MORPHOLOGY AND SYSTEMATICS OF SCIUROTHAMNION STEGENGAE GEN. ET SP. NOV. (CERAMIACEAE, RHODOPHYTA) FROM THE INDO-PACIFIC

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A new ceramiaceous alga, Sciurothamnion stegengae De Clerck et Kraft, gen. et sp. nov., is described from the western Indian Ocean and the Philippines. Sciurothamnion appears related to the tribe Callithamnieae on the basis of the position and composition of its procarps and by the majority of post-fertilization events. It differs, however, from all current members of the tribe by the presence of two periaxial cells bearing determinate laterals per axial cell. Additionally, unlike any present representative of the subfamily Callithamnioideae, no intercalary foot cell is formed after diploidization of the paired auxiliary cells. The genus is characterized by a terminal foot cell (“disposal cell”), which segregates the haploid nuclei of the diploidized auxiliary cell from the diploid zygote nucleus. The nature of three types of foot cells reported in the Ceramiaceae (intercalary foot cells containing only haploid nuclei, intercalary foot cells containing haploid nuclei and a diploid nucleus, and terminal foot cells containing only haploid nuclei) is discussed.

Key index words: algae; Ceramiaceae; cytology; morphology; Rhodophyta; Sciurothamnion gen. nov.; Sciurothamnion stegengae sp. nov.; systematics; taxonomy

During recent studies of the marine benthic floras of South Africa and eastern Africa in the western Indian Ocean, numerous specimens of a conspicuous ceramiaceous alga were collected at several localities. Because of its distinctive features it was recognized as identical to tetrasporophytes and female gametophytes collected by the second author in the Philippine Islands in 1968 and filed as “Callithamnieae gen. nov?” in the Kraft Herbarium at the University of Melbourne. This entity was later recorded as “Callithamnion (?) sp. nov.” and characterized as “a likely new genus” by Kraft et al. (1999) in a survey of Rhodophyta from the collection locality in southeastern Luzon. Detailed examination of the recent southeastern African collections reveals that they do indeed represent a new genus and species with affinities to members of not only the tribe Callithamnieae but also the tribe Pilolitae. For these algae we propose the new genus Sciurothamnion, containing at present a single highly disjunct species, Sciurothamnion stegengae.

Some features of Sciurothamnion are unique and seemingly at odds with what is known about members of both the Callithamnieae and Pilolitae, particularly in regard to early post-fertilization events. This has led us to consider carefully the defining features of ceramiaceous tribes. At present these are mostly based on a combination of vegetative and reproductive characters, the latter particularly involving the position of the procarp, the number of periaxial cells per fertile axial cell, the presence and configuration or absence of sterile cell groups on the supporting cell, the orientation of the carpogonial branch, and early events after diploidization of the auxiliary cells (Kylin 1956, Hommersand 1963, Itono 1977). Detailed reports on the immediate post-fertilization events at both anatomical and cytological levels tend to be very incomplete or inconsistent (Hommersand 1997), particularly in regard to how a derivative of the zygote nucleus reaches the auxiliary cell and how the segregation of the haploid and diploid nuclei take place, which causes a persistent difficulty in adequately defining ceramiaceous tribes and properly placing newly discovered taxa within them. Consequently, the absolute taxonomic importance of characters relating to the diploidization of the auxiliary cell remains uncertain, and it seemed appropriate to investigate and review these events in detail in the present study.

MATERIALS AND METHODS

Morphological observations were made on specimens preserved in 5% formalin-seawater. Whole mount and sectioned material was stained either with aniline-blue and mounted in Karo syrup or stained with Wittmann’s aceto-iron-hematoxylin-chloralhydrate and mounted in Hoyer medium as described in Hommersand et al. (1992). Drawings were made with a camera lucida and photographs were taken with an Olympus DP50 digital camera (Melville, NY, USA) mounted on a Leitz Diaplan compound
RESULTS

Sciurothamnion De Clerck et Kraft, gen. nov.

Plantae ceramiaceaee plurimis cellulis axialibus centralibus procerantibus duas cellulas periaxiales lateralia determinata pseudodichotoma eorticata fertentes, paribus lateraliem successivis, decessatis. Axes primarii et indeterminati dense corticati usque ad cellulas paucus infra apices; axes indeterminati ex augmente renovato ad apices lateraliem determinatorum exoriente. Tetrasporangia in tetrahedro divisa, sessilia singulae in cellulis lateraliem determinatorum. Spermatisangia in axibus nanis spermatangialibus, axibus 1–2 in quaque cellula proximali lateraliem determinatorum portatis, prope basis semel vel bis ramosis, ad 8 cellulas longis, cellula omni pro cellulam spermatangialiam maternam fungenti et 2–4 spermatisangia ovaidea statim producenti. Procarpia in cellulis intercalarios axium indeterminatorum portata, quaeca cellula axialis fertili efferenti laterali determinate vegetative et cellulas duas periaxiales perpendiculariter plano lateraliem vegetative abscissas, una cellula periaxialis pro cellula sustinenti fungenti et ramum carpogonius 4-cellulam lateraliem fertili, altere evoluto e cellulis 2–3 proximalibus et 2 distalis cellulae centes; gonimoblastus maturus circumcinctus ab involucro deinceps efferenti usque ad 5 gonimolobos simul maturates; initia gonimoblastorum divisione inaequali cellulae sustentantia et periaxialis fertili carpogonium; intercalary foot cellulae auxiliares gemellae e cellulis remanenti et cellulam auxiliarem secundam sub fecundati ramum carpogoniale 4-cellulam fertenti, altera abscissa, una cellula periaxiali pro cellula sustentante funduas periaxiales perpendiculariter plano lateraliem vegetativo efferenti laterale singulum determinatum vegetative et cellulas axium indeterminatorum portata, quaque cellula axiali fertili ovoidea statim producens. Procarpia in cellulis intercalarios.

Species typicum: Sciurothamnion stegengae De Clerck et Kraft

Ceramiaceae plantae with two periaxial cells bearing pseudo-dichotomous uncorticated determinate laterales on most central-axial cells, successive pairs of laterales being decussate. Primary and indeterminate axes densely corticated to within a few cells of the apices, indeterminate axes being formed by renewed growth at the tips of determinate laterales. Tetrasporangia tetrahedrally divided, sessile and single on cells of determinate laterales. Spermatisangia in dwarf spermatisangial axes borne 1–2 per proximal cell of determinate laterales, the axes once or twice branched proximally, to eight cells in length, every cell acting as a spermatisangial mother cell and producing 2–4 ovoid spermatisangia directly. Procarpi borne on intercalary cells of indeterminate axes, each fertile axial cell producing a single determinate vegetative lateral and two periaxial cells cut off perpendicular to the plane of the vegetative lateral, one periaxial cell functioning as the supporting cell and bearing a four-celled carpogonial branch, the other remaining unbranched and giving rise to a second auxiliary cell upon fertilization of the carpogonium; paired auxiliary cells formed by unequal division of the supporting cell and fertile periaxial cell; diploidization of the auxiliary cells by means of two connecting cells cut off on opposite sides of the fertilized carpogonium; intercalary foot cells not formed, haploid nuclei of auxiliary cells being segregated in a disposal cell; gonimoblast initials sequentially producing up to five synchronously maturing gonimolobes; mature gonimoblast surrounded by a well-developed involucrum derived from the 2–3 cells proximal as well as the 2 cells distal to the fertile axial cell.

Type species: Sciurothamnion stegengae De Clerck et Kraft

Etymology: From the Greek word skiouros, in reference to the resemblance of the ultimate branches of the alga to the tail of a squirrel, and the Greek word thamnos, for bush (Backer 2000).

Sciurothamnion stegengae De Clerck et Kraft

Thalli erecti, singuli vel caespitosi ex hafttero discoidea, usque ad 15 cm longi, rosaceo-rubri, splendide iridescentes in vivo; axes primarii irregulariter dichotomi, valde corticati a filamentis descendentibus e cellulis proximalibus lateraliem determinatorum, prope basis ad 1.5 mm in diametro; laterali determinata ad 700–800 μm longa; laterali adventititia e cellulis corticalibus superficialebus axium determinatorum exoriente, plerumque rudimentalia remanentia. Structureae reproductionis ut in geneere.

Thalli erect, single or in clusters from a discoid holdfast, to 15 cm in length; color pinkish-red, brightly iridescent when living; main axes irregularly dichotomously branched, heavily corticated by downgrowing filaments derived from the proximal cells of determinate laterales; to 1.5 mm in diameter near the base; determinate laterals to 700–800 μm in length; adventitious laterals arising from surface cortical cells of indeterminate axes, usually remaining rudimentary. Reproductive structures as for the genus.

Etymology: The specific epithet honors a fine individual and dedicated student of the marine algae of South Africa, Dr. Herre Stegenga, whose critical studies of African Ceramiaceaee are a major contribution to our understanding of the diversity and complexity of this family.


Distribution: At present, known from Tanzania, KwaZulu-Natal (South Africa), and the island of Luzon in the Philippines.


Habit and vegetative morphology. Plants grow from a small discoid holdfast from which one to several erect axes arise (Fig. 1, B and F) and reach lengths of 7–15 cm. Fronds consist of repeatedly and irregularly dichotomously branched indeterminate axes that are densely beset with decussate pairs of determinate laterals (Fig. 1, B and E). Freshly collected plants are soft in texture but not gelatinous, pinkish-red in color, and exhibit a bright-bluish iridescence in situ.

Determinate laterals reach 15–20 cells and 700–800 μm in length and are inserted at angles of 55–75 degrees to the parent axes. They are aligned in four orthostichous rows, are completely uncorticated, and branch subdichotomously at a 30–50 degree divergence in a more or less single plane (Fig. 1, D and E). The final branch order at maturity consists of 20–35 divisions that are five to six cells in length and that are the result of four to eight basal subdichotomies separated by a single unbranched cell and laxer branching distally, where two to seven cells separate successive subdichotomies (Fig. 2D and 3A). The first determinate lateral initial originates as a protrusion from the high side of the axial cell immediately subverting the apical cell and is offset by 90 degrees from the lateral on the preceding and subsequently succeeding contiguous axial cells. Three to six axial cells proximal to the apical cell a second lateral is formed opposite the first, resulting in the orthostichous opposite-decussate branching pattern. Growth of the laterals proceeds through transverse divisions of their apical cells (Fig. 2D) and elongation of the derivatives. The periaxial cells of mature laterals are generally shorter (20–30 × 12–15 μm) and more rounded than other cells, the epibasal cells reaching 50–60 × 16–21 μm and tapering gradually toward ultimate cells 12–18 × 9–12 μm. The ultimate cells often produce a long rapidly deciduous hair (Fig. 3B). Adventitious determinate laterals frequently issue from peripheral cortical cells in the lower parts of the thallus and usually remain rudimentary.

Growth of indeterminate axes takes place by oblique divisions of the apical cells, with the high sides of successive axial cells spirally offset in a 1/4 divergence (Figs. 2A and 4A). Axial cells in the distal parts of the thallus are cylindrical (sometimes with a slight median constriction) and measure 18–25 μm in width by 40–65 μm in length (L/B: 2–2.5) (Fig. 2, B and D). Mature axial cells are more broad than long (80–125 × 40–60 μm; L/B: 0.4–0.7), linked by stout primary pit connections with conspicuous torus-shaped pit plugs, and usually contain several conspicuous globular inclusions that stain prominently with aniline blue (Fig. 2E). Proximal axial cells reach 485 μm in diameter and are connected by slender lengthy pit-connections (Fig. 2I).

Indeterminate laterals form at irregular intervals along primary axes by direct conversion of determinate laterals, the transition from determinate to indeterminate lateral being at the point where paired, rather than single laterals are borne on an axial cell (Fig. 2C). The new indeterminate axis then forms cortication that extends to and merges with that of the parent primary axis, although the basal cells of the converted determinate lateral remains distinctive in that it still bears only a single lateral.

Primary and indeterminate axes are terete, heavily corticated to within a few cells of the apices, and reach diameters of 1–1.5 mm near the thallus base, which is mostly denuded of branchlets (Fig. 1F). Corticating filaments initially arise singly from the basal cells of determinate laterals approximately 14–22 cells proximal to the apices (Fig. 2B). Within a few axial segments proximal to the site of cortex initiation, a second and third corticating filament then issues from each of the basal cells, the filaments branching irregularly and initially enveloping the axial cells in a single layer (Fig. 2D). Cortication thickens basipetally and differentiates into an inner tissue to 550 μm in width (Fig. 1G) composed of narrow rhizoidal cells 3–10 μm wide by 110–220 μm in length. This layer is surrounded by a consolidated surface covering of small isodiametric cells, which divide by oblique and longitudinal divisions (Fig. 2, F and H). All vegetative cells are uninucleate.

Reproductive features (Figs. 4–6). Tetrasporangia are tetrahedrally divided, sessile, and formed singly and mostly adaxially at the distal ends of cells of determinate laterals (Fig. 3, B and C). When fully mature they are ovoid and 20–25 μm in width by 25–35 μm in length.

Gametophytes are dioecious, the spermangia forming on dwarf fertile axes borne singly or in pairs at the distal ends and mostly adaxial sides of determinate laterals (Fig. 3, D–F). Each cell of the fertile axis functions directly as a spermangial mother cell and produces two to four ovoid spermangia 3–4 × 5–7 μm.

Carpogonial branches form in series near the apices of short relatively young indeterminate axes, although only one ever produces a carpogonial branch, which is mostly denuded of branchlets (Fig. 6, A and B). Procarps in varying stages of development are usually separated by two or three segments on any given lateral but may also develop on adjacent segments (Fig. 6C). Unlike sterile determinate-axis cells, fertile axial cells bear only one rather than an opposite pair of determinate laterals.
Fig. 1. Habit and vegetative morphology. (A) Habit of the holotype (GENT KZN 695). Scale bar, 1 cm. (B) Habit of a wet-preserved highly branched frond. Scale bar, 1 cm. (C) Detail of the apical portion of the thallus. Scale bar, 1 mm. (D) Detail of a branch apex of a relatively sparsely branched axis under dark-field conditions. Scale bar, 1 mm. (E) A densely branched portion of a thallus under dark-field conditions. Scale bar, 5 mm. (F) Detail of a small discoid holdfast giving rise to two erect axes. Scale bar, 1 mm. (G) Transverse section of an axis near the base of the thallus. Scale bar, 250 μm.
Fig. 2. Vegetative morphology. (A) Detail of a lightly squashed apex showing the opposite decussate arrangement of the determinate laterals. Scale bar, 25 μm. (B) Initials (arrowhead) of the first-formed rhizoidal filaments growing down the abaxial side of the basal cells of determinate laterals. Scale bar, 25 μm. (C) Transition between a determinate lateral with each cell bearing a single lateral (arrows) and an indeterminate axis with opposite branching (arrowheads). Scale bar, 50 μm. (D) Aspect of a corticated axes approximately 2 mm below the apex, with rod-shaped axial cells. Scale bar, 100 μm. (E) Axial cells in the mid-thallus region with prominent inclusions. Scale bar, 50 μm. (F) Longitudinal section of an axis showing the differentiation of the corticating filaments, consisting of long and rhizoidal-like cells toward the center of the axis and small isodiametric cells in the outer layers. Scale bar, 50 μm. (G) Detail of rhizoidal-like inner corticating filaments. Scale bar, 50 μm. (H) Detail of isodiametric outer corticating filaments. Scale bar, 50 μm. (I) Aspect of the axial cells near the base of the thallus with prominently elongated pit connections (arrowheads). Scale bar, 100 μm.
The procarp arises by a concavo-convex division at the middle of the fertile axial cell. This results in a first periaxial cell, which arises at 90-degree angle to the plane that the determinate lateral would occupy if a second was cut off opposite it, as normally happens on sterile axial cells. The first periaxial cell becomes the supporting cell with the progressive development of a four-celled, L-shaped, carpogonial branch, of which the first (cb1) and second (cb2) cells are ellipsoidal; the third cell (cb3) is more angular and bears distally the much smaller carpogonium. The carpogonium, very much the smallest cell of the carpogonial branch (Figs. 4, B and C, and 6C), lies opposite the determinate lateral borne on the fertile axial cell. The trichogyne is long (to 500 μm). The mature second and third cells are usually binucleate, whereas the first cell and the carpogonium itself are uninucleate. In most instances the carpogonial branch is fully formed before a second fertile periaxial cell is cut off from the fertile axial cell opposite the supporting cell. No further cells are cut off from the supporting cell or the fertile pericentral cell, sterile cell groups being completely absent from the procarp.

After presumed fertilization, the carpogonium expands laterally and the trichogyne breaks down completely. Zygote formation results in an enlargement of the supporting cell and fertile pericentral cell, both of which soon divide by an uneven and oblique cross-
wall into a small basal cell and a large auxiliary cell. The diploid nucleus in the carpogonium undergoes a single mitotic division that is unaccompanied by cytokinesis (Figs. 5A and 6D). Instead, two small protrusions are formed on each side of the carpogonium, adjacent to the auxiliary cells (Figs. 5B and 6E). This is followed by a second division of both carpogonial nuclei that results in the formation of two connecting cells. Both division products then migrate to the two small protrusions formed on each side of the carpogonium adjacent to the auxiliary cells. They are then segregated into two connecting cells that are not pit-connected to the carpogonium (Figs. 5C and 6F), each consisting of a densely compacted nucleus surrounded by a narrow hyaline region. Concurrently, both auxiliary cells become pyriform and their haploid nuclei migrate toward the base (Figs. 5B and 6E and F). Adjacent to the pit connection between the auxiliary cell and its subtending cell, a darkly staining proteinaceous body starts to form (Fig. 7A) that later becomes a well-developed plug separating diploid and haploid tissue (Fig. 7D). Diploidization of the auxiliary cells is followed by an immediate mitotic division of the diploid nucleus. One of the daughter nuclei migrates toward the center of the auxiliary cell, whereas the other is extruded in the form of a persistent “residual cell” (sensu Hommersand 1997) (Figs. 5D and 6G). The original haploid nuclei, which at this stage are situated at the pyriform bases of the auxiliary cells, are cut off by a cleavage perpendicular to the longitudinal axes of the auxiliary cells to form a “disposal cell” (sensu Huisman and Kraft 1992) in which the haploid nucleus may divide once mitotically (Figs. 5D, 6G, and 7, A and B). The carpogonium and hypocystous cells have fused by this stage, but the basal and epibasal cells of the carpogonial branch remain discrete (Fig. 7C). As events proceed, the entire carpogonial branch withers.

The auxiliary cell, which acts as the gonimoblast initial after segregation and removal of its haploid nucleus, divides apically to form the first gonimolobe initial (Fig. 7, A and B), after which a second lateral gonimolobe initial soon arises. Eventually each gonimolobe initial can produce up to five rounded secondary gonimolobes that mature sequentially and are composed of synchronously maturing carposporangia (Fig. 7, F and G). All gonimolobe cells become carposporangia except for the basal cells, which elongate into distinctive stalk cells. Mature carposporangia are irregularly contoured and 10–16 μm in diameter.

Directly after a fertilization event, the two to three axial cells proximal to and two axial cells distal to the fertile axial cell initiate involucral filaments from their distal poles, there being as many as seven borne on the hypogenous cell (Fig. 7E). Unbranched and five to six cells long when young, each mature involucral filament branches ternately from the distinctive ovoid to obvoid basal cell and pseudo-dichotomously from the cells above it. Elongation of the indeterminate branchlet ceases with initiation of the gonimoblast, resulting in subapical cystocarps borne on stunted heavily corticated laterals (Fig. 6, A and B).

DISCUSSION

The huge diversity of ceramiaceous algae, as well as the cryptic and esoteric features that one often needs to observe to classify them, necessitates close attention to the precise details of procarp position and makeup.
Fig. 5. Post-fertilization stages of Sciurothamnion stegengae. (A) Early post-fertilization stage showing a fertilized carpogonium (cp) with divided diploid nuclei, the auxiliary cell and fertile pericentral cell have divided to produce a basal cell (bc) and a distal auxiliary cell (au). Scale bar, 10 μm. (B) The fertilized carpogonium has initiated a small beak (arrowhead) directed toward at least one auxiliary cell (au); the latter have become pyriform and their haploid nuclei (hn) have migrated basally. Scale bar, 10 μm. (C) Two small connecting cells (cc) are cut off from the carpogonium but have not fused yet with the auxiliary cell. Scale bar, 10 μm. (D) The auxiliary cells are diploidized and have subsequently cut off each a residual cell (rc), a disposal cell (dc), and a terminal primary gonimolobe initial (gi1); in one disposal cell the haploid nucleus has undergone a mitosis; one auxiliary cell has already cut off a second lateral gonimolobe initial (gi2). Scale bar, 10 μm.
Fig. 6. Female reproductive structures of *Sciurothamnion stegengae*. (A) Portion of an axis bearing several mature gonimoblasts, situated near the distal end of short axes. Scale bar, 500 μm. (B) Detail of a maturing gonimoblast placed distally on a short axis. Note the well-developed involucral filaments subtending the gonimoblast. Scale bar, 10 μm. (C) A mature procarp with a four-celled horizontally oriented carpogonial (cp) branch (the supporting cell and trichogyne are not in focus; the determinate lateral of the fertile axial cell is situated on the site directly opposite the carpogonium). fpc, fertile pericentral cell. Scale bar, 10 μm. (D) Early post-fertilization stage showing a fertilized carpogonium (cp) with a diploid nucleus that has divided; the fertile axial cell has divided to produce a basal cell (bc) and a distal auxiliary cell (au). Scale bar, 10 μm. (E) The carpogonium has initiated a small beak (arrowhead) directed toward the auxiliary cell; the latter has become pyriform and its haploid nucleus (hn) has migrated basally. Scale bar, 10 μm. (F) The carpogonium has cut off two connecting cells (cc, only one in focus), which have not fused with the auxiliary cells. Scale bar, 10 μm. (G) A diploidized auxiliary cell with a residual cell (rc) cut off at the site where the connecting cell fused; the haploid nuclei of the auxiliary cell are cut off in a disposal cell (dc).
whenever putative new genera and species are encountered (Hommersand 1963, Itono 1977, Huisman and Kraft 1992, Athanasiadis 1996). Important also is the complex series of events succeeding zygote formation, although these are presently less taxonomically critical because so few detailed studies have been made of them.

Procarp features of *Sciurothamnion* strongly indicate placement in the tribe Callithamnieae as defined by Schmitz and Hauptfleisch (1897), Feldmann-Mazoyer (1941), and Kylin (1956). Procarps in this group are situated on intercalary axial cells of indeterminate laterals and have carpogonial branches that are oriented horizontally to the long axis of the bearing indeterminate lateral. They consist of two initially undivided periaxial cells, of which the first-formed functions as the supporting cell and the second, arising opposite the first, mirrors it by cutting off a second auxiliary cell after fertilization. In addition to carpogonial and auxiliary cell features, another consideration that can be an important tribal attribute is whether or not sterile cell groups are associated with the supporting cell, and if so of what kind. *Sciurothamnion* lacks any sterile cell groups, a further feature allying it with the Callithamnieae, although a number of other tribes (Crouanieae, Rhodocallicladeae, Spyridieae [Feldmann-Mazoyer 1941, Hommersand 1963, Wollaston 1968, Hommersand et al. 1998]) and some members of the

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**Fig. 7.** Female reproductive structures of *Sciurothamnion stegengae*. (A) Detail of a single developing gonimoblast showing the terminal primary gonimolobe initial (gli), the gonimoblast initial (gi), a withering disposal cell (dc), and the residual cell (rc). Scale bar, 10 μm. (B) Paired gonimoblasts in an early stage of development. Scale bar, 10 μm. (C) Detail of a withering carpogonial branch showing a carpogonium (cp) which is fused with the third carpogonial branch cell (cb3); the first and second carpogonial branch cells remain discrete (arrowheads). Scale bar, 10 μm. (D) Detail of the basal cells and gonimolobe initials that are separated by a prominently staining proteinaceous body (arrowheads). Scale bar, 25 μm. (E) Transverse section of the hypogenous cell showing the presence of seven involucral filaments. Scale bar, 25 μm. (F) Detail of a maturing gonimoblast with several gonimolobes at different stages of development; note the elongate basal cell in each gonimolobe. Scale bar, 25 μm. (G) A fully mature gonimoblast. Scale bar, 50 μm.
Ptilotoea (Moe and Silva 1983, Hommersand and Fredericq 2001) are similar in this regard. As a consequence the vegetative structure of Sciuromothamnion becomes important to consider when eliminating all tribes but the Callithamnieae and Ptilotoea from serious consideration, the other tribes all being characterized by whorled periaxial cells to greater or lesser extents and additionally lacking the paired auxiliary cells and horizontal alignment of their carpogonial branches.

A procarp structure nearly identical to that of the Callithamnieae is reported for mostly southern hemisphere members of the Ptilotoea such as Euptilota, Diapese, Falklandiella, and Georgiella (Itono 1977, Moe and Silva 1979, 1983, Hommersand and Fredericq 2001), although not for other mostly northern hemisphere representatives. This apparent disparity, however, is likely to reflect the polyphyletic nature of the tribe as indicated by both morphological and molecular evidence (Hommersand 1989, Hommersand et al. 1998, Saunders and Kraft, unpublished data).

Sciuromothamnion also relates to the Callithamnieae and most southern hemisphere Ptilotoea in regard to immediate post-fertilization events. In Callithamnion corymbosum (J. E. Smith) Lyngbye (Oltmans 1898) and Aglaothamnion halliae (Collins) Aponte, Ballantine and J. N. Norris (Hommersand 1997), the transfer of the diploid nucleus from the carpogonium to the auxiliary cell by means of small connecting cells and the subsequent formation of a residual cell on the auxiliary cell mirrors these processes as they occur in Sciuromothamnion. Unlike Aglaothamnion and Callithamnion, however, the fertilized carpogonium of Sciuromothamnion does not undergo a mitosis followed by cytokinesis (O’Kelly and Baca 1984, Hommersand 1997), although this is also true for Seirospora (Aponte and Ballantine 1991, 1995, Kraft 1988) and Carpathothamnion (Wollaston 1992, as Thamnocarpus). The carpogonia of two representatives of the Ptilotoea, Georgiella and Euptilota, apparently also do not divide after fertilization (Moe and Silva 1983, Hommersand and Fredericq 2001). This linking feature appears to have taxonomic implications that, in combination with anatomical and molecular studies to be reported separately (M. H. Hommersand, personal communication), will result in the alliance of Sciuromothamnion with Seirospora, Carpathothamnion, and some former Ptilotoea into a tribe, sister to but distinct from both the Callithamnieae and Ptilotoea.

In most Ceramiaceae, diploidization is followed by a division of the auxiliary cell into an intercalary, subtending foot cell and a terminal gonimoblast initial. Three different types of cell apparently “designed” to segregate extraneous nuclei from the gonimoblast have been identified. The first type contains only the original haploid nucleus of the auxiliary cell (Hommersand 1997) or two haploid nuclei in cases where a single mitosis has taken place after diploidization by the connecting cell. This type arises from the basal part of the auxiliary cell and is segregated from the latter by an incomplete septum (Hommersand 1997). The foot cell, placed eccentrically between the gonimoblast initial and the basal cell, remains pit connected to the basal cell and is accompanied by the formation of a distinct residual cell, containing a diploid nucleus. The second type contains one or two haploid nuclei and a diploid nucleus. The foot cells are usually slender, attached to the gonimoblast initial by an incomplete septum, and two-lobed, one lobe containing either one or two haploid nuclei, the other a single diploid nucleus. It seems reasonable to hypothesize that the diploid nucleus in such foot cells is homologous to the one that becomes segregated into the lateral residual cell in type 1 species, because none of the authors illustrating this type of structure has observed a separate residual cell. Well-documented examples include Callithamnion corymbosum (J. E. Smith) Lyngbye (Oltmans 1898), Spyridia filamentosa (Wulfen) Harvey (Hommersand 1963), Seirospora orientalis Kraft (1988), Seirospora occidentalis Børgesen (Aponte and Ballantine 1991), and Rhodocallis elegans Kützing (Hommersand et al. 1998). The third type contains the haploid nucleus of the auxiliary cell but which is cut off completely and terminally from the proximal pole of the latter. This type was named a “disposal” cell by Huisman and Kraft (1992) when they introduced the genus Guiryella, a representative of the Monosporaeae (Huisman and Gordon-Mills 1994). Such cells had been previously observed in some tribes of the subfamily Compsothamnioideae as defined by Itono (1977) (e.g. the Spermothamnieae, Sphondylothamnieae, and Spongoclonieae (Gordon 1972, Stegenga 1986, as “rest” cells, Gordon-Mills and Norris 1986)), but Huisman and Kraft (1992) were the first to directly attribute their function to the elimination of extraneous haploid nuclei from diploidized auxiliary cells. Possession of a disposal cell may, as in the case of Sciuromothamnion, also be accompanied by the production of a residual cell, unlike the case of species with two-lobed foot cells in which a separate residual cell is never present. It also appears that many Ceramiaceae have lost the ability to produce any type of cell that rids the auxiliary cell of superfluous nuclei. In such cases the haploid nuclei appear to become quiescent in the auxiliary cell as it goes on to produce the wholly diploid cells of the gonimolobe initials.

Huisman and Kraft (1992) questioned the strict homology of residual, foot, and disposal cells, but we consider that all three types are possibly more than just analogous structures even though it is thought that the family Ceramiaceae as presently constituted is polyphyletic (H.-G. Choi, G. T. Kraft, I. K. Lee, and G. W. Saunders, unpublished data). This is because they equally function to eliminate haploid nuclei from the gonimoblast initial, leaving it and succeeding cells of the carposporophyte wholly diploid. Differences between the three types can be reduced to the orientation of the initial cleavage plane of cytokinesis in the auxiliary cell. If the cleavage plane is more or less per-
pendicular to the longitudinal axes of the auxiliary cell, the resulting cell will be a foot cell only containing the haploid nucleus/nuclei, positioned eccentrically between the auxiliary cell and basal cell. The diploid nucleus resulting from the mitosis of the fusing connecting cell is extruded simultaneously and forms a distinct residual cell (Hommersand 1997). In case of a cleavage plane more parallel to the longitudinal axes of the auxiliary cell, the resulting foot cell will be two-lobed. In the extreme case, where the cleavage plane does not include the pit-connection between the auxiliary cell and basal cell, a disposal cell is formed.

The different types of cells that eliminate extraneous nuclei from auxiliary cells appear to be genetically fixed within species, but their value as a diagnostic character at the genus and tribal levels in the Callithamnieae/Ptiloteae complex remains to be determined. Most representatives of the genus Seirospora possess two-lobed foot cells (Feldmann-Mazoyer 1941, Aponte and Ballantine 1995), but both foot and residual cells have been reported for Hirsutithallia (Womersley and Wollaston 1998, Fig. 121E, J), Aglaothamnion and Callithamnion (Oltmans 1898, Hommersand 1997).

Development of the carposporophyte in Sciurothamnion is typical of the Callithamnieae, the morphology of the gonimolobes and carposporangia being similar to most Aglaothamnion, Callithamnion, Carpothamnion, and Hirsutithallia species. The elongate sterile cells that subtend each gonimolobe in the new genus, however, have only been reported for the South African Carpothamnion molle (Wollaston) Silva (Wollaston 1992, as Thammocarpus mollis Wollaston) and appear to be a specialization, one independently arrived at in unrelated genera such as Dasyphila (Kraft and Wilson 1997) and Hirsutithallia (Womersley and Wollaston 1998). Despite similarities between Sciurothamnion and Seirospora in procarp and early gonimoblast features, their mature carposporophytes differ significantly, Sciurothamnion having multiseriate rounded gonimolobes whereas those of Seirospora are composed of uniseriate chains (Miranda 1932, Feldmann-Mazoyer 1941, Kraft 1988, Maggs and Hommersand 1993). This appears to be an autapomorphic feature of Seirospora, one finding roughly parallel expression only in the genus Arvadenum of the Ceramiaceae (Norris and Abbott 1992).

Male structures of Sciurothamnion are similar to those encountered in many tribes of the Ceramiaceae, including the Callithamnieae and Ptiloteae. Two forms of spermatal branchlets are known in the former tribe, erect filaments and hemispherical cushions. Because it is easy to visualize the pulvinate type being derived from erect filaments through reduction of fertile axial cell numbers and their reorientation, perhaps more phylogenetic importance should be attached to the location of the spermatal nuclei. In Aglaothamnion, Callithamnion (Feldmann-Mazoyer 1941), and apparently also in Carpothamnion and Hirsutithallia (Wollaston 1992, as Thammocarpus, Womersley and Wollaston 1998), the nucleus lies in a median position, whereas in Seirospora and Sciurothamnion it is located distally (Aponte and Ballantine 1995, this study). The absolute taxonomic significance of this distinction is not clear, but it does constitute yet one more way in which Sciurothamnion and Seirospora share a feature that other Callithamnieae apparently lack.

Although in many ways secondary to reproductive processes in the higher level taxonomy of the Ceramiaceae, vegetative construction is important to establish tribes and, as a practical matter, largely guides the tribal placement of most genera. Patterns of division of the apical cell are correlated with the primary growth patterns that tend to be diagnostic of tribes (Moe and Silva 1979). A 1/4 spiral branching pattern in species that form only one or two periaxial cells per indeterminate-axisial cell seems to be encountered only in some genera of the Callithamnieae and Spongoclonieae (Itono 1977, Norris 1985, Wollaston 1990), a 1/2 spiral being the norm in many Callithamnieae, most Spongoclonieae, and all Compsothamnieae and Ptiloteae. Although several unrelated groups exhibit a decussate branching pattern when bearing opposite determinate laterals, the combination in Sciurothamnion of 1/4 spiral first-lateral phyllotomy followed by the development of a second periaxial cell directly opposite the first is unique among the Ceramiaceae. The absolute phylogenetic value of this character is probably limited, however, because it seems likely that various types of apical divisions and resulting primary branching patterns have arisen several times independently. Assuming that the most primitive structure in Ceramiaceae is a primary-axial filament bearing whorls of laterals (Hommersand 1963, Wollaston 1971), the branch structure of the Callithamnieae can perhaps best be explained by the loss of the second-formed lateral, a feature that Sciurothamnion has relicly retained.

Apart from the number of laterals per axial cell, the entire vegetative thallus of Sciurothamnion is very Callithamnion-like. In Sciurothamnion, the Callithamnieae generally (e.g. Dixon and Price 1981, Coomans and Hommersand 1990), the Rhodolcallieae (Hommersand et al. 1998), and possibly other genera such as Gymnothamnion, Plumaria, and some species of Ptilota (M. H. Hommersand, personal communication), indeterminate axes are formed by direct transformation of the apical cells of determinate laterals, although this feature is difficult to determine in the Callithamnieae because the branching pattern of determinate and indeterminate branches is virtually identical. In Sciurothamnion, on the other hand, it is possible to see where the pseudo-dichotomies of determinate laterals undergo a transition to opposite-decussate branching and thus the precise point at which the indeterminate lateral has been produced. This sort of phenomenon allowed Millar and Kraft (1984) to establish the analogous process of indeterminate-axis transition in the gigartinean genus Acrosymphyton.

A further vegetative character linking Sciurothamnion to the Callithamnieae is its cortical morphology.
Wollaston (1992, as Thamnocarpus) described a nearly identical cortex for both the Australian *Carpothamnion gunnianum* (Harvey) Kützing and the South African *C. molle*, for in all three a thick cortex envelops all but the extreme tips of the indeterminate laterals and is produced by means of downward growing rhizoidal filaments that originate from the proximal cells of determine laterals. As in *Carpothamnion*, the peripheral corticating filaments of *Sciurothamnion* cut off small isodiamic cells that form a continuous mosaic over the axes.

Based on the combination of reproductive and vegetative characters detailed above, we believe that *Sciurothamnion* is distinct from any described genus of the Ceramiaceae. Its closest affinities in most respects appear to lie with some of the Callithamnieae, particularly the genera *Seirospora* and *Carpothamnion*, although there are sufficient differences in branching and processes by which haploid nuclei are eliminated from auxiliary cells to suggest that the present generic makeup of the Callithamnieae needs reassessment. Challenges to the monophyly of the present Piloteae, some members of which show reproductive and vegetative similarities to *Sciurothamnion*, are soon to be reported (M. H. Hommersand, personal communication) and will include molecular data on *Sciurothamnion*. Because those studies will determine the final tribal placement of our new genus, we limit our present treatment to its description and consideration of its most distinctive features.

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