

PROPOSAL OF THE EUPTILOTEAE HOMMERSAND ET FREDERICQ, TRIB. NOV.
AND TRANSFER OF SOME SOUTHERN HEMISPHERE PTILOTEAE TO THE
CALLITHAMNIEAE (CERAMIACEAE, RHODOPHYTA)¹

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Morphological and molecular studies demonstrate that the tribe Ptiloteae (Ceramiaceae, Ceramiales) is polyphyletic. The Ptiloteae, *sensu stricto*, occur only in the Northern Hemisphere and all Southern Hemisphere representatives belong in other tribes. Three genera (*Euptilota*, *Seirospora*, and *Sciurothamnion*) are transferred to the Euptiloteae Hommersand et Fredericq, trib. nov., and the Callithamnieae is revised to include three *Ptilota*-like genera, *Georgiella*, *Falklandiella*, and *Diapse*, and two new genera. *Heteroptilon* Hommersand, gen. nov. is erected to receive *Euptilota pappeana* Kützing 1849 and *Aglaothamnion rigidulum* De Clerck, Bolton, Anderson et Coppejans 2004 from South Africa, and *Aristoptilon* Hommersand et W. A. Nelson, gen. nov. is established to receive *Euptilota mooreana* Lindauer 1949 from New Zealand. The principal difference between the Euptiloteae and the Callithamnieae is seen in the earliest stages after fertilization. The fertilized carpogonium enlarges and forms a pair of tube-like protuberances directed toward the auxiliary cells that are cut off as connecting cells in the Euptiloteae, whereas in the Callithamnieae the carpogonium usually divides into two cells, each of which cuts off a small connecting cell that fuses with an adjacent enlarging auxiliary cell. Nuclei are terminal in spermatangia of the Euptiloteae, subtended by mucilaginous vesicles, and are medial in the Callithamnieae situated between apical and basal vesicles. The Euptiloteae and Callithamnieae (including the *Ptilota*-like members) are each strongly supported in maximum-likelihood tree topologies resulting from analyses of

combined 18S rDNA, 28S rDNA, 16S rDNA, and *rbcL* data sets. Their sister relationship is also well supported.

Key index words: *Aristoptilon*, gen. nov.; Callithamnieae; Ceramiaceae; *Diapse*; *Euptilota*; Euptiloteae, trib. nov.; *Falklandiella*; *Georgiella*; *Heteroptilon*, gen. nov.; Rhodophyta

Abbreviations: ML, maximum likelihood; PHT, partition homogeneity test; SH, Shimodaiva–Hasegawa; TBR, tree bisection reconnection

Large, pinnately branched Ceramiaceae with a conspicuous central axis surrounded by a small-celled cortex and exposed tetrasporangia were highly prized by collectors during the voyages of the 19th century that visited temperate waters of the Northern and Southern Hemispheres. A few received new generic names, but most were placed in *Ptilota* C. Agardh (1817). All were treated under *Ptilota* by J. Agardh (1876) who stressed the importance of bilateral alternate branching of the apices and who recognized four sections in the genus: (I) a group with similar opposite pinnae, (II) one with dissimilar opposite pinnae, (III) one with strictly alternate pinnae, and (IV) one with sloping alternate and opposite pinnae. The taxonomic history of each of these groups is summarized in Table 1 in Hommersand et al. (2004a). *Euptilota* Kützing (1849) was resurrected by Schmitz (1896) and revised by Hommersand et al. (2004a). *Georgiella*, *Falklandiella*, and *Diapse* were established by Kylin (1956) and placed alongside *Euptilota* in his *Ptilota* group. Although a few genera have been added, our concept of the Ptiloteae has not changed significantly since Kylin (Hommersand 1963, Womersley 1998). Recently, Hommersand

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TABLE 1. Species, collection data and GenBank accession numbers for Ceramiaceae taxa sequenced in this study.

Species	Collection data	GenBank accession number			
		18S	28S	<i>rbcL</i>	16S
<i>Aglaothamnion halliae</i>	Wrightsville Beach, New Hanover Co., North Carolina; coll. D. W. Freshwater, May 6, 1996	DQ022771	DQ022796	DQ022820	AY731508
<i>Antithamnionella spirographidis</i>	Burghaluis, Zeeland, The Netherlands coll. M. H. Hommersand, August 8, 1997	DQ022761	DQ022786	DQ022810	DQ026680
<i>Aristoptilon mooreanum</i>	Drift, Spirits Bay, Far North, New Zealand coll. W. Nelson, August 26, 2003	DQ022767	DQ022792	DQ022816	DQ026686
<i>Callithamnion collabens</i>	Yzerfontein, western Cape Province, South Africa; coll. M. H. Hommersand and O. De Clerck, January 25, 2001	DQ022769	DQ022794	DQ022818	DQ026688
" <i>Callithamnion</i> " <i>pikeanum</i>	Lone Ranch Beach, Josephine Co., Oregon, USA; coll. M. H. Hommersand, May 18, 1999	DQ022770	DQ022795	DQ022819	DQ026689
<i>Carpothamnion gunnianum</i>	Carnac Is., Western Australia, Australia coll. J. M. Huisman & T. Schills, December 12, 2001	DQ022772	DQ022797	DQ022821	DQ026690
<i>Centroceras clavulatum</i>	Falmouth, Trelawny Province, Jamaica coll. D. T. Thomas, vii.1999	DQ022759	DQ022784	DQ022809	DQ026679
<i>Ceramium</i> " <i>diaphanum</i> "	Wrightsville Beach, New Hanover Co., North Carolina, USA; coll. D. W. Freshwater, December 20, 1995	DQ022760	DQ022785	U04020	AY731509
<i>Crouania elisiae</i>	Content Key, Florida Keys, Florida, USA coll. M. H. Hommersand, March 12, 1997	DQ022763	DQ022788	DQ022812	DQ026682
<i>Diapse pilota</i>	Warrnambool, Victoria, Australia coll. M. H. Hommersand & G. T. Kraft, July 13, 1995	DQ022766	DQ022791	DQ022815	DQ026685
<i>Euptilota articulata</i>	Drift, Warrnambool, Victoria, Australia coll. M. H. & F. C. Hommersand, November 12, 1995	DQ022777	DQ022802	DQ022826	DQ026695
<i>Euptilota fergusonii</i>	2 mile reef, Sodwana Bay, KwaZulu-Natal, South Africa; coll. O. De Clerck, October 2, 2001	DQ022779	DQ022804	DQ022828	DQ026697
<i>Euptilota formosissima</i>	Mataikona, Wairarapa, N. Island, New Zealand coll. W. Nelson, April 25, 1994	DQ022778	DQ022803	DQ022827	DQ026696
<i>Euptilota molle</i>	Southern Pinnacle, Protea Banks, Kwazulu-Natal, South Africa; coll. O. De Clerck et al., February 4, 2001	DQ022780	DQ022805	DQ022829	DQ026698
<i>Falklandiella harveyi</i>	Drift, Rookery Bay, Stanley, East Falkland I. coll. M. H. Hommersand, December 31, 1997	DQ022764	DQ022789	DQ022813	DQ026683
<i>Georgiella confluens</i>	Bahía Collins, King George I., Antarctic Peninsula; coll. S. Fredericq, February 10, 1994	DQ022765	DQ022790	DQ022814	DQ026684
<i>Heteroptilon pappeanum</i>	Kommetjie, Cape Peninsula, South Africa coll. O. De Clerck, January 24, 2001	DQ022768	DQ022793	DQ022817	DQ026687
<i>Neoptilota densa</i>	Greyhound Rock, Anno Nuevo, San Mateo Co., California, USA; coll. M. H. Hommersand, July 17, 1996	DQ022757	DQ022782	DQ022807	DQ026677
<i>Plumaria plumosa</i>	West Angle Bay, Pembrokeshire, Wales coll. M. H. & F. C. Hommersand, July 22, 1997	DQ022758	DQ022783	DQ022808	DQ026678
<i>Ptilocladia pulchra</i>	Queenscliff, Victoria, Australia coll. M. H. & F. C. Hommersand, September 7, 1995	DQ022762	DQ022787	DQ022811	DQ026681
<i>Ptilota serrata</i>	Appledore I., Isles of Shoals, York Co., Maine, USA; coll. M. Volovsek, vi.2000	DQ022756	DQ022781	DQ022806	DQ026676
<i>Sciurothamnion</i> sp.	Hungtou, Orchid Is., Taiwan coll. S.-M. Lin, April 28, 2002	DQ022776	DQ022801	DQ022825	DQ026694
<i>Sciurothamnion stegengae</i>	9 Mile Reef, Sodwana Bay, Kwazulu-Natal, South Africa; coll. O. DeClerck, February 12, 2001	DQ022775	DQ022800	DQ022824	DQ026693
<i>Seiospora interrupta</i>	Wear Point near Neyland, Milford Haven, Pembrokeshire, Wales coll. C. Maggs, March 31, 2002	DQ022774	DQ022799	DQ022823	DQ026692
<i>Seiospora viridis</i>	La Parguera, Puerto Rico coll. D. L. Ballantine	DQ022773	DQ022798	DQ022822	DQ026691

and Fredericq (2001) suggested that *Euptilota* belongs in a separate tribe related to the Callithamnieae.

Hommersand et al. (2004b) listed the genera formerly placed in the Ptiloteae along with suggestions regarding their present tribal affinities. This paper considers only those genera and species that are correctly placed in the Euptiloteae or the Callithamnieae. Proposal of the Euptiloteae and transfer of three existing and two new genera to the Callithamnieae are supported by morphological evidence and molecular analyses of the nuclear-encoded small subunit ribosomal RNA gene (18S), nuclear-encoded large subunit ribosomal RNA gene (28S), plastid-encoded 16S rRNA gene (16S) and plastid-encoded *rbcL*, the gene that codes for the large subunit of RUBISCO.

MATERIALS AND METHODS

Species examined, collection localities, and GenBank accession numbers for generated sequences are listed in Table 1. The DNA was extracted from silica gel dried (Chase & Hills 1991) or fresh specimens following the method of Hughey et al. (2001) or using a Qiagen DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA). Specific gene regions were amplified by PCR and prepared for sequencing following the protocols described in Freshwater et al. (2000), Fredericq et al. (2003), and Gavio & Fredericq (2002). The oligonucleotide primers used for amplification and sequencing reactions were as follows: nuclear-encoded 18S rRNA gene (18S)—primers G01, G02, G10, G14, G08, G04, and G07 of Saunders and Kraft (1994) plus the following primers, listed as amplification pairs, that were designed in this study: CER-A (5'-TGCCAGTGGWATATGCTTGTC-3') and CER-E (5'-CTATTATTCCATGCTAATGTATTC-3'), CER-D (5'-GCAAGTCTGGTGCCAGCAG-3') and CER-H (5'-TAACCAGACAGATCACTCCAC-3'), CER-G (5'-AGCCTGCGGCTTAATTTGAC-3') and CER-J (5'-TCTCCTTCTCTAAGTGATAA-3'); nuclear-encoded 28S rRNA gene (28S)—primers C, X, H, and F of Freshwater et al. (1999) and LSU-F449 and LSU-R831 of Lin et al. (2001); plastid-encoded 16S rRNA gene (16S)—primers F16S-A, F16S-A.2, F16S-A.3, F16S-B, R16S-C, R16S-D, and R16S-E of Olson et al. (2004), and *rbcL*—primers FrbcLstart, F57, F753, R753, R1150, and RrbcSstart of Freshwater & Rueness (1994), *rbcL*-F64 and *rbcL*-F645 of Lin et al. (2001). Sequencing reactions were set up using the Big Dye kit and protocol (Applied Biosystems, Foster City, CA, USA), and run on ABI 3100 and 310 Genetic Analyzers (DNA Analysis Core Facility, CMS; Biology Department, UL-Lafayette). Reaction results were edited and sequence contigs assembled using Sequencher (Gene Codes Corp., Ann Arbor, MI, USA). Sequence data sets were compiled and aligned using MacClade (v.4, Maddison & Maddison 2000) and CLUSTAL X (Thompson et al. 1997). Regions of the alignments, where site homology was uncertain, and 5' and 3' regions, where a majority of taxa had missing data, were excluded from the analyses. Data set characteristics and rate models were determined using MacClade, Modeltest (Posada & Crandall 1998), and PAUP* 4.0b10 (Phylogenetic Analyses Using Parsimony) (Swofford 2002). Unrooted phylogenetic analyses using maximum likelihood (ML) were performed using PAUP*. ML searches for all data sets consisted of 10 random sequence additions with the MULTREES setting and tree bisection reconnection (TBR) branch swapping using the evolutionary models derived with Modeltest. The resulting unrooted topologies were drawn in a ladderized left form (Fig. 1) and relationships interpreted based on branch connections and not vertical placement in the ladderized left trees. A partition homogeneity test (PHT)

consisting of 1000 random partitions with heuristic searches using simple addition of sequences, TBR and MULTREES was performed following editorial recommendations although the use of this test to determine combinability of data sets is questionable (Yoder et al. 2001, Goldblatt et al. 2002). ML bootstrap analyses of the four individual data sets consisted of 100 replications of one random sequence addition with MULTREES and TBR branch swapping. Bootstrap analysis of the combined data set consisted of 191 replications. One-tailed Shimodaira-Hasegawa (SH) (Shimodaira & Hasegawa 1999) tests implemented in PAUP* with 1000 fully optimized bootstraps were used to test hypotheses of relationships based on the prior taxonomy against the combined data set ML tree topology.

Morphological observations were made on specimens preserved in 10% formalin in seawater and stored in 5% formalin-seawater. Whole-mount and sectioned material was stained either with a preparation of 1% acidified aniline blue in 25% Karo[®] solution or with aceto-iron-hematoxylin-chloral hydrate (Wittmann 1965) and mounted either in 1:1 Hoyer's medium: H₂O or transferred through an alcohol-xylene series and mounted in Piccolyte[®] (Hommersand & Fredericq, 1997). Photographs were taken with a Zeiss (Montpelier, MD, USA) Photomicroscope III using Kodak[®] T-Max film. Specimens are deposited at the herbarium of the University of North Carolina (NCU). Herbarium abbreviations follow Holmgren et al. (1990).

RESULTS

Molecular data sets and analyses. The generated 18S, 16S, and *rbcL* sequences included a majority of the genes except for the 5' (*rbcL*) or 5' and 3' regions (18S and 16S). Sequences for only the middle third of the 28S gene were generated. Alignment of the rRNA gene sequences required the inclusion of a variable number of inferred insertion-deletion mutations (indels). The 16S alignment required relatively few and mostly small indels, and only a small portion of the alignment was excluded from analyses because of uncertainty in site homology. The 18S alignment included more and larger indels, but uncertain site homology similarly required the exclusion of a relatively small part of the alignment. The 28S alignment included the most and largest indels despite these sequences being the shortest generated. Site homology was uncertain in a larger portion of the 28S alignment, and a large part of the 3' sequenced region was excluded from analyses because it could not be confidently aligned. The number of sites included in the analyses of separate data sets were *rbcL*, 1374; 16S, 1369; 18S, 1647; and 28S, 1010.

A PHT test showed heterogeneity among the four gene data sets ($P = 0.013$), but this test often rejects the hypothesis of homogeneity among data partitions when only weakly supported incongruence is seen between rival topologies (Reeves et al. 2001; Goldblatt et al. 2002). Yoder et al. (2001) also found that PHT tests were a misleading indicator of potential phylogenetic accuracy in combined data analyses (Yoder et al., 2001). Weakly supported incongruence may be the result of stochastic processes of sequence evolution, and is very different from incongruence between data partitions that is based on different branching histories

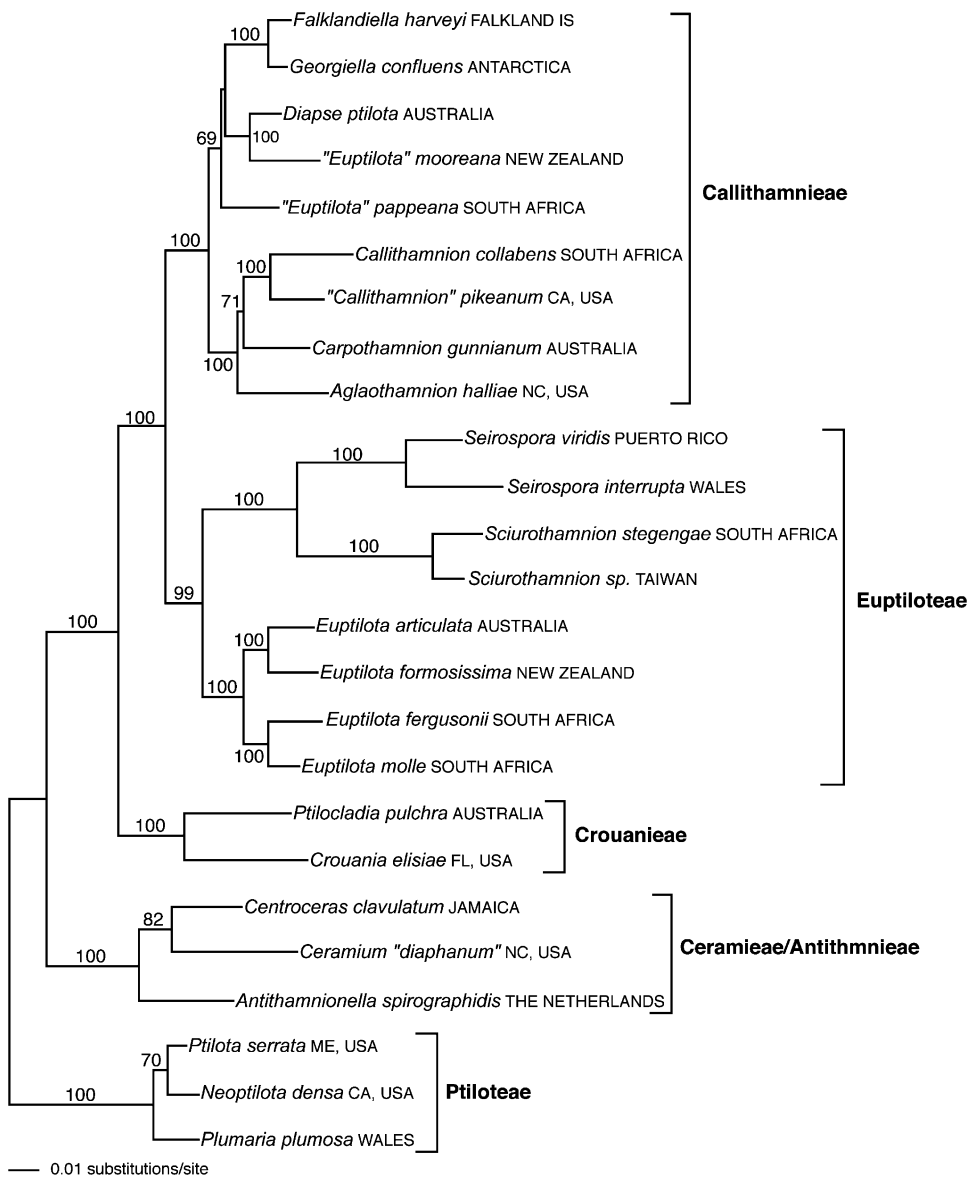


FIG. 1. Maximum-likelihood (ML) tree drawn in a ladderized left configuration resulting from unrooted analysis of a combined nuclear-encoded 18S, nuclear-encoded 28S, plastid-encoded *rbcL*, and plastid-encoded 16S DNA sequence data set for 25 Ceramiaceae species. ML bootstrap proportion values are shown for branches when greater than 60.

(Van der Neit et al. 2005). Comparison of bootstrap support for incongruent nodes has been used to discriminate between incongruence owing to stochastic processes or different branching histories (Pridgeon et al. 2001). ML analyses of the four complementary data sets in this study did not result in strictly identical topologies; however, there was never bootstrap support for both conflicting branches in the non-identical portions of trees. This suggests a lack of conflict in the phylogenetic signal present in the four data sets, and they were combined as a total-evidence approach for further analyses.

The combined data set ML analysis resulted in a tree within which most relationships were strongly supported (Fig. 1). The genera *Sciurothamnion*, *Seirospora*, and *Euptilota* are all strongly supported monophyletic clades. The tribes Callithamnieae, Crouanieae, and Ptiloteae are also strongly supported,

as well as a monophyletic group containing the Ceramieae and Antithamnieae. A Euptiloteae, containing the genera *Euptilota*, *Sciurothamnion*, and *Seirospora*, is also strongly supported. The Callithamnieae and Euptiloteae are resolved as sister taxa with strong support. Two separate monophyletic clades of species are resolved within the Callithamnieae. The one that includes the *Callithamnion*-like species is strongly supported, while the other that includes *Ptilota*-like species is only weakly supported.

Two taxa that were considered species of *Euptilota* until recently (Hommersand et al. 2004a), "*E.*" *pappeana* and "*E.*" *mooreana*, are resolved in all analyses within the Callithamnieae and not within the monophyletic clade of other *Euptilota* species. An SH test comparing the topology resulting from a ML analysis constrained to include a monophyletic *Euptilota* containing "*E.*" *pappeana* and "*E.*" *mooreana* was found to be signifi-

cantly different from the unconstrained ML topology ($P < 0.001$). The genus *Euptilota* has traditionally been placed in the tribe Ptiloteae, but this relationship was not resolved in any of the analyses. The topology resulting from an ML analysis constrained to include *Euptilota* within a monophyletic Ptiloteae was also found to be significantly different from the unconstrained ML topology ($P < 0.001$).

Morphological observations.

Euptiloteae Hommersand et Fredericq, trib. nov.

Plantae unis aut duo lateralibus initiis formatis deinceps e quoque cellula axiali, evolvantes in filamenta ecorticata aut ramos determinatos corticatos; axes nudi, corticati externo cortice parvicellulari filamentisque internis rhizoidealibus, solum filamentis rhizoidealibus, aut filamenta rhizoidea absentia praeter prope basem. Cellulae uninucleatae. Omne spermatangium continens nucleum terminalem subtentum vesicula mucosa. Procarpia solitaria vel seriatim, formata prope apices in ramos indeterminatos transformatos breves versus longos. Cellula sustinens filamentum carpogoniale formata proxime infra vel latere opposito ramum lateralem cursu cellulae periaxiali secunda formata opposita primo. Cellulae steriles absentes. Cellulae auxiliares formatae transversaliter e cellulis periaxialibus post fecundationem, carpogonium dilatans horizontaliter formans protuberationes versus cellulas auxiliares producentes cellulas conjunctivas conspicuas coalescentes; nucleus diploideus dividens situs fusionis unico nucleo ingredienti cellulam auxiliarem alteroque extruso extus in cellulam residualem. Omnis cellula auxiliaris discedens in basalem cellulam pedalem continentem nucleum haploideum originalem, qui interdum dividens, initiumque gonimoblasti terminale; primarii gonimolobi terminales, secundarii gonimolobi laterales aut non evolutantes. Tetrasporangia tetraedrice aut raro cruciatim divisa.

Genus typicum: Euptilota Kützing (1849, p. 671).

Plants with one or two lateral initials formed successively from each axial cell and either developing into ecorticate filaments or corticated determinate branches; axes naked, corticated by a small-celled outer cortex and inner rhizoidal filaments, by rhizoidal filaments alone, or rhizoidal filaments absent, except at the base. Indeterminate branches produced from the tips of determinate lateral filaments or branches, less often arising adventitiously. Cells uninucleate. Spermatangia formed singly or in pairs in dense clusters on dwarf fertile filaments, less often from surface cortical cells; each spermatangium containing a terminal nucleus subtended by a mucilaginous vesicle. Procarps solitary or in series, formed near the apices on short to long modified indeterminate branches. Supporting cell of the carpogonial branch cut off either directly beneath or on the side opposite a vegetative lateral in the plane of branching (except in *Sciurothamnion* in which the fertile periaxial cells are formed perpendicular to the plane of branching) and with a second periaxial cell cut off opposite the first. Carpogonial branch horizontal, straight or in a zigzag, with the carpogonium cut off acropetally by a transverse division; sterile cells absent. Auxiliary cells cut off transversely from the periaxial cells after fertilization, the carpo-

gonium expanding horizontally and forming protuberances directed toward the auxiliary cells and cutting off conspicuous connecting cells that fuse with them; the diploid nucleus dividing at the site of fusion with one nucleus entering the auxiliary cell and the other extruded to the outside in a residual cell, which may separate or remain attached to the base of the auxiliary cell. Each auxiliary cell cleaving into a terminal gonimoblast initial and a basal foot cell containing the original haploid nucleus, which may divide, or containing both haploid and diploid nuclei, or the haploid nucleus sometimes cut off in a disposal cell (*Sciurothamnion*); primary gonimolobes terminal, secondary gonimolobes lateral or failing to develop; gonimolobe stalk cells present or absent and the gonimolobes compact, or forming branched moniliform chains. Tetrasporangia solitary, sessile, or pedicellate from the upper ends of cells of the last three orders of filaments, or borne adventitiously on cortical filaments or superficial cortical cells; subspherical or ellipsoidal, tetrahedrally or rarely cruciately divided; binucleate bisporangia present in some, and branched moniliform chains of asexual sporangia (seiosporangia) known in one genus (*Seiospora*).

Type genus: Euptilota Kützing (1849, p. 671).

If one excludes the doubtful genus, *Podospora* (Schiffner, 1931), the Euptiloteae contains three genera, which are represented in the molecular analyses shown here. All three have previously been investigated morphologically.

Euptilota Kützing (1849, p. 671).

Type species: Euptilota formosissima (Montagne) Kützing (1849, p. 671), (1862, p. 18, pl. 59, Figs. a–f); Adams (1994, p. 254, pl. 95); Hommersand et al. (2004a, pp. 371–377, Figs. 1–30); *Ptilota formosissima* Montagne (1842, p. 8), (1845, pp. 97–99, pl. 9, Fig. 3a–i); Harvey and Hooker (1845, pp. 190–191, pl. 17, Figs. 1–4).

Sciurothamnion De Clerck et Kraft in De Clerck et al. (2002, p. 1177).

Type species: Sciurothamnion stegengae De Clerck et Kraft in De Clerck et al. (2002, pp. 1176–1189, Figs. 1A–G, 2A–I, 3A–F, 4A–C, 5A–D, 6A–G, 7A–G).

Seiospora Harvey (1846, pl. 21).

Type species: Seiospora griffithsiana Harvey (1846, pl. 21) [= *S. interrupta* (J. E. Smith) Schmitz, [1893, p. 281]; Maggs and Hommersand (1993, pp. 118–123, Figs. 40A–H). [For additional references, see Guiry and Nic Dhonncha 2004.]

Pseudospora Schiffner (1931, p. 168).

Type species: Pseudospora adriatica Schiffner (1931, pp. 168–171, Figs. 8a–k, 9a–e).

A poorly known genus that may be a taxonomic synonym of *Seiospora*

Callithamnieae J. Agardh, Sp. Alg. 2: 4. 1851.

Thalli erect from a discoid or rhizoidal holdfast and consisting of three to four orders of indeterminate branches and two to three orders of determinate branches; axes monosiphonous and uniseriate or cylindrical to compressed and consisting of a central axis

covered by a surface layer of small, irregularly rectangular cells; axes naked or surrounded throughout by descending rhizoidal filaments, or rhizoidal filaments present only at the base, or absent. Growth of an indeterminate axis by oblique division of a uninucleate apical cell with each segmental cell initially producing a single lateral from the high side of a segmental cell; a second lateral branch absent and the branching alternate-distichous or spiral, except in *Falklandiella*, *Georgiella*, and *Diapse*, in which a second lateral is produced directly opposite or subopposite the first; rhizoidal cortication absent throughout, present only at the base or extensively developed and either forming a rhizoidal surface layer or producing a small-celled outer cortex; intercalary vegetative cells remaining uninucleate or becoming multinucleate in *Callithamnion*. Indeterminate branches transformed from the tips of determinate laterals, rarely from adventitious branchlets. Spermatangia borne in clusters on the determinate laterals with the nucleus centrally located in each spermatangium and with a mucilaginous vesicle above and below. Procarps solitary or in series, formed along the lengths of indeterminate axes or clustered near their apices. Supporting cell of the carpogonial branch cut off at right angles to a vegetative lateral with a second fertile periaxial cell opposite the first. Carpogonial branch oriented horizontally, the cells cut off by longitudinal divisions and with the carpogonium oriented vertically, cut off by a transverse division, or with the carpogonial branch sometimes cut out in a zigzag, formed by oblique divisions; sterile cells absent. Supporting cell and opposite periaxial cell extending and cutting off auxiliary cells after fertilization; the carpogonium partly cleaving into two cells without the formation of a pit connection and with each cell cutting off a small connecting cell that fuses toward the base of the enlarging auxiliary cell; the diploid nucleus dividing at the surface of the auxiliary cell with one nucleus entering and moving toward its center and the other extruded to the outside in a residual cell; each auxiliary cell cleaving into a foot cell containing the original haploid nucleus, which may divide, and a terminal gonimoblast initial; the primary gonimoblast cell first cutting off one or more terminal gonimolobe initials and later producing lateral gonimolobe initials that form the gonimolobes; basal cells of gonimolobes extending to form stalk cells, or stalk cells absent. Cystocarps naked, subtended at the base by involucreal filaments, or completely surrounded by involucreal filaments or involucreal branches. Tetrasporangia adaxial, solitary and terminal, or sessile on determinate laterals; tetrahedrally or irregularly divided; bisporangia and polysporangia known for some species.

Type genus: *Callithamnion*, Lyngbye (1819, p. 123).

The Callithamnieae presently contains: *Callithamnion* Lyngbye (1819, p. 123); *Carpothamnion* Kützing (1849, p. 668); *Aglaothamnion* Feldmann-Mazoyer (1941, p. 451); and *Hirsutithalia* Wollaston et Womersley in Womersley and Wollaston (1998, p. 250). To these four genera we add *Georgiella* Kylin (1956,

p. 391); *Falklandiella* Kylin (1956, p. 391); *Diapse* Kylin (1956, pp. 390–391), each with one species; and two new genera: *Heteroptilon* Hommersand gen. nov., with two species and *Aristoptilon* Hommersand et W. A. Nelson gen. nov., with one species.

Falklandiella Kylin 1956, p. 391 nom cons. (see Silva, 1993 and Figs. 2a, b, f in this paper).

Type species. *Falklandiella harveyi* (J. D. Hooker) Kylin (1956, p. 391); *Ptilota harveyi* in Hooker and Harvey (1845, p. 271), Hooker (1847, p. 487, pl. 187); *Euptilota harveyi* (J. D. Hooker) Kützing (1849, p. 671), (1862, p. 18, pl. 59, Figs. g–k); Taylor (1939, p. 153, pl. 6, Figs. 5 and 6); *Dasyptilon harveyi* (J. D. Hooker) Papenfuss (1958, pp. 104–105), Mendoza (1969, pp. 318–321, Figs. 19, 1–4 and 20, 5–7), Wiencke and Clayton (2002, p. 75). (For additional references, see Papenfuss, 1964, p. 49.)

Lectotype. Hermite I., Cape Horn, 1842, Mr. Robertson, Hooker at BM (= reverse of PL CLXXXVII in Hooker, 1847), selected by M. H. Hommersand, 1978 (barcode BM000640265); *Syntypes:* Maxwell Harbor, Cape Horn, 1842, Mr. Davies, Hooker at BM (barcode BM 000640267); Falkland I., 1842, Sir J. C. Ross, Hooker at BM (barcode BM000640270); Outer Sea coast, Cape Pembroke, East Falkland I., May 1842, favellae, Hooker at BM (barcode BM000640268, cystocarpic!); N. W. Bay, Hermite I., Cape Horn, TCD!; Hooker at BM (barcode BM000640269); Outer Sea coast, Cape Pembroke, East Falkland I., May 1842, TCD, two specimens, tetrasporic!; Hooker at BM, (barcode BM000650271).

Specimens examined. Drift, Rookery Bay, 7 km east of Stanley, West Falkland I., 31.xii.1997 to 5.i.1998, M. H. Hommersand, sterile (NCU); Drift, Slogget Bay, Tierra del Fuego, 16.iii.1909, C. Skottsberg, tetrasporic (UC 205731).

Georgiella Kylin (1956, p. 391 and Figs. 2c–e and g in this paper).

Type species. *Georgiella confluens* (Reinsch) Kylin (1956, p. 391, Fig. 307A), Moe and Silva (1983, pp. 275–283, Figs. 1, 5, 7, 9–12, 13, 16, 18, 20, 23–30), Wiencke and Clayton (2002, p. 76, pl.18); *Ptilota confluens* Reinsch (1888, p. 154), (1890, p. 376, pl. 3, Figs. 5–9); *Euptilota confluens* (Reinsch) De Toni (1903, p. 1373), Kylin and Skottsberg (1919, pp. 66–69, Figs. 33 and 34). (For additional references, see Papenfuss 1964, and Wiencke & Clayton 2002).

Lectotype. ‘Nordstrand de Landzunge, Pinguin Bay’ (leg.?, 3 Juli 1883, tetrasporic), Botanische Staatssammlung, Munich (M), selected by R. W. Ricker, 28.iii.1983 (barcode M-0100496). *Syntype:* HBG (See Ricker, 1987, p. 240).

Specimens examined. Drift, Bahía Skua, King George I., South Shetland Islands, Antarctic Peninsula, 6.ii.1994, S. Fredericq & M. E. Ramírez (NCU); 7 m, Laggard I. in Arthur Harbor, Anvers I., Antarctic Peninsula, 1.v.1974, R. L. Moe 449 (NCU).

Diapse Kylin (1956, p. 390) (and Figs. 3a–f in this paper).

Type species. *Diapse ptilota* (Hooker and Harvey) Kylin (1956, p. 390, Fig. 307D), Womersley (1998,

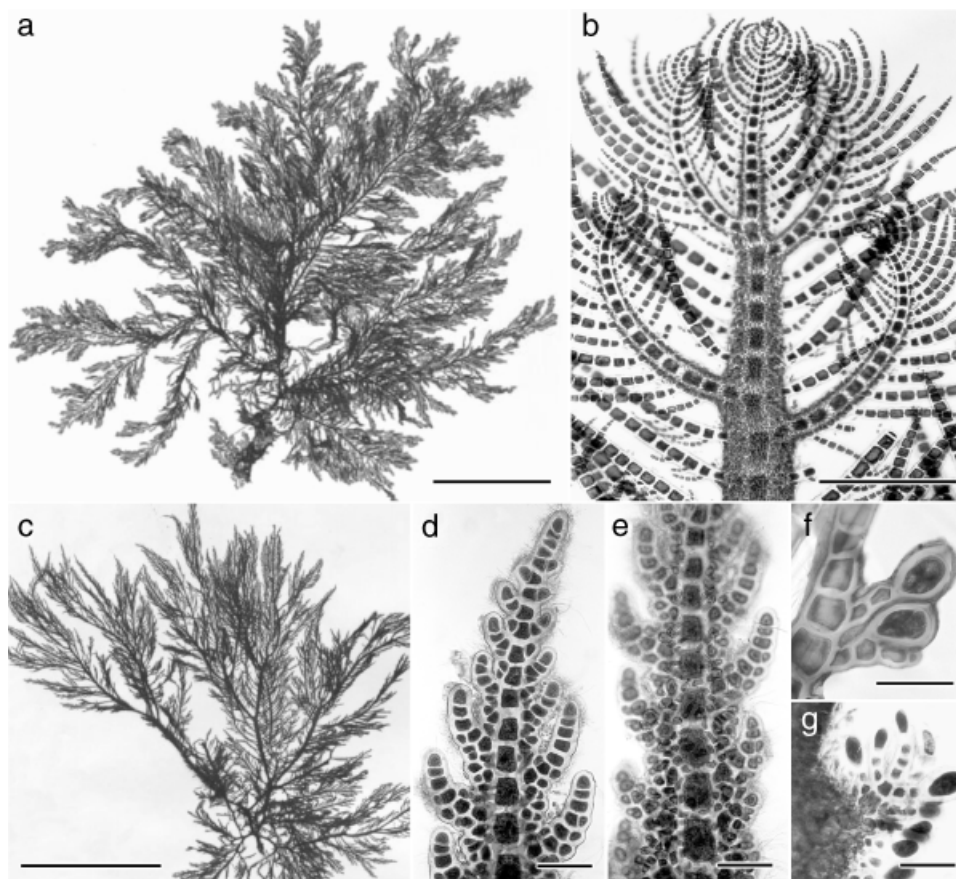


FIG. 2. *Falklandiella harveyi* and *Georgiella confluens*. (a and b) *Falklandiella harveyi*, Rookery Bay, W. Falkland I. (a) Habit. (b) Vegetative tip. (c–e) *Georgiella confluens*. (c) Habit, Bahía Skuja, S Shetland Is. (d and e) Vegetative tip, two successive views, Anvers I., Antarctic Peninsula. (f) *F. harveyi* terminal tetrasporangia, Slogget Bay, Tierra del Fuego. (g) *G. confluens*, terminal tetrasporangia, Anvers I., Antarctic Peninsula. Scale bars: a and c, 5 cm; b, 500 μ m; d and e, 50 μ m; f and g, 100 μ m. (b, d–g, aniline blue).

pp. 361–364, Figs. 167A–F); *Thamnocarpus ptilota* J. D. Hooker and Harvey (1847, p. 409); *Carpothamnion ptilota* (Hooker and Harvey) Kützing (1849, p. 669); *Ptilota jeannerettii* Harvey (1859, p. 331), (1862, pl. 198); *Euptilota jeannerettii* (Harvey) Schmitz (1896, p. 7). (For additional references, see Womersley, 1998.)

Lectotype. Port Arthur, Van Diemens Land (Tasmania), leg. D. Lyle in Herb. Hooker at BM, selected by H. B. S. Womersley (barcode BM000610844).

Specimens examined. Drift, Warrnambool, Victoria, Australia, 13.vii.1995, M. H. Hommersand & G. T. Kraft (NCU); Drift, Warrnambool, Victoria, Australia, 12.xi.1995, M. H. Hommersand & F. C. Hommersand (NCU).

***Heteroptilon* Hommersand, gen. nov.**

Plantae alternatim ramosae in unicum planitiem, uno initio laterali e quoque cellula axiali successiva, initia lateralia evolvantia in filamenta rigida, curvata, eramosa, ecorticata primo superantia axem principalem. Filamenta lateralia remanentia eramosa, vel addentia ramos irregulariter alternatimque prope apicem thalli aut solum versus basim. Cellulae basales omnis filamenti lateralis formantes initium unicum ramificans crescens circum axem formans corticem parvicellulatum 2–3-stromaticum aut producens filamenta rhi-

zoidalia cingentia axem statim; si formantes corticem externum igitur producentes filamenta rhizoidalia interna postea cingentia axem centralem. Cellulae vegetativae uninnucleatae. Procarpia genita subterminaliter vel seriatim in ramos indeterminatos transformatos ubi filamenta terminalia disposita irregulariter in caespite vice alternati-disticha; omnis cellula peraxialis producens unicum vegetativum initium laterale, cellula sustinens quadricellularis filamenti carpogonialis ad angulos rectos versus initium laterale vegetativum, denique secundam cellulam peraxialem oppositam primam; turmae steriles absentes. Gradi postfecundationis, ubi cogniti, ut in Callithamnidae; gonimoblasti typice binati compositi duo rotundatorum gonimoloborum circumcinctique serie filamentorum involucralium ramosorum exorientorum alternatim e segmentis subter interdum super segmentum fertile. Tetrasporangia divisa tetraedrice.

Species typicum: *Heteroptilon pappeanum* (Kützing) Hommersand, comb. nov. (*Euptilota pappeana* Kützing, Species Algarum, 1849, p. 671).

Plants alternately branched in one plane, with one lateral initiated from each successive axial cell, and with the laterals developing into stiff, curved, unbranched, ecorticate filaments that initially overtop the main axis. Lateral filaments remaining un-

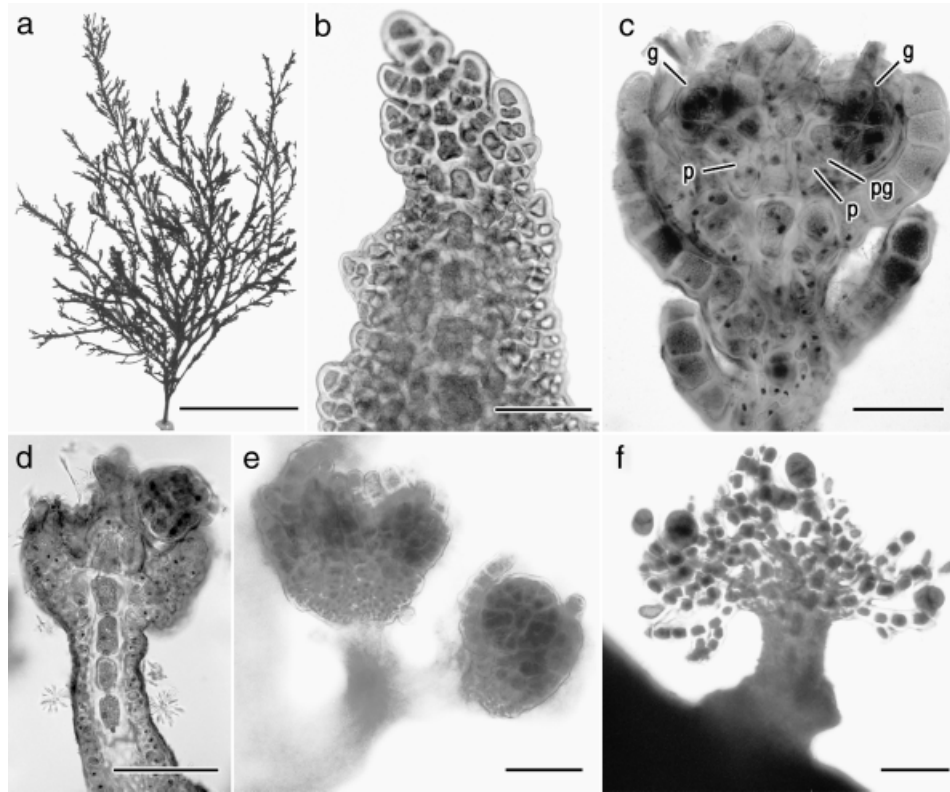


FIG. 3. *Diapse ptilota*. Warrnambool, Victoria, Australia. (a) Habit. (b) Vegetative tip. (c) Median longitudinal section of fertile tip with two fertile periaxial cells (p), two primary gonimoblast cells, one not visible (pg), and two gonimoblasts (g). (d) Median longitudinal section of fertile tip with mature and released gonimoblasts. (e) Gonimoblasts inside involucre. (f) Terminal tetrasporangia on branched stalk. Scale bars: a, 5 cm; b and c, 50 μ m; d–f, 100 μ m. (b, e, and f, aniline blue; c and d, hematoxylin).

branched, or adding branches irregularly and alternately near the thallus apex or only toward the base. Basal cells of each lateral filament forming a single initial that branches and either grows around the axis forming a small-celled two to three layered cortex or produces rhizoidal filaments that clothe the axis directly; if forming an outer cortex, then producing internal rhizoidal filaments that later envelop the central axis. Vegetative cells uninucleate. Gametophytes presumably dioecious; however, male plants unknown. Procarys borne subterminally or in series on modified indeterminate branches in which the terminal filaments are arranged irregularly in a tuft instead of being alternate-distichous; each fertile periaxial cell producing a single vegetative lateral, a supporting cell of a four-celled carpogonial branch at right angles to the vegetative lateral, and lastly a second periaxial cell opposite the first; sterile groups absent. Early post-fertilization stages, where known, as in the Callithamniae; gonimoblasts typically paired, composed of two rounded gonimolobes and surrounded by a series of branched involucre filaments arising alternately from the segments below and sometimes those above the fertile segment. Tetrasporangia in short, second series, one per cell, on the adaxial sides of unbranched filaments, or on highly branched dwarf filaments and then mostly sessile or sometimes pedicellate; mature tetrasporangia ellipsoid and tetrahedrally divided.

Type species. *Heteroptilon pappeanum* (Kützing) Hommersand, comb. nov. (*Euptilota pappeana* Kützing, Species Algaeum (1949, p. 671).

Etymology. From the Greek word *heteros*, meaning different, and the Greek word *ptilon*, for feather.

Heteroptilon pappeanum (Kützing) Hommersand, comb. nov. In: Hommersand, Freshwater, Lopez-Bautista and Fredericq [Figs. 4a–c, 5a–i and 6a–i].

Euptilota pappeana Kützing, Species Algaeum (1849, p. 671), (1862, p. 18, pl. 60, Figs. a–c); Stegenga et al. (1997, pp. 429–431, pl. 166, Figs. 1 and 2). *Ptilota pappeana* J. Agardh (1851, p. 100). *Rhodocallis setigera* Kützing (1849, p. 670), (1862, p. 18, pl. 57, Figs. e–h).

Lectotype of *Euptilota pappeana*. One of two specimens on a sheet in Leiden, L.937, 273–307 labeled (scr. Kützing): *Euptilota Papeana* KG (sic!), Tab. Phyc. XII, 60, C.B.S selected by Willem Prud'homme van Reine (barcode L539673), labeled C.B.S., *Ptilota pappeana* J. Ag. MSS, Tafelbay, 75.

Holotype of *Rhodocallis setigera*. Fragments in Leiden (barcode L539674) labeled *Rhodocallis setigera* Kg, Tab. Phyc. XII, 57. Cap, and also *Ptilota setigera* Harv. and *Rhodocallis*, Cap (in pencil by Kützing). The words “Type” and the identification “*Euptilota pappeana*” are added.

Specimens examined. Drift, Kommetjie, Cape Peninsula, South Africa, 24.i.2001, O. De Clerck (NCU).

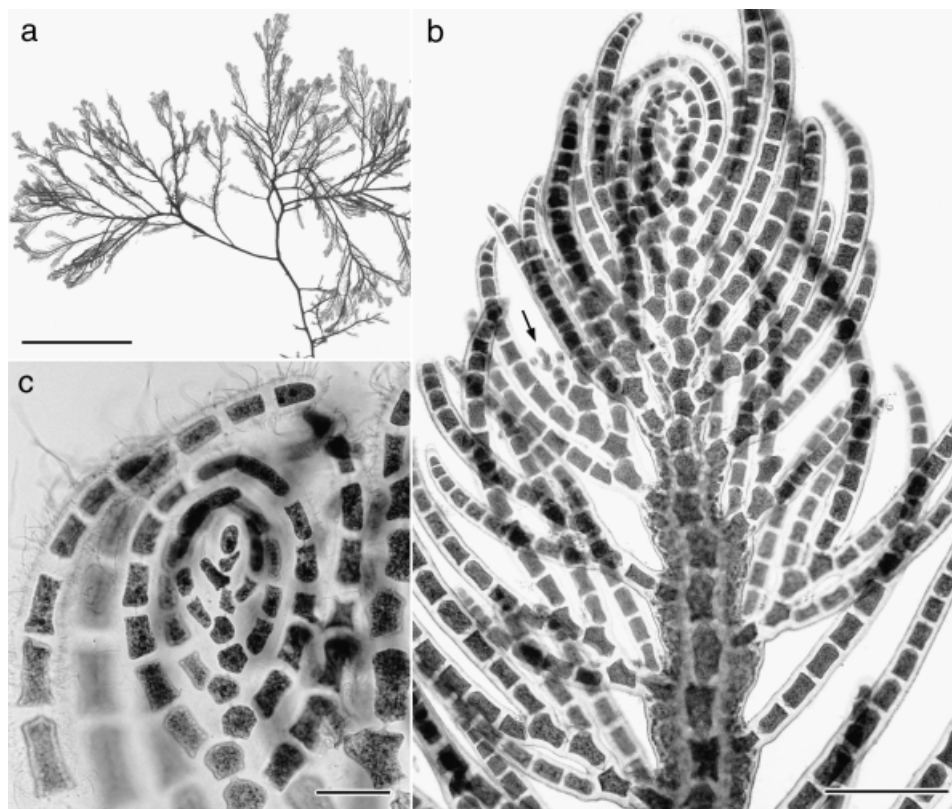


FIG. 4. *Heteroptilon pappeanum*, Kommetjie, Cape Peninsula. (a) Habit. (b) Vegetative tip showing lateral filaments and cortication. Arrow points to a developing indeterminate branch. (c) Vegetative apex. Scale bars: a, 2 cm; b, 200 μm , c, 100 μm . (b and c, aniline blue).

Drift, Olifantsbos, Cape Peninsula, South Africa, 7.ix.1983, M. H. Hommersand (NCU).

Description. Plants are rose-red with a grayish tinge, attached to solid substratum by a discoid holdfast, solitary, erect, up to 20 cm tall, alternately branched in one plane, and consisting of up to six orders of indeterminate and determinate branches that are not formed in a fixed sequence. Branching is initially pinnate, although most indeterminate branches reach the same length as the main axis, with the result that the branching often appears to be subdichotomous (Fig. 4a). Branches are clothed with stiff, alternately arranged ecorticate lateral filaments that persist in the last two to three orders of branches, but are ultimately deciduous. These may be unbranched, may bifurcate, or may be alternately branched from one to four (5) successive segments (Fig. 4b). Axes are compressed in the plane of branching and oval to circular in cross-section, with the central file of axial cells surrounded by an inner layer of larger cells and two outer layers of small cells. Longitudinally oriented rhizoidal filaments envelope the central axis beginning with the penultimate branches. All cells are uninucleate.

Growth of an indeterminate axis takes place by oblique division of the apical cell with the high sides of successive axial cells alternately offset and elongating before cutting off the initials of the determinate laterals (Fig. 4c). Axial cells are nearly

isodiametric and slightly offset in a zigzag near the apex (Figs. 4b and c). They elongate below to become about twice as long as broad approximately 20 segments below the apex. Branching is strictly alternate-distichous. Young laterals curve upwardly and overtop the apical cell (Fig. 4c). Vegetative laterals are ecorticate, except for the basal cells, and are either unbranched and setaceous with acute tips or branched from the lower one to four (5) segments. When present, the basal segment bears an adaxial branch, the second segment an abaxial branch, the third an adaxial branch, and the fourth an abaxial branch (Fig. 4b). Laterals may develop in any sequence on an unbranched lateral filament, although the first branch is most commonly formed from the second segment. Growth normally ceases after four branches have been produced and all segments, except the basal segment, remain ecorticate, or the tip may convert to regular alternate-distichous branching and give rise to a potentially indeterminate branch or a branch of limited growth (Fig. 4b, arrow).

There is no sharp distinction between indeterminate branches and determinate branchlets. Both originate by the conversion of an apical cell or branch initial to a pattern of regular alternate-distichous branching. In actively growing tips such branches typically form near the apex from the terminal segment of an ecorticate filament four to five segments distal to the

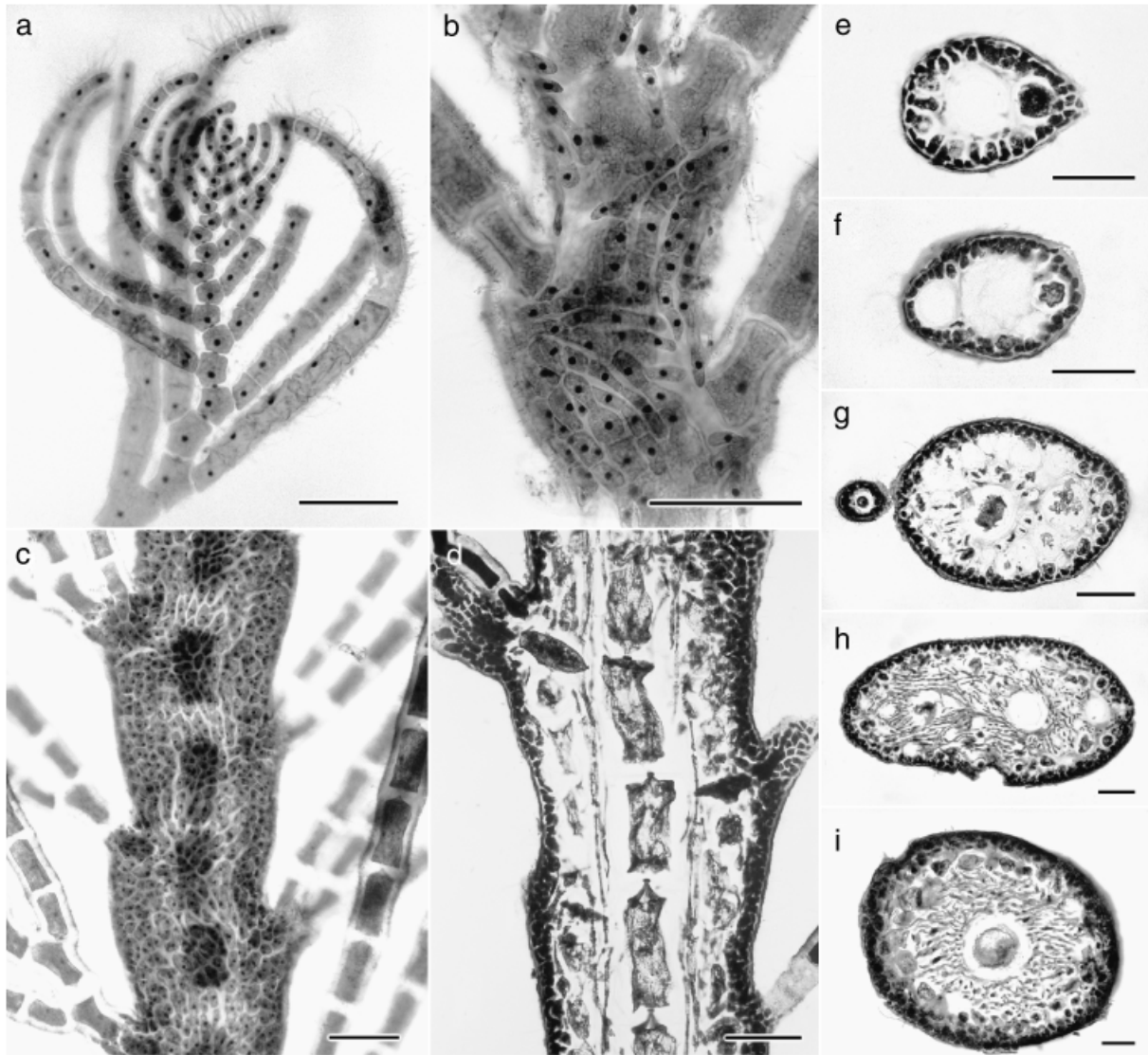


FIG. 5. *Heteroptilon pappeanum*, Kommetjie, Cape Peninsula. (a) Initiation of an indeterminate branch. (b) Axis and laterals with developing cortex. (c) Corticated axis and lateral filaments. (d) Median longitudinal section of corticated axis. (e–i) Cross-sections of axis at different levels. (e and f) Near tip. (g) Middle of axis. (h) Lower axis at branching point. (i) Near base. Scale bars: a–i, 100 μm . (a–c, hematoxylin; d–i, aniline blue).

basal cell (Fig. 5a). Alternatively, they may form adventitiously from the basal cells of deciduous ecorticate filaments or from their terminal cells, or from the tips of deciduous corticated branchlets. Laterals that have converted to normal alternate-distichous branching ultimately become corticated in the same manner as the main axis.

Cortical filaments issue singly from the basal cells of ecorticate lateral filaments beginning eight to ten segments below the apical cell. At first they grow downward for the length of two segments and branch on opposite sides from each segmental cell. The opposite branches formed in this fashion spread across the nodal axial cell and the cell below and some filaments turn upward to meet the filaments descending from the node above (Fig. 5b). Some of the filaments also turn upward and enclose the basal cell of the otherwise

ecorticate lateral (Figs. 4b and 5c). The cortical filaments initially form a single layer; however, each cortical cell cuts off small rectangular and triangular cells from its sides and corners producing short, branched filaments that align in one to two layers next to the innermost layer (Fig. 5c). At first the cortical layers are densest in the nodal region above the axial cells and less dense in the internodal region where ascending and descending filaments meet. The result is a banding pattern with dark areas above the axial cells and lighter lines in between (Fig. 5c). This distinction disappears as more layers of cells are added to the internodal regions. The three or so proximal cortical cells that form a file alongside the axial cell directly below the basal cell of an ecorticate lateral filament elongate and expand to a greater degree than any of the other cortical cells (Fig. 5d). As a result the axis is broader in

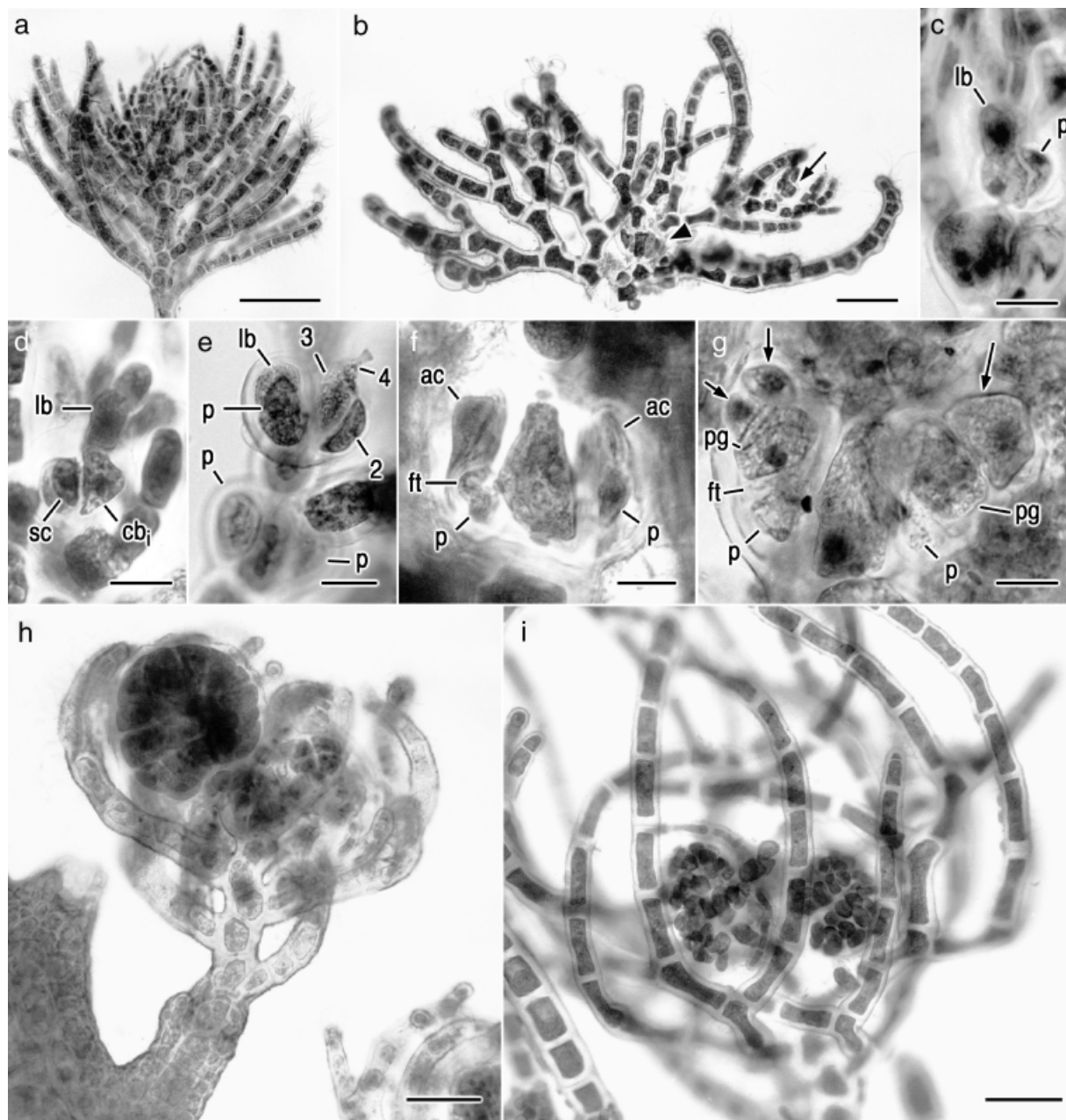


FIG. 6. *Heteroptilon pappeanum*. Olifantsbos, Cape Peninsula. (a) Densely branched tip of female plant. (b) Squash of tip showing young procarp (arrow), early postfertilization stage (arrowhead), and branched involucrel filament (left-hand side). (c–g) Developing procarps and cystocarps. (c) Tip with periaxial cell (p) at right angles to lateral branch (lb). (d) Tip with supporting cell (sc), carpogonial branch initial (cb_i), and lateral branch (lb). (e) Two successive fertile axial cells, one below with two periaxial cells (p), and one above with cells 2, 3, and 4 of the carpogonial branch, a periaxial cell (p) and a two-celled lateral branch (lb) underneath. The carpogonium (4) bears a rudimentary trichogyne. (f) Optical section of axial cell bearing two fertile periaxial cells (p) and two auxiliary cells (ac). A foot cell (ft) is seen on the left. (g) Optical section of axial cell bearing two fertile periaxial cells (p) and two primary gonimoblast cells (pg), with two terminal gonimolobe initials seen on the left and one on the right (arrows). A foot cell (ft) is visible on the left. (h) Young cystocarp with developing gonimoblasts surrounded by branched involucrel filaments. (i) Mature cystocarp with paired gonimoblasts surrounded by branched involucrel filaments. Scale bars: a and b, h and i, 100 µm; c–g, 20 µm. (a, b and i, aniline blue; c–h, hematoxylin).

the plane of branching than in the transverse plane, and cross-sections tend to be oval rather than circular, especially at the nodes (Figs. 5e–i). Cross-sections made at a node often show three large cells (Figs. 5f and h) corresponding to the three axes illustrated by Kützing (1862, pl. 60, Fig. 2) for *Euptilota pappeana*, whereas

sections through the internode usually show a single large central cell (Figs. 5e, g, i) that corresponds to the single axis illustrated by Kützing (1862, pl. 57, Fig. h) for *Rhodocallis setigera*. Rhizoidal filaments originate from subcortical cells and descend in parallel arrays alongside the axial cells (Fig. 5d). They are absent in

the ultimate branches (Figs. 5e, f), few in number in the penultimate branches (Fig. 5g), become increasingly more numerous lower down, where they traverse from the side branches into the main axis (Fig. 5h), and form a solid core between the inner cortical cells and the central axis toward the base (Fig. 5i).

Gametophytes are presumably dioecious, although male plants were not seen. The tips of female plants are brush like as a result of a shift from alternate-distichous to irregularly spiral branching (Fig. 6a), in which each cluster contains several fertile branchlets. Most axial segments in a fertile tuft produce ecorticate lateral filaments that branch subdichotomously, with up to five orders of branches, which become more robust after fertilization (Fig. 6b, left-hand side). Procarps form toward the tips of potentially indeterminate branches and arise intermittently, alternately, or successively from segments along the axis (Figs. 6a–e). In this way, large numbers of procarps may be produced in succession, ceasing only when one has been fertilized or a young cystocarp has begun to develop. At maturity, fertile branchlets bear cystocarps subterminally surrounded by branched, ecorticate involucreal filaments (Figs. 6h, i). Carpogonial branches are initiated within three to four segments from the apex (Figs. 6b–d). A fertile axial cell forms a vegetative lateral followed by a single periaxial cell oriented at approximately a 90° angle with respect to the associated vegetative lateral (Fig. 6c). The periaxial cell serves as a supporting cell and divides longitudinally to produce a carpogonial branch initial (Fig. 6d), which, in turn, divides longitudinally twice to produce first a two-celled and then a three-celled carpogonial branch. Finally, the third cell divides transversely or diagonally to initiate a carpogonium and trichogyne (Fig. 6e). The trichogyne had not elongated in any of the carpogonia observed, and attached sperm were not seen. A second periaxial cell is cut off opposite the first once the carpogonial branch has fully formed (Fig. 6e). A carpogonial branch breaks down and disappears in the absence of fertilization and its former position along an axis is indicated by the presence of the two persistent, opposite periaxial cells perpendicular to the lateral branch (Fig. 6e). Paired periaxial cells are seen intermittently over long distances in some axes, indicating that procarps continue to be produced on the same axis as long as fertilization has not taken place.

After fertilization, the supporting cell and the opposite periaxial cell each cut off an auxiliary cell, which, in turn, cuts off a foot cell (Fig. 6f). The events associated with the transfer of the diploid nucleus to the auxiliary cell were not seen. A broad supporting cell, a narrow foot cell and a large primary gonimoblast cell bearing gonimolobes were seen in several instances. In one case, the primary gonimoblast cell bore two terminal gonimolobe initials on one side and an undivided gonimolobe initial on the other side (Fig. 6g). Both large and small gonimolobes in different stages of development were common (Fig. 6h). Paired spherical gonimoblasts composed of fused gonimolobes were

also frequent (Fig. 6i). In all instances, the gonimoblasts were surrounded by branched ecorticate involucreal filaments derived from four to six successive segments situated below the fertile segment. No involucreal filaments were produced above the gonimoblasts.

Tetrasporangial plants were not seen in this study; however, Stegenga et al. (1997, pl. 106, Fig. 2) illustrated tetrasporangial plants in which the tetrasporangia were terminal or lateral on much branched ecorticate filaments in older parts of the thallus. The tetrasporangia were ovoid and tetrahedrally divided.

Heteroptilon rigidulum (De Clerck, Bolton, R. J. Anderson et Coppejans) Hommersand et De Clerck, comb. nov. *In*: Hommersand, Freshwater, Lopez-Bautista and Fredericq.

Aglaothamnion rigidulum De Clerck, Bolton, Anderson et Coppejans *In*: De Clerck, O., Bolton, J. J., Anderson, R. J. & Coppejans, E. (2004) *Aglaothamnion rigidulum* nov. spec. (Rhodophyta, Ceramiaceae) from South Africa. *Botanica marina* 47: 431–436.

Description. See De Clerck et al. (2004). Comparison of an *rbcL* sequence for *H. rigidulum* provided by O. De Clerck with that of *H. pappeanum* showed that the two species varied at 42 of 1311 compared sites (3.2%).

Aristoptilon Hommersand et W. A. Nelson, gen. nov.

Plantae alternatim ramosae in unicum planitiem, uno initio laterali e quoque cellula axiali. Filamenta lateralia ecorticata, initio ramificantia e primis, tertiis quinque segmentis, sed addunt ramos postea ad interjacentia segmenta eramosa; rami lateralia in axialibus principales toti convertantes ad ramificationem alternati-distichum omnes efferentes ramulum determinatum corticatum vel ramum indeminatum. Cellulae basales omnes filamentorum lateralium formantes initium unicum crescens ramificansque circum cellulas axiales formans corticem bistratosum. Filamenta rhizoidalia emanantia e strato corticali externo crescentia intime deorsunque, cingentia axem centralem. Cellulae vegetativae uninucleatae. Gametophyti dioecii. Filamenta spermatangialia formantia fasciculum unicum dense filamentorum ramosorum multistromaticorum tectorum pallio spermatangiorum; omne spermatangium continens nucleum medialem subtentum vesicula mucosa terminalia proximaliaque. Procarpia genita subterminaliter in pumilos ramos determinatos, unica in ramum fertilem; omnis cellula axialis fertilis producens unicum vegetativum initium laterale, cellula sustinens quadricellularis filamentum carpogoniale ad angulos 45° versus axem initii lateralis vegetativi, denique secundam cellulam periaxialem oppositam primam. Gradi postfecundationis ut in Callithamniae; gonimoblasti initia omnia abscissa duo initia terminalium gonimoloborum cuorum filamentorum conjungentium enim producere gonimolobum terminalem unicum gonimolobis terminalibus formatis postea. Gonimoblasti tecti basaliter per canistrum filamentorum parvicellularium formatorum in cellulam axialem fertilem circumcincti involucreo filamentorum eramo-

sorum exorientium cellula axiali fertili aliquotque infra cellularum axialium. Tetrasporangia in pumilos ramos genita in ecorticata lateralibus filamenta in ramulos determinatos; tetrasporangia divisa tetraedrice.

Species typicum. *Aristoptilon mooreanum* (Lindauer) Hommersand et W. A. Nelson comb. nov. (*Euptilota mooreana* Lindauer, 1949, p. 391).

Plants alternately branched in one plane, with one lateral initiated from each successive axial cell and forming a curved filament that overtops the main axis. Lateral filaments ecorticate, initially branching from the first, third, and fifth segments, but adding branches later to the intervening unbranched segments; laterals on main axes all converting to alternate-distichous branching and each producing a corticated determinate branchlet or an indeterminate branch. Basal cells of lateral filaments each cutting off a single initial that grows and branches around the axial cells to form a two-layered cortex, with the inner layer composed of larger cells and the outer layer of smaller cells; rhizoidal filaments issuing from the outer cortical layer and growing inward and downward, enveloping the central axis. Vegetative cells uninucleate. Gametophytes dioecious. Spermatangial filaments typically developing from two initials on the adaxial sides of cells of the ultimate or penultimate branches of lateral filaments and forming a single cluster of densely branched filaments several cell layers thick covered by a mantle of spermatangia; each spermatangium containing a median nucleus and terminal and proximal mucilaginous vesicles. Procarps formed subterminally on dwarf determinate filaments, one per fertile branch; each fertile axial cell producing a single vegetative lateral, a supporting cell of a four-celled carpogonial branch at a 45° angle to the axis of the vegetative lateral, and lastly a second periaxial cell opposite the first. Early postfertilization stages as in Callithamnieae; gonimoblast initials, each cutting off two terminal gonimolobe initials whose filaments unite to form a single terminal gonimolobe with lateral gonimolobes formed later. Gonimoblasts covered basally by a basketwork of small-celled filaments produced on the fertile axial cell and surrounded by an involucre of unbranched filaments arising from the fertile axial cell and several of the axial cells below. Tetrasporangia one per cell, and terminal or lateral on dwarf branches borne on ecorticate lateral filaments in determinate branchlets; mature tetrasporangia obovoid, tetrahedrally divided.

Type species. *Aristoptilon mooreanum* (Lindauer) Hommersand and W. A. Nelson comb. nov. (*Euptilota mooreana* Lindauer, 1949, p. 391).

Etymology. From the Greek word *aristos*, meaning best, and the Greek word *ptilon*, for feather.

Aristoptilon mooreanum (Lindauer) Hommersand et W. A. Nelson, comb. nov. *In:* Hommersand, Freshwater, Lopez-Bautista and Fredericq. [Figs. 7a–i, 8a–j, 9a–l]

Euptilota mooreana Lindauer (1949, Transactions of the Royal Society of New Zealand, vol. 77, part 3, pp.

391–392, pl. 38, Figs. 13–14; pl. 40, Fig. 19); Adams (1994, p. 255, pl. 95, upper right).

Lectotype. Pihama, Taranaki, North Island, New Zealand, 13.iv.1946, V. W. Lindauer (AK 46) (See Nelson & Phillips 1996)

Paratype. Pihama, Taranaki, North Island, New Zealand, 22.ii.1946, V. W. Lindauer, Algae Nova-Zelandicae Exciccatae, No. 273. (See Nelson & Phillips 1996)

Specimens examined. On *Pterocladia lucida*, Kapowairua, NE end of Te Horo Beach, Spirits Bay, Far North, New Zealand, 26.x.2003, W. A. Nelson, ASD 206, female. On *Pterocladia lucida*, Shipwreck Bay, Ahipara, Far North, New Zealand, 13.xi.2004, D.W. Freshwater, NZ04-470, male, female (NCU). On *Sarcothalia marginifera*, Erangi Pt., Bethels Beach, North Island, New Zealand, 14.xi.2004, D.W. Freshwater NZ04-483, female, tetrasporic (NCU). Pihama, Taranaki, North I., New Zealand, 13.iv.1946, V.W. Lindauer (AK 46). Pihama, Taranaki, North I., New Zealand, 22.ii.1946, V. W. Lindauer, ANZE 273 (UC 735861, male), (NCU, tetrasporangial). Drift, Campbells Beach, Taranaki, North I. New Zealand, 10.ii.1947, L. B. Moore (UC 761025). On *Pterocladia lucida*, Allan's Beach, Pihama, Taranaki, New Zealand, 27.ii.1945, V. W. Lindauer 5687, male (AK). On *Pterocladia lucida*, Oeo Beach, Pihama, Taranaki, New Zealand, 12.vii.1945, V. W. Lindauer 6085, male, tetrasporic (AK).

Description. Plants are rose-red to red-purple in color, epiphytic, attached by a rhizoidal holdfast, and consist of one to several erect axes up to 20 cm tall, although commonly much smaller. Indeterminate axes branch irregularly two to four times in one plane, often from the same side of the axis, and bear distichously arranged branchlets alternately from successive axial cells. These are variable in length, with the shorter ones about 1 mm long and the longer ones approaching the length of young indeterminate branches. Branchlets stand 1 mm apart, with the shorter ones giving the plant a banded appearance (Fig. 7a). Axes are circular to broadly oval in cross-section, with the central file of axial cells surrounded by a two-layered cortex consisting of a large-celled inner layer and a small-celled outer layer in the ultimate branches (Fig. 7g). They are interspersed by rhizoidal filaments in the mid-region (Fig. 7h), and the rhizoidal filaments coalesce to form a core around the central axis toward the base (Fig. 7i). Rhizoidal filaments orient longitudinally in parallel arrays that appear as fine lines in optical longitudinal section (Fig. 7f).

Growth of an indeterminate axis takes place by oblique division of the apical cell with the high sides of successive axial cells alternately offset and elongating to initiate the determinate lateral filaments. Arrangement of the lateral filaments is not strictly planar. If two successive laterals are deflected toward the viewer, the next two recede into the background, and so on (Fig. 7b). Axial cells are initially aligned in a zigzag near the apex (Figs. 7b and c). As they elongate and inflate, the axis straightens and the lateral branches line up in a

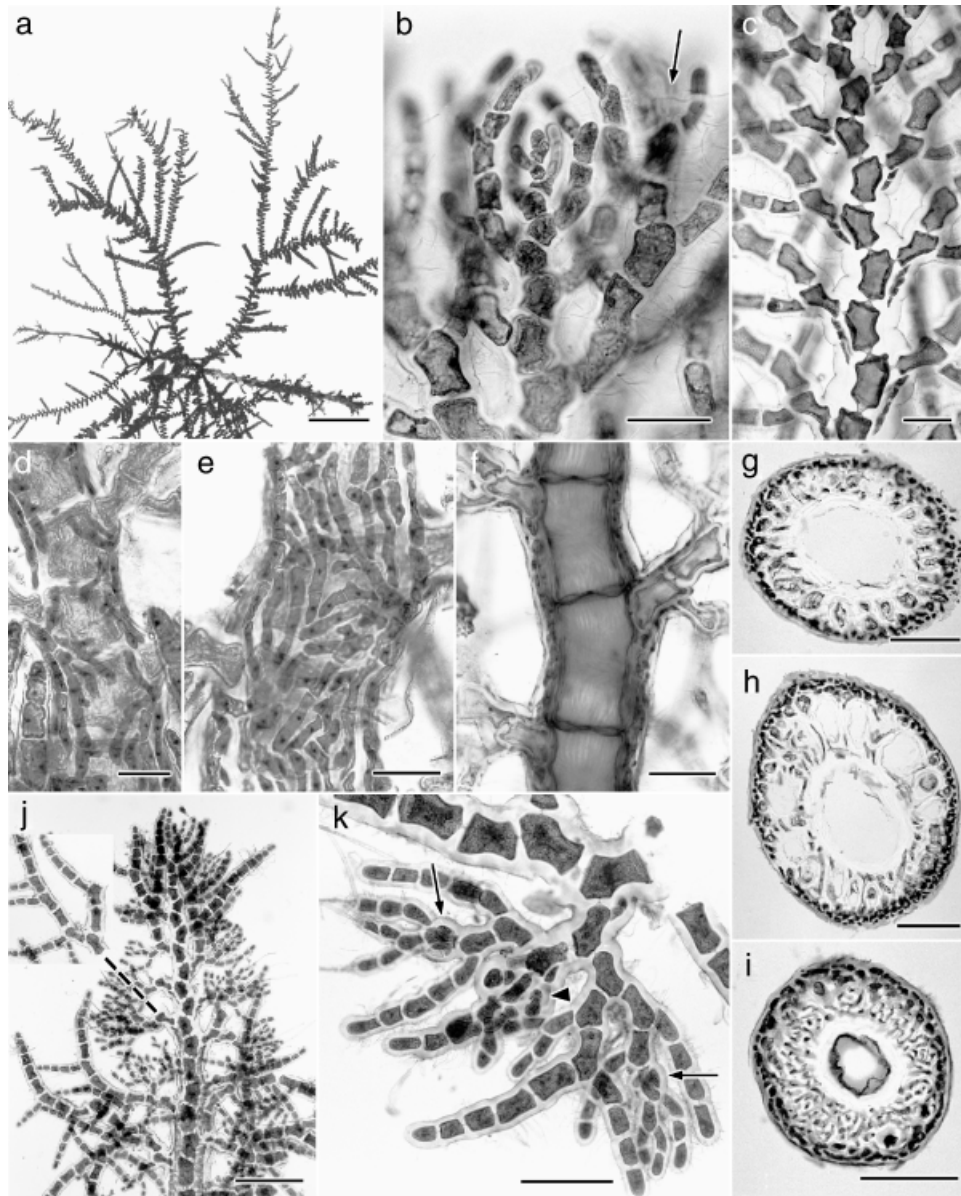


FIG. 7. *Aristoptilon mooreanum*. (a) Habit of male plant, Lindauer, No. 273, Pihama, Teranaki Bight (UC 735861). (b–k) Vegetative anatomy, Ahipara, Far North, NZ. (b) Vegetative tip showing alternate branching in and out of plane of view. A lateral indeterminate branch is seen on the right (arrow). (c) Zigzag axis near tip showing lateral filaments and young cortical filaments. (d) Axis near tip showing branching of cortical filaments. (e) Axis a little below that in (d) surrounded by cortical filaments. (f) Optical section of axis in middle of thallus. The fine lines seen in surface view are images of longitudinally oriented rhizoidal filaments. (g–i) Cross-sections of axis. (g) Two-layered cortex below apex. (h) Two-layered cortex and rhizoidal filaments midway down axis. (i) Cortex and rhizoidal filaments near base of axis. (j) Determinate branchlet on female plant bearing ordinary and dwarf lateral filaments. A detached vegetative filament is seen on the left (dashed line). (k) Fertile dwarf filaments originating from the basal cell of ecorticate vegetative lateral, showing location of prefertilization (arrows) and postfertilization (arrowhead) female stages. Scale bars: a, 2 cm; b–e and g–i, 50 μm; f and j, 200 μm, k, 100 μm. (b, c, and g–k, aniline blue; d–f, hematoxylin).

plane. Initially slightly broader than long, the axial cells elongate rapidly to become about twice as long as broad. Young laterals curve upwardly and overtop the apical cell (Fig. 7b). Initially unbranched, the lateral filaments branch abaxially from the first, third, and fifth segments, and sometimes the seventh and ninth segments, beginning five to six segments below the apex. Laterals that will become indeterminate branch-

es rapidly shift to an alternating pattern of growth with new branches forming from each successive segment (Fig. 7b, arrow). All other laterals on main axes form branches of limited growth (branchlets). Branchlets develop from ecorticate lateral filaments by a process in which adaxial laterals develop from unbranched segments situated between the segments that bear the abaxial branches. Once this stage is completed, the

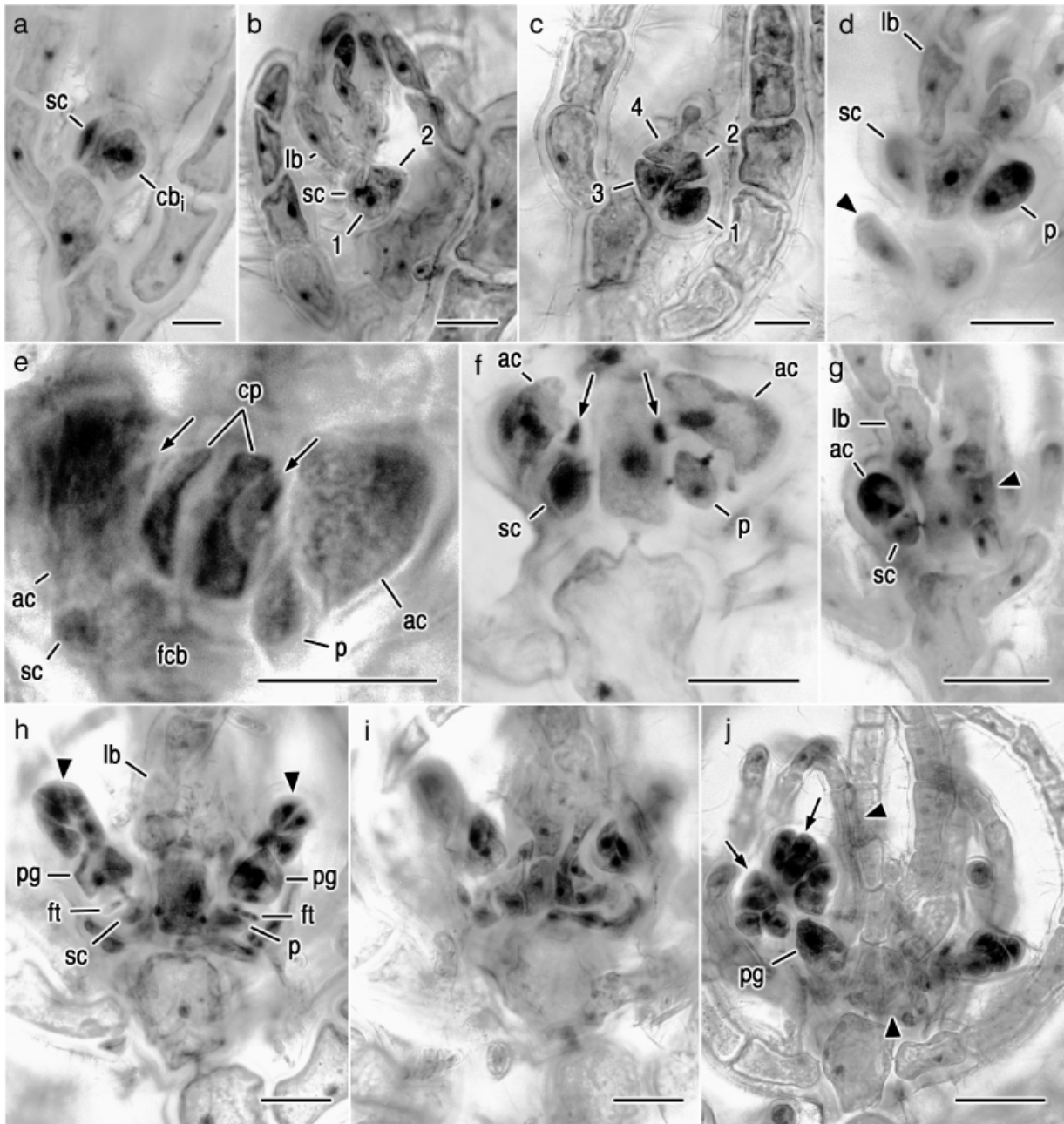


FIG. 8. *Aristoptilon mooreanum*. Procarys and young cystocarps. Material as follows: (a–d) Point Erangi, Bethels, North Island; (e) Hooper Point, Spirit Bay, Far North; (f–j) Ahipara, Far North. (a) Supporting cell (sc) and a one-celled, binucleate carpogonial branch initial (cb_i). (b) Tip with fertile axial cell bearing a lateral branch (lb), a supporting cell (sc), and a two-celled carpogonial branch (1, 2). (c) four-celled carpogonial branch (1–4) showing the carpogonium (4) with a developing trichogyne. (d) Procaryp seen from the backside showing a supporting cell (sc) and fertile periaxial cell (p) and a vegetative lateral branch (lb). Note involucrel branch initial originating from the hypogynous axial cell (arrowhead). (e) Early post-fertilization stage showing a divided carpogonium (cp), two connecting cells (arrows), a supporting cell (sc), and fertile periaxial cell (p), and two auxiliary cells (ac). Remnants of the fused carpogonial branch (fcb) are still visible. (f) Stage after the connecting cells have fused with the auxiliary cells showing a supporting cell (sc) and fertile periaxial cell (p), and two auxiliary cells (ac). Two daughter nuclei have entered the auxiliary cells and two are extruded inside residual cells (arrows). (g) View from the backside of an axial cell bearing a lateral branch (lb) at a 45° angle with respect to the supporting cell (sc), which bears an auxiliary cell (ac). The fertile axial cell also bears an adventitious branched filament (arrowhead) that will form the filamentous network around the base of the gonimoblasts. (h) Optical section showing an axial cell bearing a pair of opposite gonimoblasts and a lateral branch (lb). The supporting cell (sc) and fertile periaxial cell (p) at the base are each connected to a foot cell (ft) and a primary gonimoblast cell (pg), and gonimolobes (arrowheads), each of which are composed of two gonimolobe filaments. (i) Optical section of axis seen in (h) at a level showing the network of small-celled filaments formed around the base of the gonimoblasts. (j) Paired opposite gonimoblasts. A primary gonimoblast cell is seen on the left bearing two gonimolobe filaments (arrows). An involucrel filament and filamentous network (arrowheads) originates from the fertile axial cell after fertilization. Other involucrel filaments formed after fertilization derived from the hypogynous cell below the fertile axial cell. Scale bars: a–i, 20 μm, j, 50 μm. (a–j, hematoxylin).

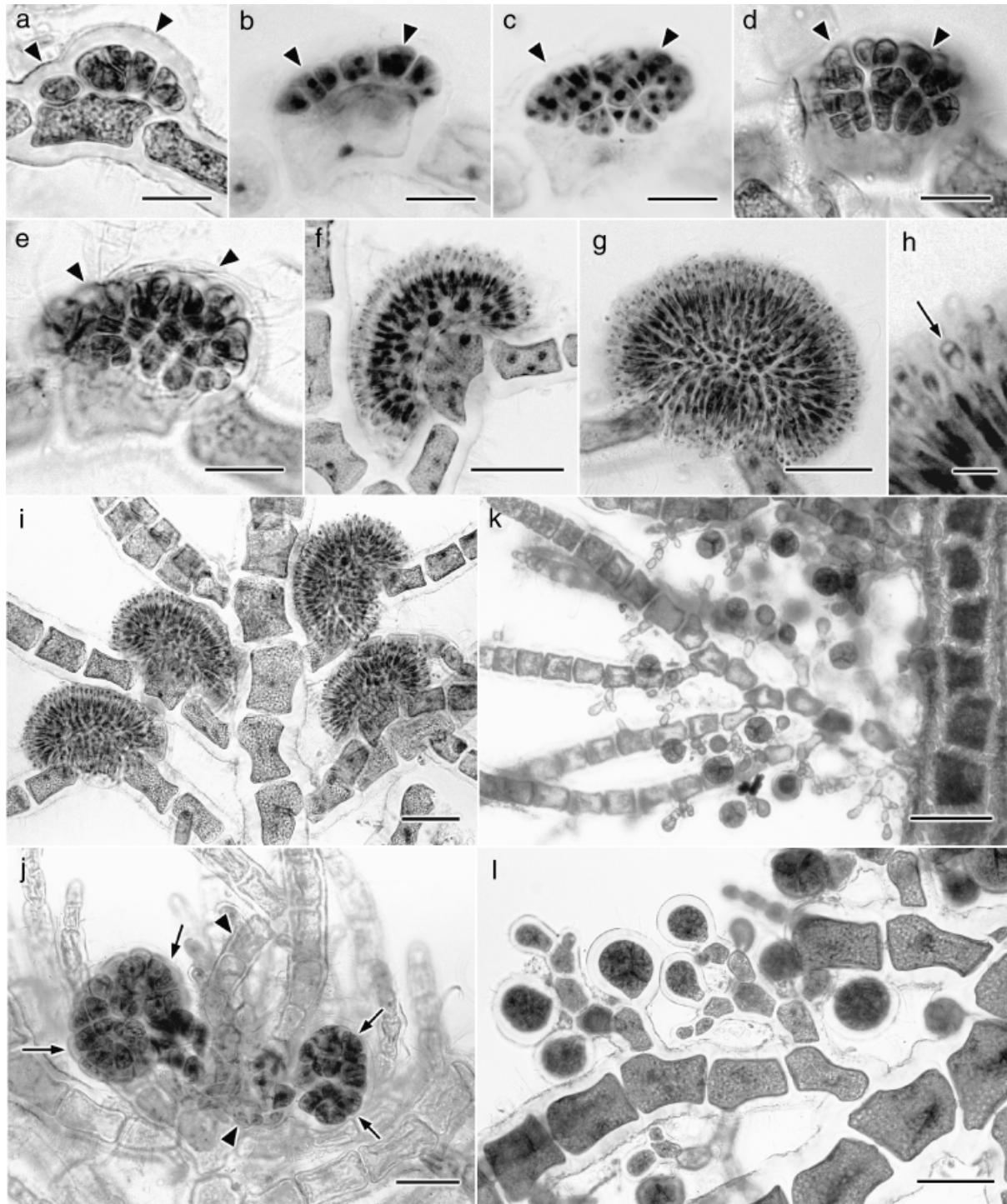


FIG. 9. *Aristotilium mooreanum*, stages from male, female and tetrasporangial plants. (a–i) Development of spermatangial filaments and spermatangia in male plants, Ahipara, Far North. Figs. (a–g) oriented to show the distal portion to the right and the proximal portion to the left. (a) Cell bearing a spermatangial filament (arrowhead on right) and a filament initial (arrowhead on left). (b and c) Distal and proximal spermatangial filaments oriented as in (a). (b) View in optical section. (c) Surface view. (d) Surface view of spermatangial filaments showing apical initials and branching. (e) Later stage before initiation of the spermatangia. (f) Optical section showing cluster of spermatangial filaments bearing a mantle of spermatangia. (g) Surface view of cluster of spermatangial filaments and mantle of spermatangia. (h) Enlarged view of a spermatangium (arrow) with a median nucleus and apical and basal muscilaginous vesicles. (i) Ecorticate filaments bearing spermatangial clusters on the ultimate branches. (j) Maturing cystocarp containing a pair of gonimoblasts surrounded by unbranched involucre filaments and filamentous network arising from the fertile axial cell (arrowheads) and involucre filaments coming from the axial cells below, Ahipara, Far North. The spherical gonimolobes each consist of two branched filaments (arrows) in which most of the cells are converted into carposporangia. (k and l) Dwarf tetrasporangial branchlets on ecorticate lateral filaments, Erangi Pt., Bethels, North I. (k) Corticated axis and ecorticate lateral filaments bearing dwarf branchlets with tetrasporangia. (l) Enlarged view of lateral filaments showing dwarf fertile branchlets bearing sessile, lateral tetrahedrally divided tetrasporangia. Scale bars: a–e, 20 μ m; f, g, i, j, and l, 50 μ m; h, 10 μ m; k, 500 μ m. (a, e, i, k, and l, aniline blue; b–d, f–h, and j, hematoxylin).

terminal cells shift to alternate branching similar to that seen in indeterminate branches. The principal difference between determinate branchlets and indeterminate branches is that the growth of the determinate branchlets soon ceases. Although the length of a branchlet is variable, most reach a length of no more than 1 mm. In general, only the determinate branchlets become fertile in male, female and tetrasporangial plants.

Potential indeterminate branches form at irregular intervals along an axis, although there is a tendency for the branching to be pectinate with successive indeterminate branches formed abaxially in rows (Fig. 7a). A lateral that has ceased growing does not convert later into an indeterminate branch, and there is no evidence that indeterminate branches arise adventitiously. Indeterminate branches and determinate branchlets become corticated in the same manner, except that the onset of cortication of a determinate branchlet is often delayed. Initials of the cortical filaments arise singly from the basal cells of the ecorticate lateral filaments beginning approximately 10–12 segments below the apical cell. The filament formed from a cortical initial grows downward within the outer cuticular layer (Fig. 7c). Proximal segments of cortical filaments branch from their tips on both sides (opposite branching); however, the branching becomes irregularly alternate as the filaments become crowded. The initial filament grows downward along one side of the axial cell for a distance of two segments and sends out laterals that spread across the face of the axial cell on both sides (Figs. 7d and e). A few branches are deflected upward and grow acropetally (Fig. 7e). Cortical filaments derived from a single initial extend across the axis for a distance of approximately two segments below and one-half segment above its attachment point. The cortex is initially only one cell layer thick. Once the axis is completely covered, cortical cells cut off smaller cells from their sides and corners to form a second, outer layer. Cells in the outer layer continue to divide and grow and spread over the inner cortical cells as the axial cells expand in circumference and grow in length; however, the cortex essentially remains two-layered throughout. Ultimately, cells in the outer cortex initiate rhizoidal filaments that grow between the cells of the inner cortex to reach the axial cell, where they are deflected downward and grow longitudinally parallel to one another (Fig. 7f), increasing in number (Fig. 7i) toward the base of the plant, where many emerge and penetrate between the host cells, anchoring the epiphyte firmly to the host.

Gametophytes are dioecious or sometimes andromonoecious with procarys present on male plants. These may not be functional, in as much as post-fertilization stages were not seen on male plants. Female plants are about the same size as tetrasporangial plants, whereas the male plants tend to be smaller. Fertile branches in male plants are isomorphic with the ecorticate lateral vegetative filaments that bear them, with cells all approximately the same size (Fig. 9i). In con-

trast, the fertile branches in female and tetrasporangial plants are dimorphic, composed of narrower and shorter cells than those of ordinary vegetative filaments. Branches that bear the procarys and cystocarys, and those that bear the tetrasporangia consist of cells about 1/2 the diameter and 1/2 the length of comparable vegetative cells (Figs. 7j and k and 9k and l).

Procarys are restricted to determinate branchlets and are only rarely found at the tips of indeterminate branches that have ceased growing. The narrow, short-celled filaments that bear the procarys appear to arise secondarily from unbranched segments on ecorticate lateral filaments. In some branch systems the procarys are most abundant on the abaxial filaments borne on basal cells of the ecorticate laterals (Fig. 7k). Otherwise, they are found primarily on secondary adaxial filaments. At the time of its initiation, a procary is situated only two to three cells below the apical cell and will be no more than three to five cells below the apical cell at maturity. A fertile segment first initiates a vegetative lateral and then cuts off a supporting cell at about a 45° angle with respect to the orientation of the vegetative lateral (Figs. 8a and b). The supporting cell cuts off a carpogonial branch initial to one side that is rhomboidal in shape. Intersecting divisions of the carpogonial initial produce first a two-celled and then a three-celled carpogonial branch, in which the cells are arranged in a zigzag (Figs. 8a–c). The carpogonium is cut off from the third cell by a transverse septum and is oriented at about a 30° angle with respect to a line drawn through the axis. Cells of the carpogonial branch are initially uninucleate, but become binucleate in cells one to three when the carpogonium matures. An unfertilized carpogonium bears a short trichogyne with a bulbous tip (Fig. 8c). In every instance in which the trichogyne had elongated, a spermatium was seen nearby or attached close to the tip of the trichogyne, or a sperm nucleus was present inside the trichogyne. It is conceivable that the trichogyne elongates only in the presence of a compatible spermatium. A second periaxial cell is cut off opposite the supporting cell after a four-celled carpogonial branch has formed. Seen from the backside, the supporting cell lies at a 45° angle with respect to the vegetative lateral and the second periaxial cell is situated opposite the first (Fig. 8d). Unfertilized carpogonial branches are evanescent and soon disappear; however, the paired periaxial cells may persist and their presence indicates the former position of a procary. In general, only one procary is formed toward the tip of a fertile branch; that is, the procarys do not tend to form in rows, and only one cystocary develops in a cluster of filaments.

A fertilized carpogonium divides longitudinally into two cells connected by a strand of cytoplasm that lacks a pit connection (Fig. 8e). The supporting cell and the opposite periaxial cell cut off auxiliary cells, and the two cells derived from the carpogonium each cut off a small connecting cell adjacent to an auxiliary cell (Fig. 8e). At the same time, the first three cells of the carpo-

gonial branch break down and disappear. The two auxiliary cells enlarge and one or both may form an extension that contacts a nearby connecting cell, if they are not already in close proximity. Normally both auxiliary cells will fuse with connecting cells leading to the formation of two gonimoblasts. Prior to fusion, the haploid nucleus moves to the base of the auxiliary cell, where it is cut off into a foot cell. The diploid fertilization nucleus divides at the margin of the auxiliary cell and one nucleus enters the auxiliary cell while the other is extruded into a residual cell (Fig. 8f). At the same time, the haploid nucleus inside a foot cell divides and each foot cell usually contains two nuclei (Fig. 8h). Completion of these events transforms the distal end of the auxiliary cell into a gonimoblast initial. In general, two gonimolobe initials are cut off from the sides at the terminal end of the gonimoblast initial, which branch to form two closely appressed filaments (Fig. 8h). These may remain separate (Fig. 8j, arrows) or may unite into a single globular mass of carpospores (Fig. 9j). Secondary gonimolobes may be produced from the sides of a primary gonimoblast cell as the first gonimolobes mature and their spores are released (Fig. 9j).

At the same time that auxiliary cells are cut off in a fertilized procarp, the central cell cuts off a vegetative cell at a 45° angle with respect to the vegetative lateral on the side opposite the original carpogonial branch that initiates both ascending and descending filaments (Fig. 8g). Further growth leads to the formation of an unbranched ascending filament and a highly branched, small-celled basketwork that encircles the axial cell at the base of the gonimoblasts (Figs. 8i and j and 9j). Shortly after fertilization the cell below the fertile axial cell initiates four filaments in addition to the original lateral filament (Figs. 8f and g) that grow upward and produce unbranched filaments that surround the gonimoblasts (Figs. 8j and 9j). These, combined with the two sterile filaments formed on the central axis and additional filaments that develop from the axial segments below, form a prominent involucre composed of a dozen or more unbranched involucre filaments.

Spermatangia occur only on determinate branchlets where they are restricted to the ecorticate lateral filaments. They tend to develop first on the abaxial branches produced from the lower sides of the basal cells of the lateral, ecorticate filaments and later on adaxial branches as well. Spermatangia form compact clusters on the adaxial sides of the ultimate, or occasionally the penultimate branches (Fig. 9i). Clusters are compact and hemispherical and are typically composed of highly branched filaments derived from two lateral initials. Rarely, a cluster will form from only one initial or sometime from three initials. In any event, the individual filaments that make up a cluster cannot be differentiated under the microscope at maturity. The first initial of a spermatangial filament is cut off from the upper side at the distal end of the bearing cell in the same position as the initial of a vegetative lateral and is indistinguishable from it. The second initial is

cut off behind the first, often from the proximal end of the cell (Fig. 9a). Initially, the divisions of the spermatangial filament are anticlinal and give rise to a cluster of small cells one cell layer thick that spreads across the upper surface of the bearing cell (Figs. 9b and c). Filaments grow laterally from the sides covering the upper half of the bearing cell (Fig. 9d) and branch toward the surface to increase the number of cell layers (Fig. 9e). At maturity, the hemispherical cluster is about four to five cell layers thick as seen in the optical section (Fig. 9f) crowned by a surface layer of spindle-shaped spermatangial mother cells, each of which bear one to two hyaline spermatangia (Fig. 9g). Individual spermatangia are teardrop shaped with a central nucleus situated between an anterior and a posterior mucilaginous vesicle (Fig. 9h, arrow).

Tetrasporangia are borne on the ecorticate laterals that fringe the sides of the determinate branchlets. Such filaments branch abaxially from the first, third, fifth, and seventh segments in the usual fashion and may add adaxial branches from the intervening naked segments as well. Naked segments between the branch-bearing segments produce narrow, short-celled filaments that bear mostly sessile, lateral tetrasporangia (Figs. 9k, l). Tetrasporangia are obovoid to teardrop shaped and divide simultaneously to produce four tetrahedrally arranged tetraspores (Fig. 9l).

DISCUSSION

A clear separation between primarily Southern Hemisphere genera presently placed in the Ptiloteae and the Northern Hemisphere Ptiloteae that includes *Plumaria*, *Ptilota*, and *Neoptilota* can be defended based on morphological evidence alone. A critical analysis would show that the two groups express different patterns of vegetative and reproductive development. Further evidence of their deep separation is seen in the molecular analyses. The largely Southern Hemisphere genera are resolved in monophyletic clades that show no close affinity to the monophyletic clade containing the Northern Hemisphere Ptiloteae (Fig. 1). In contrast, the placements of most Southern Hemisphere *Ptilota*-like taxa in two tribes, Euptiloteae and Callithamnieae, as proposed here, are problematic and require explanation.

Saunders et al. (1996) and Choi et al. (2002) have shown that the order Ceramiales is monophyletic, even though some of the families may be polyphyletic and the Ceramiaceae is paraphyletic. Our first clue concerning the affinities of genera and species that comprise the Euptiloteae and Callithamnieae came from global analyses of *rbcL* sequences that included approximately 150 species of Ceramiales (data not shown). In these analyses the Euptiloteae and Callithamnieae came out in separate clades nearest to the Crouanieae among currently accepted tribes, were more distantly related to the Ceramiaceae/Antithamnieae assemblage, and were remote from a cluster of tribes that included the Ptiloteae.

The sister relationship between the Euptiloteae and the Callithamnieae and their affinity with the Crouanieae are all strongly supported in global analyses, and received 100% bootstrap support in the ML tree inferred from the combined data (Fig. 1). Sterile groups are absent in the procarps in all three tribes and the carpogonial branches are borne on naked supporting cells and are directed horizontally or in a zigzag manner rather than vertically in all three (Feldmann-Mazoyer 1941, Wollaston and Womersley 1959, Hommersand 1963, Wollaston 1968). The only other tribe in the Ceramiaceae that exhibits these characters is the Spyrideae (Hommersand 1963), a tribe that differs in other respects and was not found to be closely related to the Crouanieae/Euptiloteae/Callithamnieae in global molecular searches (data not shown). Species belonging to the Crouanieae are never confused with the other two tribes because their apical cells undergo transverse rather than oblique divisions and axial cells each produce three or four whorl-branches per segment rather than just one or two. There are also differences in their reproductive development that will be discussed later on.

The conspicuous character that unites the Euptiloteae and Callithamnieae is the structure and position of the procarps. Each fertile axial cell bears a determinate vegetative lateral and two opposite periaxial cells, one of which forms the carpogonial branch and both of which potentially cut off auxiliary cells after fertilization that bear the gonimoblasts. The fertile periaxial cells lack vegetative laterals; that is, sterile groups are absent. Kylin (1956) circumscribed his Callithamnion group to contain genera in which the carpogonial branches are formed on special cells borne laterally in the upper parts of long shoots rather than being cut off from the basal cell of a determinate lateral branch or borne subterminally close to the apical cell. In Kylin's interpretation, axial cells bearing procarps are scattered along the length of potentially indeterminate branches, usually separated by one to several sterile segments, each of which bears a single vegetative lateral. When one procarp is fertilized and cuts off auxiliary cells, the development of the others on the same branch is inhibited or they abort. Such an arrangement of procarps and the associated reproductive strategy is seen in *Aglaothamnion*, *Callithamnion*, *Carpothamnion*, and *Heteroptilon* of the Callithamnieae and in *Seirospora* and *Sciurothamnion* of the Euptiloteae, and may be plesiomorphic in both tribes (Maggs and Hommersand 1993, Womersley and Wollaston 1998, De Clerck et al. 2002; this paper). The fertile branch is shorter and contains fewer procarps or may be subterminal with just one procarp in the more robust species of both tribes. A tendency toward having fewer procarps and ultimately only one subterminal procarp is seen in *Euptilota* progressing from the most lax species, *E. molle*, to *E. fergusonii*, *E. articulata*, and *E. formosissima* (Hommersand et al. 2004a). Procarps are formed close to the apices of fertile branches and the gonimoblasts are involucrate in two species of *Hirsutithallia*

(Womersley and Wollaston 1998) and in *Falklandiella*, *Georgiella*, *Diapse*, and *Aristoptilon* (Mendoza 1969, Moe and Silva 1983; this paper). All bear their procarps near the apices on modified indeterminate branches and, since all are only distantly related, no associated evolutionary progression is indicated.

Perhaps the most striking character that separates the two tribes is the position of the nucleus in the spermatangia: terminal subtended by muscilaginous vesicles in the Euptiloteae (Hommersand et al. 2004a) and medial with a vesicle above and below in the Callithamnieae (McIvor et al. 2002; this paper). In general, there is also a difference in the position of the supporting cell of the carpogonial branch in relation to the vegetative filament in the fertile axial segment: directly below or on the opposite side in the Euptiloteae and at right angles to the vegetative filament in the Callithamnieae. The one exception appears to be *Sciurothamnion* of the Euptiloteae, in which the supporting cell and vegetative filament are borne at right angles (De Clerck et al. 2002). The earliest stages in which auxiliary cells are cut off and derivatives of the fertilization nucleus are transferred to the auxiliary cells provide some of the most significant characters both for uniting and for separating the Euptiloteae and Callithamnieae. The carpogonium expands and auxiliary cells are cut off from the supporting cell and the opposite periaxial cell; the diploid nucleus undergoes two divisions and ultimately cuts off a pair of connecting cells that fuse with the auxiliary cells in both tribes. Despite superficial similarities, no other ceramiaceous tribes undergo these processes in precisely the same way. There are differences in the details that distinguish the two tribes. In the Euptiloteae, the carpogonium expands without dividing and forms prominent protuberances that may contact the auxiliary cell before being cut off as connecting cells. This behavior was recognized as a distinguishing feature in two species of *Seirospora* (Aponte and Ballantine 1991, 1995) and has been documented in species of *Euptilota* (Hommersand et al. 2004a) and *Sciurothamnion* (De Clerck et al. 2002). This behavior stands in contrast to that described numerous times in *Aglaothamnion* and *Callithamnion*, in which the carpogonium undergoes nuclear division and cleavage into two cells after fertilization (Oltmanns 1898, O'Kelly and Baca 1984, Hommersand 1997). Division of the fertilized carpogonium into two cells may be diagnostic for the Callithamnieae; however, the carpogonium is said not to divide in *Georgiella* (Moe and Silva 1983). The connecting cell is a minute cell that does not enlarge appreciably in members of the Callithamnieae. Fusion between the connecting cell and the auxiliary cell appears to be initiated by the expanding auxiliary cell, sometimes with the formation of a prominent extension directed toward the connecting cell. Further studies are needed to determine just how variable this feature is among species in the Callithamnieae. The membranes of the connecting cell and auxiliary cell fuse and the diploid nucleus divides at the site of fusion

TABLE 2. Defining features of Pilota-like Callithamniaceae.

Species category	<i>Falklandiella harveyi</i> ^a	<i>Georgiella confluenta</i> ^b	<i>Heteropilton pappeanum</i> ^c	<i>Heteropilton rigidulum</i> ^d	<i>Aristopilton mooreanum</i> ^c	<i>Diapse pilota</i> ^c
Division of the apical cell	Alternate-oblique	Alternate-oblique	Alternate-oblique	Alternate-oblique	Alternate-oblique	Alternate-oblique
Initiation of first lateral	Alternate, two to six segments below apex	Alternate, two to six segments below apex	Alternate, one to two segments below apex	Alternate, one to two segments below apex	Alternate, one to two segments below apex	Alternate, one to two segments below apex
Initiation of second lateral	Opposite the first, two to five segments below	Opposite the first, one to five segments below	Absent	Absent	Absent	Obliquely opposite first, one segment below
Habit of the determinate laterals	Curved, initially unbranched, some abaxial branches later, ecoriicate	Branching first from abaxial then adaxial side, coriicate	Curved, stiff, unbranched but adding branches irregularly near apex, ecoriicate	Curved, stiff, unbranched but adding branches irregularly near base, ecoriicate	Curved, first branching abaxially then adaxially, ecoriicate	Five to seven times sub-dichotomously branched in a plane, coriicate
Branching of basal cell of a lateral	Naked	Abaxial, adaxial branchlet absent	Naked or adaxial	Naked or adaxial	Abaxial	Abaxial, then opposite
Origin and growth of the cortical filaments	Three initials from basal cells of laterals, down and around axis, up to three layers	One initial from basal cells of laterals, down, up and around axis, two to six layers	One initial from basal cells, bidirectional and around axis, up to three layers	Absent	One initial from basal cells, down and around axis, two layers	Several, to form densely branched small-celled cortex covering axis
Rhizoidal cortication	From subcortical cells, growing between cortical cells and enveloping axis	From subcortical cells, growing between cortical cells and investing axis	Bidirectional, in thin layer between cortical cells and central axis	Singly from basal cells of laterals, growing downwards and enveloping the central axis	From outer cortical cells, growing inwards and downwards enveloping the central axis	From subcortical cells, growing between them and forming a core around axis
Origin of the indeterminate branches	Replacing determinate laterals, often subopposite	Transformed irregularly from tips of determinate laterals	Transformed from tips of determinate laterals or adventitious	Transformed from tips of determinate laterals	Replacing determinate laterals or formed adventitiously	Transformed irregularly from tips of determinate laterals
Origin and structure of the spermatangia	Unknown	In groups of one to three in superficial sort, nuclei medial	Unknown	Unknown	Mantle covering dense cluster of filaments, nuclei medial	Unknown
Location of the procarps	Subterminal on modified lateral branches	One to two near apex of indeterminate or transformed determinate branches	In series of indefinite length on modified indeterminate branches	Single, five to six cells below apex on modified indeterminate branches	Subterminal on dwarfed determinate filaments, one per fertile branch	Subterminal on modified indeterminate branches
Shape of procarps	Unknown	Horizontal, at right angle to the plane of the vegetative lateral	Horizontal, at right angle to plane of the vegetative lateral	In a zigzag, at right angle to plane of the vegetative lateral	In a zigzag, at oblique angle to plane of the vegetative lateral	Unknown
Structure and arrangement of mature gonimoblasts	Paired, globular, subterminal on modified lateral branches	Paired, globular, from one to two gonimolobe initials	Single or paired, globular, or with secondary gonimolobes	Paired, with two rounded gonimolobes	Paired, globular, with secondary gonimolobes and basketwork	Single or paired, globular, often clustered
Presence and organization of cystocarp involucre	Up to four ecoriicate filaments from each of two to three cells below fertile axial cell	Four branched, ecoriicate filaments plus other coriicate filaments below fertile axial cell	Two to three times branched ecoriicate filaments three to four cells below fertile axial cell	One to two times branched filaments two to three cells above and below fertile axial cell	From ordinary and additional unbranched filaments at and below fertile axial cell	From branched, coriicate filaments two to three cells below fertile axial cell
Position of the tetrasporangia	Sessile, bilateral in series on marginal lateral branches	Terminal on short, marginal unbranched filaments	Terminal or lateral on highly branched filaments	Sessile, in series on adaxial side of determinate laterals	Terminal or lateral on dwarfed lateral filaments	Terminal or lateral at margin on branched filaments on coriicate stalks

^aMendoza (1969, and Fig. 2, this paper).^bMoe & Silva (1983, and Fig. 2, this paper).^cThis paper.^dDe Clerck et al. (2004).^eWomersley (1998, and Fig. 3, this paper).

between the two, with one daughter nucleus entering the auxiliary cell and the other extruded to the outside into a 'residual cell'. This behavior is not too different from that seen in members of the Crouanieae (Feldmann-Mazoyer 1941, Wollaston and Womersley 1959, Hommersand 1963, Wollaston 1968), or in *Spyridia* (Hommersand 1963) and *Rhodocallis* (Hommersand et al. 1998) of the Ceramiaceae, in which the diploid nucleus and its associated cytoplasm remain attached to the auxiliary cell and are subsequently cut off along with the haploid nucleus into a foot cell. Indeed, this is exactly what happens in *Seirospora orientalis* (Kraft 1988). In *Sciurothamnion*, the haploid nucleus is cut off from the foot cell into a 'disposal cell' (De Clerck et al. 2002). The variety of structures cut off basally or laterally from an auxiliary cell after its diploidization are related morphologically and can be regarded as aspects of the 'foot cell'. De Clerck et al. (2002) have discussed the technical differences between 'foot cells', 'residual cells', and 'disposal cells'.

Most characters that are considered to be diagnostic at generic and species levels in the Ceramiaceae are homoplasious with character states converging to the same end points in distant and closely related taxa. This is especially true of the Euptiloteae and Callithamnieae, in which unrelated species may look very similar or even be confused. For example, species having a conspicuous central axis and a small-celled outer cortex are seen in both tribes in addition to uniseriate, uncorticated "callithamnioid" species. Likewise, rhizoidal cortication may surround the axes, be spread among the subcortical cells, include descending or both descending and ascending elements, be limited to basal parts, or be absent in both tribes. The range of characters and the extent of homoplasy are recorded for *Euptilota* (Hommersand et al. 2004a), *Sciurothamnion* (De Clerck et al. 2002), and *Seirospora* (Aponte and Ballantine 1995) among the Euptiloteae, and for the filamentous Callithamnieae (Maggs and Hommersand 1993, Womersley and Wollaston 1998, McIvor et al. 2002). The variation seen in vegetative and reproductive characters in the *Ptilota*-like Callithamnieae investigated here is summarized in Table 2.

The Callithamnieae, including the newly transferred *Ptilota*-like members, is strongly supported in the ML analysis of the combined molecular data, receiving 100% bootstrap support. In contrast, the relationships among the *Ptilota*-like members of the tribe are only weakly supported. One might argue that the *Ptilota*-like clade could be recognized as a separate tribe. *Falklandiella* and *Georgiella* are strongly resolved as sister taxa within the *Ptilota*-like Callithamnieae, and they share some morphological features in common. In contrast, the strongly supported sister relationship of *Aristoptilon* from New Zealand and *Diapse* from southern Australia is counterintuitive, as they do not share any unique morphological characters. On the other hand, the two appear to have originated in Australasia and may have been separated in the course of time by plate tectonics and seafloor spreading that ac-

companied the opening of the Tasman Sea, as has been documented for many species and genera of algae (Hommersand 2006). *Heteroptilon* from South Africa is very different morphologically and does not appear to be closely related to any other *Ptilota*-like Callithamnieae. In short, while it is entirely possible that the *Ptilota*-like Callithamnieae may have originated from a common ancestor, it is equally likely, at this point in time, that they represent two or more separate evolutionary lines within the Callithamnieae.

We have already argued that *Euptilota*, *Sciurothamnion*, and *Seirospora* of the Euptiloteae originated in the Tethyan Ocean (Hommersand et al. 2004a). All of the *Ptilota*-like Callithamnieae are presently found in the Southern Ocean and may well have originated in the antiboreal Pacific Ocean. The ancestor of *Heteroptilon* may have been distributed to South Africa through a seaway between West and East Antarctica during periods of minimal glaciation in the manner described by Hommersand (1986) and Hommersand and Fredericq (2003) for some other temperate South African species.

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