b], 14[c], 18
Ch. cultratum	1	1	1	0	0	?	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	0	1	9[b], 11, 14[c], 21
*Haliptilon roseum** (form A[l], OK244)	1	1	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	5[c], 9[b], 12, 22
*H. roseum** (form A[l], OK245)	1	1	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	5[c], 9[b], 12, 22
*H. roseum** (form B[l], OK242)	2	0	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	5[c], 9[b], 12, 22
*H. roseum** (form C[l])	1	0	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	5[c], 9[b], 12
H. roseum (''*H. gracilis*'')	1	0	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	4[g], 9[b], 12, 22
H. roseum (South Africa)	2	0	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	9[b], 12, 21, 22
H. squamatum	1	0	0	1	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	16, 9[b], 22
Haliptilon sp. 1	2	0	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	9[b], 19, 22
Haliptilon sp. 2	2	0	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	5, 9[b], 22
Jania adhaerens	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	3[h], 9[b,c], 15, 21
J. pulchella	1	1	1	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	9[b,c], 16[i], 18, 20[j]
J. rubens var. *rubens**	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	9[b,c], 16[i], 22
J. rubens var. *corniculata*	1	0	0	1	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	9[b,c], 16[i]
J. verrucosa (CH768)	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	9[b,c], 17, 21
Jania sp. 1 (OK239)	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	5[c], 9[b,c], 17, 21

*Type species of a genus.

[a] 1, Decaisne (1842); 2, Manza (1940); 3, Yendo (1902); 4, Dawson (1953); 5, Johansen (1970); 6, Johansen (1971a); 7, Johansen (1971b); 8, Johansen (1973); 9, Johansen and Silva (1978); 10, Johansen (1981); 11, Garbary and Johansen (1982); 12, Johansen and Womersley (1986); 13, Womersley and Johansen (1988); 14, Srimanobhas et al. (1990); 15, Choi (1993); 16, Irvine and Johansen (1994); 17, Johansen and Womersley (1994); 18, Womersley and Johansen (1996); 19, Choi et al. (1997); 20, Huisman (2000); 21, De Clerck et al. (2005); 22, this study.

[b] Information at level of tribe, not specific to the species used in our analyses.

[c] Information at generic level, not specific to the species used in our analyses.

[d] As *A. linearis* Manza; [e] as *A. gardneri* Manza; [f] as *Amphiroa declinata* Yendo; [g] as *C. gracilis* var. *verticillata* Dawson; [h] as *C. adhaerens*; [i] characteristics showed in *J. rubens* var. *rubens* and *J. rubens* var. *corniculata*; [j] as *J. affinis*; [k] as *C. ungulata* Yendo.

[l] Forms A, B, C referred from Johansen and Womersley (1986); although forms A, B, C belong to Johansen and Womersley's forms, they do not represent three forms.

tative characters (6, 7, and 8–10 in Tables 1 and 2), and nine synapomorphic reproductive characters (11, 14, 16, 17, 19–22, and 26 in Tables 1 and 2). *Haliptilon* and *Jania* species within this lineage were weakly defined by reversals in two reproductive characters (13 and 23 in Tables 1 and 2) from *Cheilosporum* spp. This parsimony analysis, however, failed to resolve relationships between *Haliptilon* and *Jania*. *Jania rubens* var. *corniculata* was allied to *H. squamatum* with weak support by one synapomorphic character (4 in Tables 1 and 2). *Jania pulchella* was resolved as a sister of the other members of the *Jania* and *Haliptilon* complex with character as sagittate intergenicular lobes (cheilosporoid intergenicula) present (character 3 in Tables 1 and 2).

Phylogeny based on combined molecular and anatomical data. In a final analysis, combined molecular and anatomical data (including 1755 characters, of which 129 were informative) were subjected to unweighted parsimony analysis, and the most parsimonious solution included 20 trees (length = 287, CI = 0.704, RI = 0.899). One of the trees is selected for presentation, with distribution of character-state changes appended (Fig. 4). Analysis of this data set generally echoed the molecular result (Fig. 2) in that the three lineages were strongly supported. Within the Janieae clade, two distinct clades, temperate North Atlantic Janieae and Indian-Pacific Janieae, were not represented by any identifiable anatomical character. All members included in the Janieae shared 14 synapomorphic and two convergent characters. Among these characters, 15 characters are traditionally diagnostic in the separation of the tribe Janieae from the tribe Corallineae. *Jania*-type epithallial surface structure (character 6 in Tables 1 and 2) is shared by *Jania* and *Haliptilon*, but the character state for *Cheilosporum* is regarded as equivocal (Garbary and Johansen 1982). Also, *Corallina*-type and *Jania*-type surface structures were reported in same materials of *Jania* as well as

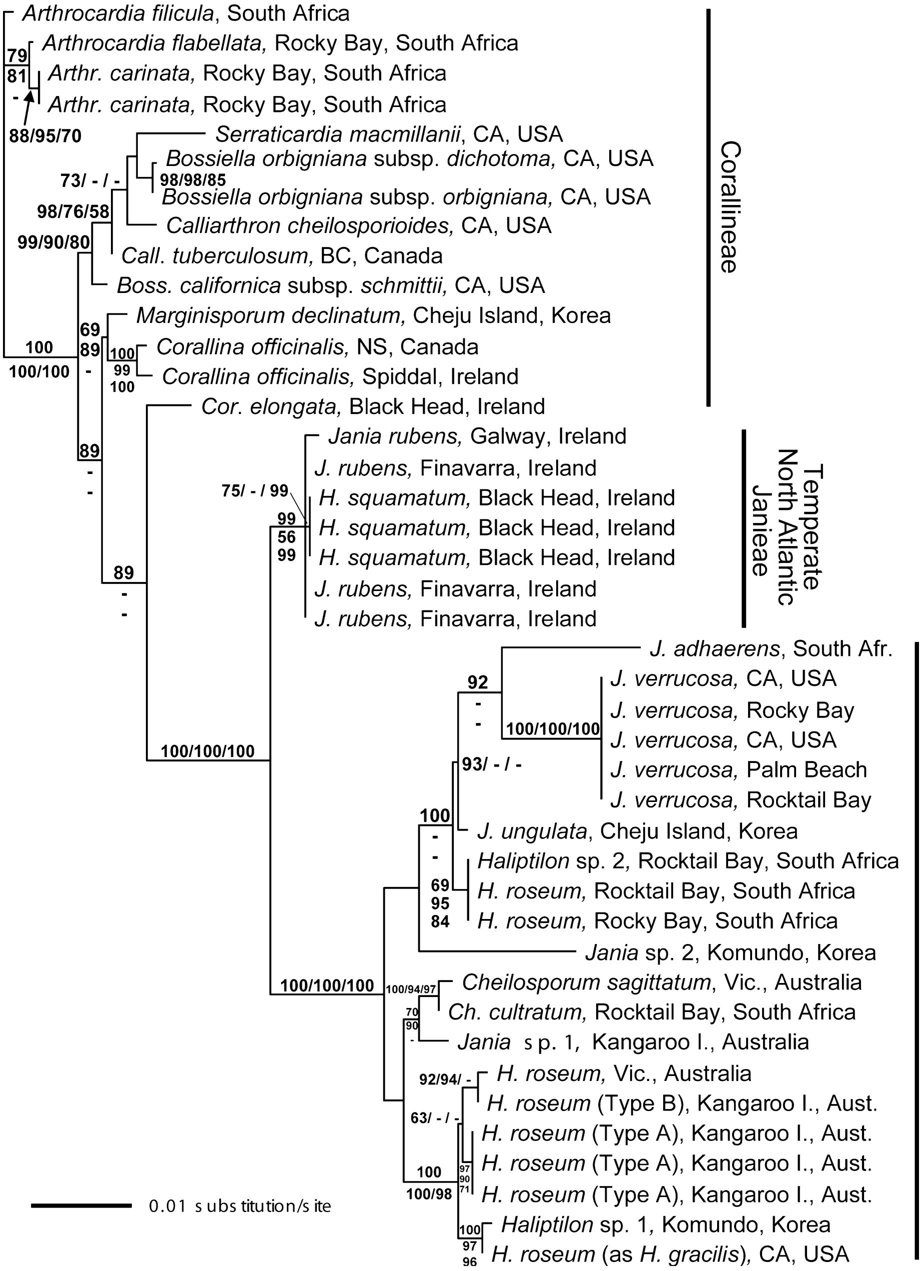

FIG. 2. Tree constructed with Bayesian inference for the SSU alignment (GTR+Γ+I model) in this study. Values at branches represent Bayesian posterior probabilities (left values) and 1000 bootstrap replicates each for distance and parsimony (middle and right values, respectively) analyses. Missing values (-) indicate <50% support. Voucher numbers correspond to records in Table S1 (see the supplementary material).

Haliptilon (Garbary and Johansen 1982, Judson and Pueschel 2002, Pueschel et al. 2002). They observed *Jania*-type surfaces near branch apices but *Corallina*-type surfaces in older parts of the same thallus in *Haliptilon.* The character of surface structure seems to be systematically insignificant.

Cheilosporum diverged from the Indian-Pacific Janieae and was defined by three anatomical characters (3, 13, and 23 in Tables 1 and 2); however, these characters have convergently evolved within *Bossiella, Corallina officinalis*, and *Marginisporum* clade.

DISCUSSION

The separation of geniculate coralline genera on the basis of conceptacle position has been generally accepted since Decaisne (1842) emphasized the axial position of conceptacles in *Corallina* and *Jania* and their lateral position in *Amphiroa.* Yendo (1905) recognized the origin of reproductive cells as an important character and distinguished *Amphiroa* and *Cheilosporum* mainly according to their origin in the cortex (*Amphiroa*) or medulla (*Cheilosporum*). Most

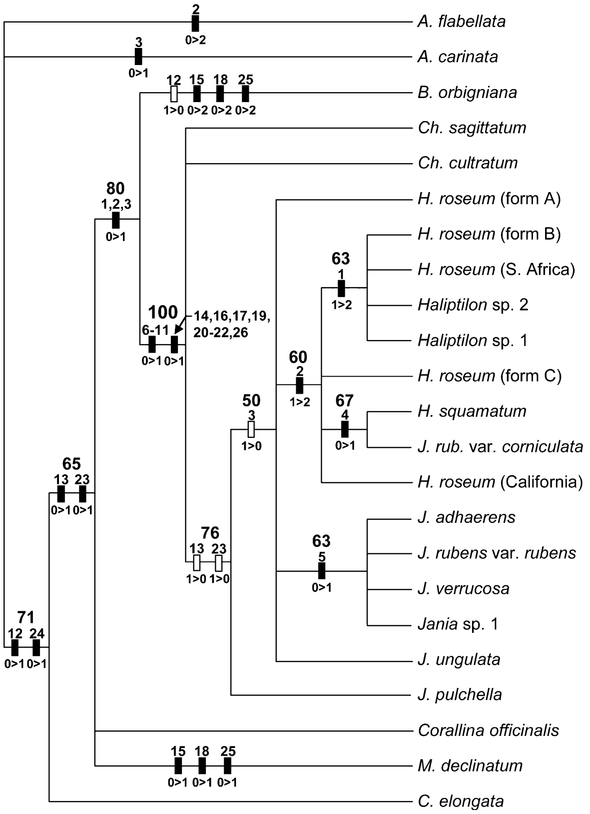

Fig. 3. Cladistic analyses of the anatomical data. One of three equally parsimonious solutions for anatomical data. Bold numbers above the branches indicate bootstrap values (% of 1000 replicates). Branches lacking values received <50% support. Numbers above and below the filled and open bars correspond to anatomical characters and character-state changes (Tables 1 and 2), respectively. Filled bars, (syn)apomorphies; open bars, reversals.

taxa that are delimited primarily on the basis of conceptacle origin correspond to genera accepted by Manza (1940). However, the feature of conceptacle position (axial, marginal, and lateral), rather than conceptacle origin, which seems natural (Johansen 1969), has been used as an important character in more recent studies (Johansen 1981, Bailey and Chapman 1998). Bailey and Chapman (1998) tested Johansen's hypothesis that conceptacle positions are phylogenetically informative, and three steps were required to fit the character states onto the corallinoidean tree (Bailey and Chapman 1998, fig. 3). They discussed the hypothesis that axial conceptacles are plesiomorphic, and that marginal and lateral conceptacles are derived within the Corallinoideae. Our results of combined molecular and anatomical data indicate that the mode of conceptacle formation (characters 15, 18, and 25) rather than the position of the conceptacles is informative; medullary conceptacles (axial and marginal) in *Corallina*, *Cheilosporum*, *Haliptilon*, and *Jania* are plesiomorphic, while medullary/cortical conceptacles in *Marginisporum* and cortical (lateral) conceptacles in *Bossiella* are derived.

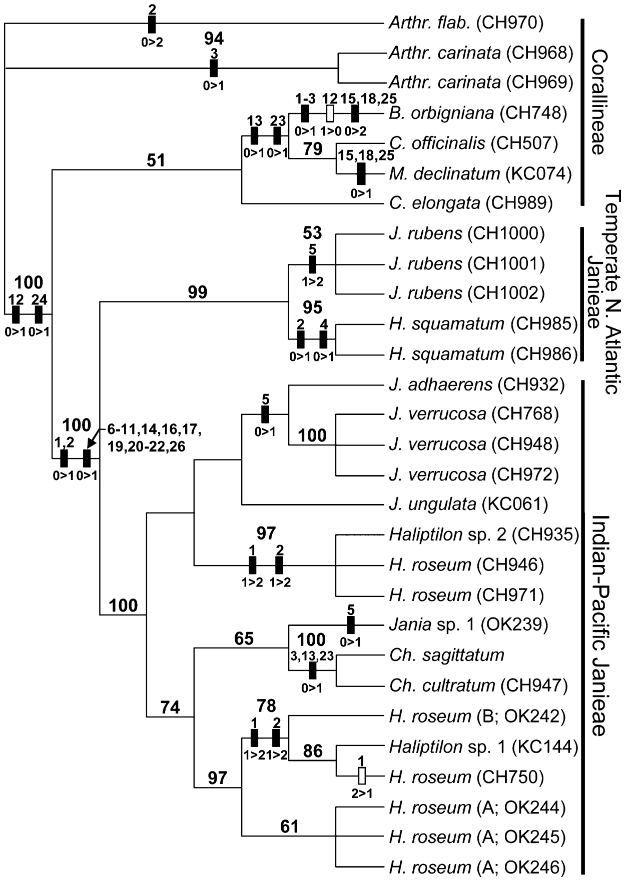

Fig. 4. Cladistic analyses of the combined molecular and anatomical data. One of 20 equally parsimonious solutions for anatomical data. Bold numbers above the branches indicate bootstrap values (% of 1000 replicates). Branches lacking values received <50% support. Numbers above and below the filled and open bars correspond to anatomical characters and character-state changes (Tables 1 and 2), respectively. Filled bars, (syn)apomorphies; open bars, reversals.

The Janieae is currently recognized as a monophyletic tribe (Johansen and Silva 1978) of the subfamily Corallinoideae (Aresch.) Foslie (1908). As in previous molecular studies (Bailey and Chapman 1998, Bailey et al. 2004), our molecular and combined molecular and anatomical data indicate that the Janieae is a monophyletic group with strong support (Figs. 2–4). Relationships among the species and genera of the Janieae are very complex, and our data indicate that both *Haliptilon* and *Jania* are polyphyletic, and that *Cheilosporum* is included within the *Haliptilon* and *Jania* complex. The three genera of Janieae—*Cheilosporum*, *Haliptilon*, and *Jania*—have been delineated traditionally by the branching pattern of the main axes (character 1), intergenicular shape (character 3), and conceptacle position. These characters have long been considered important in generic separation (Decaisne 1842, Zanardini 1844, Lindley 1846, Johansen 1969, Johansen and Silva 1978, Bailey and Chapman 1998). However, *Jania* and *Haliptilon* are so closely related that certain species may be difficult to assign to one genus or another using these morphological criteria. *Jania* species have been distinguished from *Haliptilon* mainly by branching, *Jania* species being dichotomous, and *Haliptilon* species primarily dichotomous and secondarily pinnate (Johansen and Womersley 1986). Having pronounced intergenicular lobes (character 3) and lacking surmounting branches on carpogonial and tetrasporangial conceptacles (characters 13 and 23)—all features of traditional significance in defining *Cheilosporum* from *Haliptilon* and *Jania*—has seemingly evolved in parallel in *Cheilosporum* and *Arthrocardia carinata* (character 3) and in *Cheilosporum* and *Bossiella–Corallina officinalis–Marginisporum* (characters 13 and 23), respectively.

In our combined molecular and anatomical data analyses, two strongly supported clades, a temperate North Atlantic Janieae and an Indian-Pacific Janieae, are defined within the Janieae. However, no anatomical features were discovered in this study with which to distinguish the clades, perhaps because they consist of limited species with representative features for the three genera in the Janieae.

Taxonomic proposals. On the basis of our molecular data, we conclude that reproductive rather than vegetative characters are phylogenetically important to delimit genera in the Corallinoideae. We also conclude that the Janieae includes only a single genus, *Jania*, in which species formerly referred to *Cheilosporum* and *Haliptilon* should be included. This genus is delineated by three reproductive features—thick and compact carposporophytic fusion cells, a narrow male conceptacle chamber with short canal, and less than 15 tetrasporangia per conceptacle—which primarily distinguish the Janieae and have been examined in all groups of *Jania* (in cheilosporoid group, Segawa 1941, Johansen 1977, Srimanobhas et al. 1990; in haliptiloid group, Johansen 1970, Johansen and Womersley 1986; in janioid group, Suneson 1937, Segawa 1946, Johansen 1970, Womersley and Johansen 1996). Of these genera, *Jania* has nomenclatural priority. We therefore propose new combinations of some species previously included in *Cheilosporum* and *Haliptilon* as follows.

Jania Lamouroux (1812, p. 186).

Emended description: Primary crustose bases reduced or replaced by stolons; main branching dichotomous; intergenicular medullary cells 90–130 μm long; genicular cells longer in the center than at the periphery; conceptacle primordia medullary in origin; carposporophytic fusion cell up to 35 μm thick and less than 130 μm broad with convex upper surface; male conceptacles long and narrow, chambers 90–250 μm broad, canal less than 120 μm long; tetrasporangial conceptacles containing less than 15 mature sporangia per conceptacle; sporeling development rapid, occasionally semiendophytic *Choreonema thurettii* present.

Type species: Jania rubens (Linnaeus) Lamouroux 1812, p. 186.

Lectotype (of Corallina rubens *Linnaeus): Herb. Burser,* vol. XX, p. 72 (Irvine and Johansen 1994).

Type locality: "in Oceano Europaeo."

Jania acutiloba (Decaisne) J. H. Kim, Guiry et H.-G. Choi, comb. nov.

Basionym: Amphiroa acutiloba Decaisne (*Ann. Sci. Nat. Bot.* Sér. II, vol. 18, p. 125, 1842).

Synonyms: Cheilosporum jungermannioides Ruprecht ex J. E. Areschoug (1852, p. 546). *Cheilosporum acutilobum* (Decaisne) Piccone (1866, p. 66).

Jania cubensis Montagne ex Kützing (1849, p. 709–10).

Synonyms: Corallina cubensis (Montagne ex Kützing) Kützing (1858, p. 37). *Haliptilon cubense* (Montagne ex Kützing) Garbary et Johansen (1982, p. 212).

Jania cultrata (Harvey) J. H. Kim, Guiry et H.-G. Choi, comb. nov.

Basionym: Amphiroa cultrata Harvey (*Ner. Aust.* 1849, p. 102, pl. XXXIX, pro parte, 1849).

Synonyms: Amphiroa cultrata var. *pectinata* Kützing (1858, p. 27). *Amphiroa multifidum* Kützing (1858, p. 27). *Amphiroa fastigiata* Decaisne (1842, p. 125). *Cheilosporum cultratum* (Harvey) J. E. Areschoug (1852, p. 545). *Cheilosporum cultratum* subsp. *multifidum* (Kützing) H. W. Johansen (1977, p. 176–7, figs. 24, 25, and 28). *Cheilosporum elegans* Harvey et Hooker (Harvey 1849, p. 101, pl. 38: figs. 1–4). *Cheilosporum fastigiatum* (Decaisne) De Toni (1905, p. 1834).

Jania prolifera (Lamouroux) J. H. Kim, Guiry et H.-G. Choi, comb. nov.

Basionym: Corallina prolifera Lamouroux (*Hist. Polyp.*, p. 291, pl. X: fig. 5, 1816).

Synonyms: Amphiroa flabellata Harvey (1849, p. 101). *Amphiroa stangeri* Harvey (1849, p. 101). *Amphiroa heterocladia* Kützing (1858, p. 28). *Cheilosporum pulchellum* Harvey (1855, p. 546). *Cheilosporum proliferum* (J. V. Lamouroux) De Toni (1905). *Cheilosporum africanum* Manza (1937, p. 570).

Jania rosea (Lamarck) Decaisne (1842, p. 123).

Basionym: Corallina rosea Lamarck (*Mém. Mus. Hist. Nat.* [Paris] 2, p. 235, 1815).

Synonyms: Haliptilon roseum (Lamarck) Garbary et Johansen (1982, p. 212), numerous other putative synonyms listed in Johansen and Womersley (1986, p. 563, appendix 1).

Jania lamourouxiana (Decaisne) J. H. Kim, Guiry et H.-G. Choi, comb. nov.

Basionym: Amphiroa lamourouxiana Decaisne (*Ann. Sci. Nat. Bot. Sér.* II, vol. 18, p. 125, 1842).

Synonyms: Corallina sagittata J. V. Lamouroux (in Quoy and Gaimard, 1824: p. 625, pl. 95: figs. 11 and

12). *Cheilosporum sagittatum* (J. V. Lamouroux) J. E. Areschoug (1852, p. 545). Note: We are precluded from using the earlier name of *Corallina sagittata* J. V. Lamouroux as the basis for a name in *Jania,* as the binomial *Jania sagittata* is already occupied by *Jania sagittata* Blainville (1834, p. 550, pl. LXXXXVI: fig. 2 and 2a); although no locality and no description are provided by De Blainville, the protologue fulfills the requirements of Article 44 of the ICBN. Unfortunately, this latter name cannot be applied with any certainty to any entity and to our knowledge has not been used by any author since. We have therefore chosen to use the next earliest valid name for this entity, which, by a most appropriate twist of phycological fate, is named for the originator of the genus *Jania.*

Jania spectabile (Harvey ex Grunow) J. H. Kim, Guiry et H.-G. Choi, comb. nov.

Basionym: Cheilosporum spectabile Harvey ex Grunow (in Grunow, *J. Mus. Godeffroy [Hamburg]*, vol. 3, p. 41, 1873).

Jania squamata (Linnaeus) J. H. Kim, Guiry et H.-G. Choi, comb. nov.

Basionym: Corallina squamata Linnaeus (*Syst. Nat.* ed. 10, p. 806, 1758).

Synonym: Haliptilon squamatum (Linnaeus) H. W. Johansen, L. M. Irvine et A. M. Webster (1973, p. 212).

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Supplementary Material

The following supplementary material is available for this article:

Table S1. Collection information or references and GenBank accession number for species used in this study.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1529-8817.2007.00410.x.

(This link will take you to the article abstract.)