**Skeletonella nelsoniae** gen. et sp. nov., representing a new tribe of marine macroalgae, the Skeletonelleae (Ceramiaceae, Rhodophyta)

ALAN J.K. MILLAR* and OLIVIER DE CLERCK

1Royal Botanic Gardens Sydney, Mrs Macquaries Rd, Sydney, NSW 2000, Australia
2Research Group Phycology, Biology Department, Ghent University, Krijgslaan 281/S8, 9000 Ghent, Belgium


*Skeletonella nelsoniae* gen. et sp. nov. is described from sublittoral habitats at Three Kings Islands (34°09′S, 172°10′E) off the northern cape of New Zealand. Plants are diminutive, reaching a height of only 2.5 mm, and consist of erect alternately branched, monosiphonous, uniseriate axes that bear two mostly simple, equal and opposite, distichously arranged determinate lateral branches from each axial cell. Laters are cut off from axial cells by a pronounced concavo-convex septum. Typical protrusions that precede cell division are absent, and the newly formed lateral branch initial sits nearly entirely within the original contour of the axial cell. Procarps are borne on the basal cell of a two-celled determinate lateral and consist of a four-celled carpogonial branch. The determinate lateral opposite the two-celled lateral, which bears the carpogonium, is suppressed and is never more than one cell long. After fertilization, the auxiliary cell is cut off from the supporting cell and then divides once into a foot cell and a gonimoblast initial. At this stage involucral branchlets are produced de novo from the hyophycean cell to enclose the maturing carposporophyte. Spermatangial heads are transformed from the distal cells of determinate laterals and each fertile axial cell divides longitudinally to form a whorl of four periaxial cells, which in turn, divide twice to form two spermatangial mother cells each bearing one to two spermatangia. This combination of features is shown to be unique in the family Ceramiaceae, and thus the new tribe Skeletonelleae is proposed.

**Key Words:** *Skeletonella nelsoniae* gen. et sp. nov., Skeletonelleae trib. nov, Rhodophyta, Ceramiaceae, Marine macroalgae

**INTRODUCTION**

The red algal order Ceramiales is one of the largest groups of marine algae and is represented on almost every coastline in the world. Of the 15 genera that make up this order (Ceramiaceae Dumortier, Delesseriaceae Bory, Dasyaceae Kützing, Sarcomeniaceae Womersley and Rhodomelaceae Areuschou) the Ceramiaceae contains genera that are the most morphologically recognisable due to their uniform monosiphonous, uniseriate filaments. Unlike the other four families that have a fundamental polysiphonous axis that is often heavily corticated, hence obscuring this feature, the Ceramiaceae have at most some periaxial cells or reduced whorl branchlets that cover the central axial cell row, and thus their monosiphonous nature can easily be detected. With the sole exception of the genus *Spyridia* Harvey, all taxa in the Ceramiaceae have naked carposporophytes that lack a true pericarp (a sterile protective covering that completely envelops the carposporophyte in which the involucral filaments are united by secondary pit-connections; Womersley 1998). Some genera of the distinctive tribe Griffithsiaceae do have substantial, synchronously developed involucral filaments of enlarged cells that surround and almost completely cover the carposporophyte (Baldock 1976; Millar 1986; Millar & Abbott 1997), but these are not secondarily pit-connected. Some would also argue that *Lejolisia* Bornet has a pericarp (Womersley 1998), but again, we argue the involucral filaments are not secondarily pit-connected and are simply encased in a mucilage sheath.

The Ceramiaceae consists of approximately 100 genera that are arranged into some 25 tribes. Australia and New Zealand host the vast majority of these, with the southern Australian coastline alone harbouring 22 tribes, 65 genera and 159 species (Womersley 1998). Vast tracks of New Zealand’s coastline remain phycologically unexplored (Adams 1994; Adams & Nelson 1985) so it was not surprising that collections from the remote and wind-swept rocky archipelago to the north of the northern cape of New Zealand, known as Three Kings Islands (Nelson & Adams 1990, fig. 1), have uncovered a diminutive red algal genus and species that is undescribed. Furthermore, whereas the vegetative morphology of this new genus superficially resembles that of several established tribes, the character combination of procarp structure, early postfertilization events, spermatangial heads, and distinctive branching pattern strongly suggests that it represents a new tribe.

Due to their diminutive stature, the plants were not knowingly collected *in situ*, but were found while undertaking laboratory microscopical examinations of numerous epiphytic species growing on the stipes of larger algae. Due to this after-the-fact discovery and the relative isolation and difficulty of returning to the type locality, it was not possible to sequence the DNA of fresh material.

**MATERIAL AND METHODS**

All collections were obtained using SCUBA and preserved in 4% formalin-seawater. Permanent whole mount microscope slides were prepared using aniline blue and corn syrup mixed according to the methods described by Millar & Wynne (1992). Voucher specimens are housed at the National Herbarium of New South Wales (NSW), Ghent University, Belgium (GENT) and the Museum of New Zealand Te Papa Tongarewa (WELT). Herbarium abbreviations are designated as

* Corresponding author (alan.millar@rbgsyd.nsw.gov.au)
RESULTS AND OBSERVATIONS

**Skeletonella** A. Millar & De Clerck *gen. nov.*

Thalli erect, eocuticatæ, ramis lateralis oppositis determinatis monosiphoniis uniseriatis et quaque cellulae axiales orientibus, per septa concavo-convexa a cellulis axialsibus abscessis; spermatangia in verticillis cellularum maternarum portata e cellulis ramorum lateraliis determinatorum orientibus; ramus carpogoniis 4-cellularis, in cellula basali rami lateraliis bicellularis determinati portatus, cellula basali se pro cellula sustinenti gerente et cellula apicali remanente affixa; carposporophyta filamentis involucralibus in cellulis hypogenesis et alteris cingentibus portatis.

Thalli erect, eocuticatæ, with opposite determinate monosiphonous, uniseriate determinate laterals arising from each axial cell, cut off from axial cells by concavo-convex septa; spermatangia borne from whorls of mother cells developed from cells of determinate laterals; carpogonial branch four-celled, borne on basal cell of two-celled determinate lateral with basal acting as supporting cell and apical cell remaining attached; carposporophytes with involucral filaments borne from hypogenous and other surrounding cells.

**TYPE AND ONLY KNOWN LOCALITY**: Arch Island, Princes Rocks, Three Kings Islands, New Zealand, 25 m deep epiphytic on the lower main axes of *Sargassum johnsonii* V.J. Chapman.

**ETYMOLOGY**: From the English word *skeleton* (as in the bones of an animal) and the Latin suffix -*ella*, meaning little or diminutive, referring to the branching pattern that is reminiscent of a little fish’s backbone and ribs.

**Skeletonella nelsoniae** A. Millar & De Clerck *sp. nov.*

(Figs 1–25)

Thalli ad 2.5 mm alti, cellulis axialsibus ad 60 μm in diametro (parietē cellulārum inclusū) et 48 μm longīs, affīxī per rhizoideae multicellularia uniseriata ramosa quae sunt rami laterales determinati muta-tī; laterales determinati ad 12 μm in diametro et 15 cellulas longīs, leniter curvī in latere abaxialī; capitula spermatangialia ad 72 μm longa et 24 μm in diametro (spermatangia ad 2 μm in diametro); carposporangia ovoidea ad 20 μm longa et 12 μm in diametro. Tetrasporangia ignota.

Thalli ad 2.5 mm in height, axial cells to 60 μm in diameter (including cell wall) by 48 μm long; attached by multicellular, uniseriate branched rhizoids that are modified determinate laterals; determinate laterals to 12 μm in diameter and 15 cells long, curved slightly abaxially; spermatangial heads to 72 μm long and 24 μm in diameter (spermatangia to 2 μm in diameter); carposporangia ovoid to 20 μm long by 12 μm in diameter. Tetrasporangia unknown.

**HOLOTYPE**: NSW 486121 (Fig. 1) collected by A.J.K. Millar & R. De Nys, 24 November 1998. This specimen is filed in WELT.

**ISOTYPES**: in NSW 486129 and 486130, NSW Slide 22-48, NSW Slide 27-56, NSW Slide 27-58 and NSW Slide 27-59; in GENT ex NSW 486128 = NSW Slide 27-57.

**TYPE AND ONLY KNOWN LOCALITY**: Arch Island, Princes Rocks, Three Kings Islands, New Zealand, 25 m deep epiphytic on the lower main axes of *Sargassum johnsonii* V.J. Chapman.

**ETYMOLOGY**: The epithet honours our friend and colleague, Dr Wendy A. Nelson (National Institute of Water and Atmospheric research, NIWA, New Zealand), who has dedicated her career to the study of marine macroalgae in New Zealand.

**Habit and vegetative structures**

Thallus erect (Figs 1–3), up to 2.5 mm high, attached by means of basal multicellular, uniseriate, irregularly branched rhizoids (Figs 4, 5). Multiple main axes may arise from a consolidated base (Fig. 1), or singly (Figs 2, 3). Fronds consist of eocuticrate, indeterminate axes that branch three to five times alternately. Axial cells initially cut off branches unilaterally on the convex side of the main indeterminate axis (Fig. 6), with the first lateral cut off two to three cells below the apex by means of a pronounced concavo-convex division. Some two to five cells below the apical cell, axial cells then cut off an opposite lateral branch, which may be determinate or indeterminate in type (Fig. 6), ultimately displaying equal and opposite branches throughout (Fig. 2). Both determinate and indeterminate laterals are borne at approximately 45° to the parent axes (Figs 1–3) and in no predetermined pattern, although indeterminate laterals arise irregularly every 2–13 axial cells by direct conversion of determinate laterals. Determinate laterals are mostly unbranched (Figs 2, 3) and reach 9–15 cells or 180–225 μm in length. In older and proximal parts, proximal cells of determinate laterals may bear a few simple branchlets in adaxial position on both (Fig. 7) or one side of the main axis (Fig. 8).

Apical cells of erect axes divide obliquely into two nearly equal cells (Fig. 11), or by a transverse concavo-convex wall so that new apical cells sit in the distal cup of subapical cells (Figs 6, 12). The initial of a second lateral, placed 180° opposite the first, is cut off from the third to sixth segment onwards. Indeterminate axes curve distinctly sinusoidally (Figs 1–3), with the first formed lateral produced in a secund series on the convex side of the curve (Figs 6, 10–12). The initiation of an indeterminate side axis causes the apical cells of the bearing axes to begin dividing such that the axis recurves abaxially and thus produces the sinusoidal nature of the axes (Figs 6, 13). Although this is evident in plants bearing spermatangial heads, it is most pronounced in female plants (Fig. 13).

Apical cells were seen to divide by transverse septa rather than oblique septa only in axes being formed from transformed rhizoidal filaments near the base of plants. These young regenerated axes are straight, showing no signs of curvature. Axes attain a width of 60 μm near their bases; axial cells themselves are mostly twice as long as broad.

The growth of determinate laterals proceeds through transverse divisions of apical cells and elongation of the derivatives. Periaxial cells (basal cells) of determinate laterals are conspicuous in their trapezoidal shape (Figs 7, 9). This is most pronounced in the middle portions of thalli, where the concavo-convex division by which determinate laterals were cut off is reflected in the broadly triangular shape of axial cells (Fig. 9). Epibasal cells of determinate laterals measure 12–16 μm in diameter × 18–22 μm long, and narrow slightly to apical cells that are 10 × 15 μm in diameter. No deciduous hairs were observed.

**Reproductive structures**

Procarps are initiated near the apices of indeterminate axes (Figs 10–12). Several carpogonial branches are formed along a single axis, usually separated by three to seven axial cells (Fig. 13). Any of them may potentially give rise to carposporophytes. The fertile axial cell is usually the cell immedi-

Fig. 1. Several plants on the Holotype microscope slide. NSW 486121, NSW Slide 27-56. Scale = 500 μm.

Fig. 2. Thallus with alternate branching. NSW 486129, NSW Slide 27-59. Scale = 500 μm.

Fig. 3. Single thallus with basal rhizoids. NSW 486129, NSW Slide 27-59. Scale = 500 μm.

Fig. 4. Base of thallus with both rhizoids and determinate lateral branches borne on basal segments. NSW Slide 22-48. Scale = 150 μm.

Fig. 5. Detail of uniseriate, branched rhizoids. NSW Slide 27-56. Scale = 100 μm.

Fig. 6. Apices of indeterminate axes showing laterals (arrows) borne by concavo-convex divisions of axial cells. NSW Slide 27-59. Scale = 50 μm.

Fig. 7. Unilaterally, branched, determinate laterals on both sides of main axis. NSW Slide 22-48. Scale = 100 μm.

Fig. 8. Branched determinate laterals on only one side of main axis. NSW Slide 22-48. Scale = 100 μm.

Fig. 9. Main indeterminate axis with distinctively shaped axial cells and basal cells of determinate laterals. NSW Slide 27-59. Scale = 100 μm.

Fig. 10. Procarp at two-celled stage. NSW Slide 22-48. Scale = 20 μm.

Fig. 11. Procarp at three-celled stage. NSW Slide 27-56. Scale = 20 μm.

Fig. 12. Mature carpogonial branch with extended trichogyne. NSW Slide 27-56. Scale = 20 μm.

Fig. 13. Series of procarps (arrows) on sinusoidally shaped main indeterminate axis. NSW Slide 22-48. Scale = 50 μm.

Fig. 14. Fertilized procarp bearing dome-shaped auxiliary cell (aux), sterile apical cell (a), basal cells of carpogonial branch (cbr), fertile axial cell (fac), and supporting cell (su). NSW Slide 27-57 (in GENT). Scale = 10 μm.

Fig. 15. Procarp with connecting cell (arrow head). NSW Slide 27-57 (in GENT). Scale = 10 μm.

Fig. 16. *De novo* involucral branches in plane perpendicular to plane of thallus. NSW Slide 27-56. Scale = 50 μm.

Fig. 17. Hypogenous cell (arrow) bearing two involucral filaments in same plane as thallus. NSW Slide 27-59. Scale = 50 μm.
Following (presumed) fertilization, the supporting cell divides unevenly to produce a large, dome-shaped auxiliary cell (Figs 14, 20). The carpogonium cuts off a distal capping cell. The fertilization nucleus (or its derivative) is most likely transferred to the auxiliary cell by what appears to be a connecting tube, which fuses to the base of the auxiliary cell. Although the actual diploidization of the auxiliary cell was not seen, detached connecting tubes were observed (Fig. 15). The auxiliary cell divides unequally to produce a small basal foot cell and a large distal gonimoblast initial (Fig. 20). The latter divides transversely to form the first gonimolobe initial (Fig. 21). Additional gonimolobe initials (up to four) are soon cut off from the sides of the gonimoblast initial. Gonimolobes mature sequentially and are composed of synchronously maturing carposporangia, 15-18 μm in diameter (Fig. 22). All cells, except the basal cells, which form distinctive stalk cells, are transformed into carposporangia. The fertile axial cell, foot cell and auxiliary cell fuse as the gonimolobes develop, but the individual cells remain recognizable (Fig. 22). The fertile axial cell does not expand once the procarp has been fertilized, and the fusion cell does not incorporate other axial cells. The result is a fertile axial cell that is much smaller than the subtending axial cells. The initial apical cell of the two-celled determinate lateral and the cells of the carpogonial branch remain recognizable during carposporophyte development. Following fertilization, the cell subtending the fertile axial cell (the hypogenous cell) initiates two involucral branches de novo (Figs 16-18, 21) and in a plane perpendicular to that of the vegetative thallus branches. The involucre thus consists mainly of four branches. One is the indeterminate lateral that always subtends the fertile axial cell and is thus richly branched. The second is the simple determinate lateral borne opposite and in the same plane, which then begins to branch much like an indeterminate lateral. The third and fourth involucral filaments are cut off simultaneously from the hypogenous cell and in the plane perpendicular to those of the thallus branches. They thus form a quadriverticate branching pattern. Indeterminate and determinate laterals from the axial cell below the hypogenous cell may also contribute to the involucre. Involutural filaments branch and envelop the carposporophyte loosely (Figs 16, 17). An axis bearing a carposporophyte may continue to grow (Fig. 18).

Spermatangia are produced in heads that develop from determinate lateral branches (Fig. 23). Distal cells of determinate lateral branches (Fig. 25) divide sequentially in a longitudinal manner to cut off up to four periaxial cells radially (in a whorl). The first periaxial cell divides transversely and obliquely into two spermatangial mother cells that each produces one to two spermatia, each with an apical nucleus. A second, then third and ultimately fourth periaxial cell then develops sequentially. Periaxial cells can also divide twice, giving three spermatangial mother cells, each of which produces one or two spermatia. Spermatangial heads ultimately occupy the last four to eight segments of determinate laterals (Figs 24, 25) and are up to 72 μm long and 24 μm in diameter. Tetrasporangia and tetrasporophytes were not observed.

**DISCUSSION**

Given that *Skeletonella nelsoniae* is a very tiny epiphyte that grows only 2.5 mm high and only on the stipes of the endemic

---

**Fig. 18.** *Skeletonella nelsoniae*, mature carposporophytes surrounded by involucral branches borne from hypogenous cell (arrows). NSW Slide 27-56. Scale = 100 μm.

Fig. 19. Mature procarp bearing carpogonium (cp), supporting cell (su), fertile axial cell (fac), carpogonial branch cells (cb1, cb2, cb3) and sterile apical cell (a).

Fig. 20. Fertilized procarp with auxiliary cell that has divided into a foot cell (ft) and gonimoblast initial (gi), with capping cell (z).

Fig. 21. Early stage of carposporophyte with gonimoblast initial (gi) and first gonimolobe initial (gli).

Fig. 22. Carposporophyte with sequentially maturing gonimolobes (gli) and carposporangia.
Skeletonelleae trib. nov. 69

Figs. 23–25. Skeletonella nelsoniae, spermatangial development. NSW 486130, NSW Slide 27-58.

Fig. 23. Male plant bearing spermatangial heads. Scale 300 μm.

Fig. 24. Spermatangial heads developing from most determinate laterals. Scale 50 μm.

Fig. 25. Fertile axial cells undergoing longitudinal divisions (short arrow) to form periaxial cells that undergo oblique divisions (long arrows) to form spermatangial mother cells. Scale 40 μm.

According to Itono (1977), features of lateral branch initiation have probably evolved independently in several members of the Ceramiaceae, but the character appears to be constant within each tribe. In the vast majority of tribes, determinate laterals are initiated by means of a protrusion of the axial cell that is then cut off, and this is expressed in tribes for a reassessment of the tribal characters of the family Ceramiaceae. While we have not been able to use molecular evidence (due to its ex situ laboratory discovery) to help guide phylogenetic placement of the genus, Skeletonella displays such distinctive vegetative and reproductive morphological characters that we believe it represents a new tribe. The placement of Skeletonella in the family Ceramiaceae is beyond doubt. The monosiphonous and monopodial thallus architecture, combined with the near naked carpogonial branchlets that lack a consolidated pericarp, preclude placement in any of the other four families of the Ceramiaceae.

Defining the affinities of species and genera in the Ceramiaceae is a complicated undertaking because of the repetitive convergent and parallel evolution of easily observable vegetative characters. Indeed, recent studies aided by molecular sequences confirm that vegetative morphology is highly homoplastic and thus unreliable as a diagnostic tool at the generic and tribal level in Ceramiaceae (e.g. De Clerck et al. 2002; Hommersand et al. 2004, 2006). It appears that the most reliable characters that reflect a natural classification within the family (or at least our best approximation of natural relationships based on comparative gene sequence analysis) are to be found mainly among characters of the male and female reproductive systems. In the absence of molecular data, a review of the vegetative and reproductive features of Skeletonella, in comparison with other genera and tribes in the family Ceramiaceae, is necessary (Table 1).

On first appearance, Skeletonella most closely resembles Gymnothamnion, especially due to the opposite, distichous arrangement of its predominantly simple determinate laterals and the complete lack of cortex. Despite this striking resemblance in vegetative morphology, essential differences in procarp structure and postfertilization events indicate that the two genera are not closely related. In Gymnothamnion, traditionally considered a representative of the Ptiloteae (Feldmann-Mazoyer 1941; Kylin 1956; Hommersand 1963), but now assigned to its own tribe, the Gymnothamnieae (Kajimura 1989; Maggs & McIvor 2002), procarps are borne on the subapical cells of axes of limited growth. In that respect, Gymnothamnion resembles Skeletonella with the exception that the female fertile branchlet is several cells long as opposed to strictly two-celled in Skeletonella. The procarps of both genera, however, are fundamentally different in that the subapical cell should be considered as a fertile axial cell in Gymnothamnion. It cuts off two pericentral cells, one of which will become the supporting cell. The supporting cell itself bears a lateral sterile cell next to a four-celled carpogonial branch. In Skeletonella, the basal cell of a fertile lateral is the supporting cell and therefore procarps are formed in series along an indeterminate axis, rather than subterminal on a female axis of limited growth as in Gymnothamnion. In addition, sterile cells borne on the supporting cell, as observed in Gymnothamnion, are entirely absent in Skeletonella. Finally, Skeletonella has a distinct involucre of branched filaments surrounding the carpogonial branchlet, which is lacking in Gymnothamnion.

According to Itono (1977), features of lateral branch initiation have probably evolved independently in several members of the Ceramiaceae, but the character appears to be constant within each tribe. In the vast majority of tribes, determinate laterals are initiated by means of a protrusion of the axial cell that is then cut off, and this is expressed in tribes brown alga Sargassum johnsonii, which grows in deep water on the isolated, wind-swept, rocky archipelago of the Three Kings Islands some 80 nautical miles north of the northern tip of New Zealand, it is surprising that it has been discovered at all. Yet so distinctive is Skeletonella that its discovery calls
Table 1. Comparison of vegetative and reproductive characters of Skeletonella and several closely related tribes.1

<table>
<thead>
<tr>
<th>Vegetative characters</th>
<th>Gymnothamnieae</th>
<th>Balliella</th>
<th>Skeletonella</th>
<th>Antithamnieae</th>
<th>Heterothamnieae</th>
<th>Pterothamnieae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apex morphology</td>
<td>Straight</td>
<td>Straight to sinusoidal</td>
<td>Sinusoidal</td>
<td>Straight to sinusoidal</td>
<td>In whorls of two to four</td>
<td>Often sinusoidal</td>
</tr>
<tr>
<td>Branching pattern of main axes</td>
<td>Distichous; indeterminate axes with two opposite whorl branches</td>
<td>Distichous; indeterminate axes with two opposite whorl branches</td>
<td>Distichous; indeterminate axes with two opposite whorl branches</td>
<td>In whorls of two to four</td>
<td>In whorls of two to four</td>
<td></td>
</tr>
<tr>
<td>Initiation of laterals</td>
<td>Protrusion followed by a concavo-convex septum</td>
<td>Concavo-convex septum</td>
<td>Protrusion followed by a straight septum</td>
<td>Protrusion followed by a straight septum</td>
<td>Protrusion followed by a straight septum</td>
<td></td>
</tr>
<tr>
<td>Lateral branches</td>
<td>Initially unbranched, becoming pinnately branched</td>
<td>Opposite branches of unequal length, unbranched to pinnately branched</td>
<td>Unbranched or with one to three rudimentary adaxial branches on the proximal cells</td>
<td>Simple to branched</td>
<td>Simple to dichotomously branched</td>
<td></td>
</tr>
<tr>
<td>Formation of indeterminate axes</td>
<td>Replacing determinate laterals</td>
<td>Replacing determinate laterals</td>
<td>Developed from proximal cells of determinate laterals</td>
<td>Developed from proximal cells of determinate laterals or replacing determinate laterals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cortication</td>
<td>Absent</td>
<td>Loosely corticated from basal cells of whorl branches</td>
<td>Absent</td>
<td>Usually absent, sometimes basally corticated</td>
<td>Absent</td>
<td>Absent to densely corticated</td>
</tr>
<tr>
<td>Gland cells</td>
<td>Absent</td>
<td>Abaxial (rarely adaxial) on the proximal cells of determinate laterals</td>
<td>Absent</td>
<td>Usually present, on reduced branchlets or terminal</td>
<td>Usually present on whorl-branchlet cells</td>
<td>Usually present on whorl-branchlet cells</td>
</tr>
<tr>
<td>Cytology</td>
<td>Uninucleate</td>
<td>Uninucleate</td>
<td>Presumably uninucleate</td>
<td>Uninucleate</td>
<td>Uninucleate</td>
<td>Uninucleate</td>
</tr>
<tr>
<td>Reproductive characters</td>
<td>Procarp position</td>
<td>In series along indeterminate axes</td>
<td>In series along indeterminate axes</td>
<td>In series along indeterminate axes</td>
<td>In series along indeterminate axes</td>
<td>In series along indeterminate axes</td>
</tr>
<tr>
<td>Supporting cell</td>
<td>The basal cell of an ordinary determinate lateral</td>
<td>The basal cell of a reduced two-cell lateral</td>
<td>The basal cell of an ordinary determinate lateral</td>
<td>The basal cell of reduced laterals (two to four cells)</td>
<td>The basal cell of an ordinary lateral</td>
<td></td>
</tr>
<tr>
<td>No. of procarps/ fertile axial cell</td>
<td>One</td>
<td>One or two</td>
<td>One, the opposite vegetative lateral reduced to the periaxial cell</td>
<td>One or two</td>
<td>One or three</td>
<td></td>
</tr>
<tr>
<td>Carposporangia branch cells</td>
<td>Rounded</td>
<td>Rounded, curving around the supporting cell, parallel to the main axis</td>
<td>Narrow and elongate, curving around the supporting cell, parallel to the main axis</td>
<td>Rounded</td>
<td>Rounded</td>
<td></td>
</tr>
<tr>
<td>Sterile cells on the supporting cell</td>
<td>Present</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Gonimoblast initials</td>
<td>Clavate</td>
<td>Clavate</td>
<td>Clavate</td>
<td>Usually, undifferentiated</td>
<td>Usually, undifferentiated</td>
<td>Undifferentiated to clavate</td>
</tr>
<tr>
<td>Involucrum</td>
<td>Absent</td>
<td>Absent</td>
<td>Present (developed from cells below the fertile axial cell)</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td>Tetrads</td>
<td>Tetrahedrally to cruciately divided, usually (sub)terminal</td>
<td>Cruciate, cut off from the proximal cell of determinate laterals</td>
<td>Unknown</td>
<td>On normal whorl branchlets or on small lateral branches</td>
<td>On normal whorl branchlets</td>
<td>On normal whorl branchlets</td>
</tr>
</tbody>
</table>
such as Crouanieae, Antithamnieae, Pterothamnieae, Heterothamnieae, Delesseriopsieae, Wrangelieae, Callithamnieae, Euptilotoeae, Spongoclonieae, Composothamnieae and Pililotoeae. Only in the second group of tribes, including Ceramiaceae, Spyridiaceae, Spermatangieae and Griffithsieae, are laterals cut off by a concavo-convex septum at the distal end of the axial cells. In Skeletonella, axial cells do not expand laterally prior to cutting off a branch initial. Consequently, the newly formed cell lies completely within the original contour of the axial cell (Fig. 11). To us, this is a significant character in the description of a new tribe because it is reflected in the further development of the thallus. Even in mature parts of the thallus, the imprint of the original concavo-convex septum is clearly seen in the shape of the axial cells (Figs 7–9). Interestingly, the general morphological resemblance of Skeletonella to Gymnothamnion extends to some degree to the formation of lateral initials. Although in Gymnothamnion laterals are initiated by means of a protrusion, the septum that finally cuts off the lateral initial is pronouncedly concavo-convex (Stegenga, pers. comm.: Womersley 1998: fig. 57C). A type of cell division identical to Skeletonella is also observed in Ballia, now placed in its own order, the Balliales, and Inkylea, tentatively retained in the Ceramiaceae (Stegenga 1986; Choi et al. 2000).

In Skeletonella, only in axes being formed from transformed rhizoidal filaments near the base are apical cells seen to divide by transverse septa in a flat plane rather than in a concavo-convex or oblique manner. These young regenerated axes are straight, showing no signs of any curvature. The main indeterminate axes, however, are sinuously curved and this may correlate with the concavo-convex oblique divisions of apical and axial cells. Among the genera of the tribes listed above, this sinuous curvature is most pronounced in Skeletonella, although we do not assign any tribal significance to it.

The vegetative anatomy of Skeletonella is also reminiscent of a few genera and tribes related to the Antithamnieae (Huisman & Kraft 1984; Millar 1990; Womersley 1998) and of Balliella, which is currently assigned to the Delesseriopsieae (Athanasiadis 1996). Besides the fact that most of the taxa in these tribes have branched rather than simple determinate laterals, nearly all of their representatives bear typical gland or vesicular cells. Furthermore, indeterminate axes may replace determinate laterals or be borne on the periaxial cells of determinate laterals in the Antithamnieae, Heterothamnieae and Pterothamnieae (Wollaston 1968). In Skeletonella, as in Balliella, an indeterminate branch replaces a determinate lateral. Despite this resemblance in the ontogeny and morphology of branches of unlimited growth, a whole suite of characters unambiguously differentiates Balliella from Skeletonella: spherical gland cells in abaxial positions on periaxial cells, a loose, rag-like cortex, pinnately branched determinate laterals, and the absence of a postfertilization involucre surrounding the carposporophyte, to name a few.

The position and structure of the procarp as well as early postfertilization events relate Skeletonella to the Antithamnieae, Heterothamnieae, Pterothamnieae (Antithamnieae sensu lato) as well as to Balliella. Those algae, together with Warrenia and Plumariella, are shown to form a natural assemblage based on SSU sequence analyses (Han-Gu Choi and colleagues, pers. comm.). To recap, procarps in Skeletonella are formed in series along indeterminate axes, and the supporting cell is the basal cell of a two-celled fertile determinate lateral. In other words, the periaxial cell acts as the supporting cell and the apical cell remains attached, but takes no part in the development of the procarp or carposporophyte. No additional sterile cells are associated with the procarp, other than the remnant apical cell of the fertile determinate lateral. In all of the abovementioned taxa, except Warrenia (Wollaston 1971; Womersley 1998), the supporting cell is always a periaxial cell, and procarps are formed in series along indeterminate axes. The monotypic genus Warrenia represents a special case in the Ceramiaceae in that about every cell of the thallus can act as a supporting cell. This may be because there is little differentiation between determinate and indeterminate branches in Warrenia. This feature formed the basis for considering Warrenia phylogenetically primitive or basal (Wollaston 1971). Although in many representatives of the Antithamnieae, Heterothamnieae and Pterothamnieae the procarp bearing lateral might be fully developed, there is a tendency towards reduction of this branch. This is most pronounced in the Heterothamnieae in which several genera (e.g. Heterothamnion, Antithamnionella p.p., Trithamnion) exhibit the same condition as Skeletonella, whereby the lateral branch is reduced to a two-celled condition. One of the features that sets Skeletonella apart is the suppression of the remaining vegetative laterals on the fertile axial cell. The vegetative lateral opposite the two-celled fertile lateral is not cut off until the carpogonial branch has fully formed. Even following fertilization, this periaxial cell remains dormant and does not participate in the formation of involucral branches, although it may divide once to form a two-celled lateral (Fig. 21). In the Antithamnietae s.l., as in Balliella, the vegetative laterals on the fertile axial cell display a morphology that is identical to that of nonfertile segments. A second contrasting character is presented by the ontogeny and shape of the carpogonial branch. Although detailed illustrations and descriptions of carpogonial branch initiation in the Antithamnieae s.l. are rare, it is most likely that the initials of the carpogonial branch are formed at a 90° angle to the sterile group as was illustrated by Wollaston (1968) for Pterothamnion nodiferum (J. Agardh) Athanasiadis & Kraft (Hommersand, pers. comm.). In Skeletonella, as in Balliella and Plumariella, the initial of the car-
pogonial branch is cut off abaxially from the supporting cell, resulting in a carposgonial branch that curves around the supporting cell. Characters of carposgonial branch initiation may be important indicators of phylogenetic relatedness among certain genera in the Ceramiaceae, but unfortunately, detailed literature reports are too scarce to allow any conclusions at this stage. Additionally, the ultimate shape of the carposgonial branch differs markedly between Skeletonella and the Antithamnieae s.l. Carposgonial branches in the Antithamnieae, Heterothamnieae and Pterothamnieae are curved upwards or straight (depending on the interpretation) and end in a characteristic conical carposgonium with the trichogyne directed along the long axis of the carposgonial branch (Wollasten 1968; Athanasiadis 1996, 2002; Cho et al. 2005). In Skeletonella, the trichogyne of the flask-shaped carposgonium is directed at nearly 90° relative to the orientation of the carposgonial branch (Figs 12–15).

In all Ceramiaceae, postfertilization events involve the formation of an auxiliary cell following fertilization of the carposgonium, but some uncertainty exists regarding the mechanism of transfer of the diploid nucleus to the auxiliary cell. Feldmann-Mazoyer (1941) and Wollasten (1968) depicted connecting cells for the Crouanieae, Antithamnieae and Heterothamnieae. Maggs & Hommersand (1993) on the other hand leave a possibility for direct fusion via a connecting tube. More recently, Cho et al. (2005) provided evidence that diploidization of the auxiliary cell in Antithamnion nipponicum proceeds by means of a connecting tube as well. Our observations in Skeletonella also point towards a connecting tube rather than a connecting cell (Fig. 15). Further development of the gonimoblast is very similar in all the aforementioned taxa, but Skeletonella stands apart in producing a clear and defined involucre (Fig. 16). The involucre itself is also distinctive, consisting mainly of four branches. One is the pre-existing indeterminate lateral that always arises from the cell that subtends the fertile axial cell (the hypogenous cell), one is the pre-existing determinate branch opposite and in the same plane as the first (Fig. 18), and the other two are produced de novo, simultaneously and in the plane perpendicular to that of the thallus (Fig. 16). Such involucral branches are absent in the Antithamnieae s.l., where carposporophytes are entirely naked or only partly surrounded by normal vegetative branches that existed before fertilization. Skeletonella thus displays quadriverticillate branching, at least in the formation of the involucre. Of interest is that many bilaterally branched Ceramiaceae exhibit this character, suggesting that quadriverticillate branching may be an ancestral condition in the Ceramiaceae.

Spermatangia generally have been given less attention in the classification of the Ceramiaceae compared with female reproductive structures. Several types of spermatangial development, however, can be discerned. In some tribes, such as the Crouanieae, outer cortical cells of ordinary lateral branch-es function as spermatangial mother cells and bear terminal spermatangia. In others, such as the Callithamnieae, spermatangia are borne on mother cells produced unilaterally along cells of determinate lateral axes. And in still others, such as the Antithamnieae, spermatangia are formed as in Skeletonella, where cells of determinate laterals divide to form whorls of periaxial cells that cut off spermatangial mother cells from which spermatangia are borne. The resulting structure forms a distinctive spermatangial ‘head’.

The cellular development of spermatangial heads differs between genera and tribes, and it is important to note how many cells are cut off in each whorl and what kinds of filaments they initiate. In Davythamniiella of the Composothamnieae, the uppermost two to three cells function as spermatangial mother cells and produce three or four spermatangia directly while the medial and lower axial cells each produce one to four short branchlets that increase in length but decrease in number towards the base. These short branches curve upwards and their cells produce two or three spermatangial mother cells (Womersley 1998, p. 275, fig. 129D). This differs from the development in Gymnofyllum (also of the Composothamnieae) in which three periaxial cells are borne in whorls from each fertile axial cell of the determinate lateral, with each periaxial cell functioning as a spermatangial mother cell and bearing two to four spermatangia (Huisman & Kraft 1983, fig. 13). In Skeletonella, each fertile axial cell produces up to four periaxial cells that may divide obliquely twice to form three spermatangial mother cells that in turn produce one or two spermatangia.

A feature that may bear closer scrutiny as a diagnostic character is the position of the nucleus of the spermatium. The nucleus appears to be apical and not median in Skeletonella as well as in Balillia (De Clerck, pers. observ.). This at first sight trivial similarity may have taxonomic relevance as was shown in recent studies involving the tribes Callithamnieae and Euptiloteae (De Clerck et al. 2002; McIvor et al. 2002; Hommersand et al. 2006).

In summation of the vegetative characters, the combination of concavo-convex oblique cell division with correspondingly regular, alternately branched, indeterminate axes, a distichous branching pattern in which two equal determinate laterals are formed, and the complete absence of vesicular (gland) cells, cortication, and prostrate parts strongly suggests that Skeletonella cannot be placed in any of the existing tribes without critically emending their respective diagnoses. In addition to and in combination with characters of the male and female reproductive structures and of the carposporophytes, we propose the new tribe, Skeletonelleae, to accommodate this new genus.

**Skeletonelleae A. Millar & De Clerck trib. nov.**

Tribus nova Ceramiacearum. Thalli rami lateralisibus duobus distichis e quaque cellula axiali, cellulis glandularibus (vesicularibus) nullis, ramis e divisionibus obliquis concavo-convexis cellularum apicalium axialiumque orientibus. Ramuli spermataangiales capitula distincta formantes, ex apicibus ramorum lateralia determinato- rum orientes; nucleus spermatii basalis. Procarpia in cellula basali rami lateralis bicuscularis fertilib determinatib portata, cellula basali se pro cellula sustentii gerente, ramum carposgonialem 4-cellularem ferente parallelo ad axem longitudinalinem cellularum fertilib axialis, cellula apicali remanente affixa ad cellulum susteniment sed sine alteris cellulis sterilibus. Carposporophyta constantia e gonomilobis effectis in ordinem, ex initio gonomilobasti et cellula pedaria orien-tibus.

**GENUS TYPICUM:** Skeletonella A. Millar & De Clerck

A new tribe of Ceramiaceae. Thalli with two distichously arranged lateral branches per axial cell; gland (vesicular) cells lacking; branches arising by concavo-convex oblique divisions of apical cells and axial cells. Spermatangial branchlets forming distinct heads, developed from distal ends of determinate laterals; sperma-
tium nucleus apical. Procarps borne on the basal cell of a two-celled fertile determinate lateral, the basal cell acting as the supporting cell and bearing a four-celled carpogonial branch directed parallel to the longitudinal axis of the fertile axial cell, and the apical cell remaining attached to the supporting cell but with no additional sterile cells produced. Carposporophytes consisting of sequentially produced gonimoblasts arising from a gonimoblast initial and a foot cell, surrounded by an involucre of four branched filaments.

**TYPE GENUS:** *Skeletonella* A. Millar & De Clerck.

**ACKNOWLEDGEMENTS**

The senior author sincerely thanks Dr Wendy Nelson, NIWA, New Zealand, for the invitation to join the Three Kings Islands expedition. Thanks are also due to Dr Rocky De Nys for partnering on all dives. Funds for this research arose from Botanic Gardens Trust funds, Australian Geographic and National Geographic Society of America sponsorship. O.D.C. is indebted to the Fund for Research Flanders for a grant as postdoctoral researcher. We also express our gratitude to the Fund for Scientific Research Flanders for a research grant to Max Hommersand and Herre Stegenga for in-depth discussions on the generic affinities of *Skeletonella*, Max (again) and Craig Schneider for critically reviewing the manuscript, Paul Gabrielson for his editorial assistance, and Han-Gu Choi and Craig Schneider for critically reviewing the manuscript, Paul Gabrielson for his editorial assistance, and Han-Gu Choi and colleagues for sharing with us their unpublished tree of Ceramiaceae phylogeny. Mark Garland’s botanical Latin services are very much appreciated.

**REFERENCES**


ATHANASIADIS A. 2002. Recent additions to the subfamily Ceramioideae (Rhodophyta) and the nature of the ceramielean ancestor. *Constance* 83.6.


Received 15 March 2006; accepted 8 August 2006

Associate editor: Paul Gabrielson