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Woelkerlingia minuta gen. et sp. nov. from the Mediterranean Sea and a reassessment of the genus *Lomathamnion*, with the description of two new genera: *Hommersandiella* gen. nov. and *Stegengaea* gen. nov. (Ceramiaceae, Rhodophyta)

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Abstract – The new genus *Woelkerlingia*, with the new species *W. minuta* (Ceramiaceae, Rhodophyta), is described from the Mediterranean Sea. This genus, belonging to the tribe Spermothamnieae, seems related to *Lomathamnion* (type species *L. epicodii*) from which it differs mainly in having terminal female fertile filaments with only the apical and subapical cells smaller than other vegetative cells, and terminal spermatangial heads with spermatangia produced directly by periaxial cells. Since the other two species of *Lomathamnion* (*L. capense* and *L. humile*) do not show the diagnostic characters of the genus and appear to be distinct from each other in main reproductive characters (except for only one periaxial cell produced by the subapical cell of the female fertile filament), two new genera, *Stegengaea* and *Hommersandiella*, are proposed to accommodate *L. capense* and *L. humile*, respectively.

Aeolian Islands / Ceramiaceae / *Hommersandiella* / *Lomathamnion* / *Stegengaea* / *Woelkerlingia minuta* / Mediterranean Sea / Rhodophyta

Résumé – *Woelkerlingia minuta* gen. et sp. nov. de la mer Méditerranée et une réévaluation du genre *Lomathamnion*, avec la description de deux nouveaux genres : *Hommersandiella* gen. nov. et *Stegengaea* gen. nov. (Ceramiaceae, Rhodophyta). Le nouveau genre *Woelkerlingia* avec l'espèce nouvelle *W. minuta* (Ceramiaceae, Rhodophyta) est décrit de la mer Méditerranée. Ce genre qui appartient à la tribu de Spermothamnieae, semble apparenté à *Lomathamnion* (espèce type *L. epicodii*) dont il diffère principalement par la présence de filaments terminaux femelles fertiles ayant seulement les cellules apicale et subapicale plus petites que les autres cellules végétatives, et les têtes terminales mâles portant des spermatocystes produits directement par des cellules périaxiales. Les deux autres espèces de *Lomathamnion* (*L. capense* et *L. humile*) ne présentent pas les caractères diagnostiques du genre et apparaissent distinctes l'une de l'autre par d'importants caractères de reproduction (sauf pour la seule cellule périaxiale produite par la cellule subapicale du filament femelle fertile) ; deux nouveaux genres, *Stegengaea* et *Hommersandiella*, sont proposés pour accommoder respectivement *L. capense* et *L. humile*.

Iles Eoliennes / Ceramiaceae / *Hommersandiella* / *Lomathamnion* / *Stegengaea* / *Woelkerlingia minuta* / Mer Méditerranée / Rhodophyta

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INTRODUCTION

The family Ceramiaceae is represented in the Mediterranean Sea by 34 genera (Gómez Garreta *et al.*, 2001) belonging to 19 tribes (Guiry, 2006). In the course of our floristic research on Mediterranean macroalgae, some specimens of a ceramiacean alga were collected at Salina Island (The Aeolian Islands, Tyrrhenian Sea) (Fig. 1). This alga shows diagnostic features of the tribe Spermothamnieae Schmitz, including prostrate axes attached by digitate haptera from which short erect axes arise, spermatangia formed in compact heads, and subapical procarps. In producing only two periaxial cells on the subapical cell of the female fertile filament, this alga appears to be related to the genus *Lomathamnion* E.M. Gordon (type species *L. epicodii*, Gordon, 1972), but it differs in an unique combination of characters that prompt us to describe herein the new genus *Woelkerlingia*, with the single species *W. minuta*.

From our study of original descriptions and illustrations of the other two species of *Lomathamnion* (*L. capense* Stegenga and *L. humile* (Kützing) Stegenga) it is clear that they do not show the diagnostic characters of the genus. Moreover, they appear distinct from each other in important reproductive characters (except for both producing only one periaxial cell on the subapical cell of the female fertile filament). Therefore, a reassessment of this genus seems necessary and the genera *Stegengaea* and *Hommersandiella* are proposed to accommodate *L. capense* and *L. humile*, respectively.

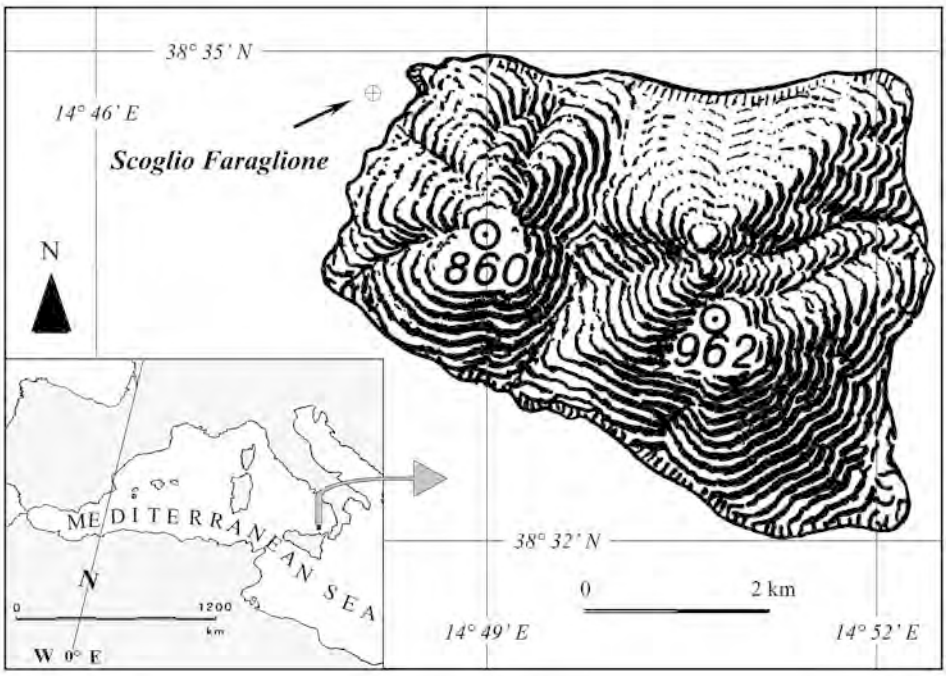


Fig. 1. Map of Salina Island. Arrow indicates the type locality (Scoglio Faraglione).

MATERIALS AND METHODS

Plants of *W. minuta* were collected in June 2004 by SCUBA at 12 m depth at Scoglio Faraglione (Salina Island, The Aeolian Islands): 38° 34' 47.54" N – 14° 48' 02.45" E, on a thallus of *Cystoseira sauvageauana* Hamel. All observations were made on material preserved in 4% formaldehyde-seawater. Microscope slide preparations were mounted in a solution of 1% aniline blue, 3% 1 N HCl, 50% Karo® syrup and 46% sea water. Photographs were made by a Nikon D1 digital camera and mounted using Adobe Photoshop 6.0. Herbarium abbreviations follow Holmgren *et al.* (1990).

Specimens examined (other than *Woelkerlingia*): *Lomathamnion epicodii* E.M. Gordon, Seal Bay, Kangaroo I., S. Australia, epiphytic on *Codium galeatum* J. Agardh, 31 October 1966, male and female gametophytes, tetrasporophyte, **Holotype**, AD A30961; *Lomathamnion epicodii*, Stanley Beach, Kangaroo I., S. Australian drift, epiphytic on *Codium galeatum*, 6 February 1957, male and female gametophytes, tetrasporophyte, **Paratype**, AD A20909; *Lomathamnion epicodii*, Head of Great Australian Bight, S Australian drift, epiphytic on *Codium galeatum*, 3 November 1968, male and female gametophytes, tetrasporophyte, AD A33186.

RESULTS

Thalli from Salina Island (Mediterranean Sea) were found epiphytic on *Cystoseira sauvageauana*. They consisted of prostrate axes creeping on cauloids of *C. sauvageauana*, to which they are attached by digitate haptera, and erect filaments (Figs 2-3). Cells of prostrate axes are 15-25 µm in diameter and 1.5-3(-4) times longer than wide. From each of these only one erect filament arises (Figs 2-3). Erect filaments are to 1 mm high and decrease in diameter gradually towards the apex where they become hair-like (Fig. 2). They are simple or scarcely branched pseudodichotomously or with unilateral pairs of branches (Figs 2-3) with basal and median cells 18-35 and 12-22 µm in diameter, respectively.

In female plants, the fertile filaments consist of two cells (apical and subapical) that are smaller than other vegetative cells and are terminal on vegetative filaments (Figs 4-5). The subapical cell bears two periaxial cells, one of which remains sterile while the other (the supporting cell) produces a sterile cell and a 4-celled lateral carpogonial branch (Figs 4-6, 10A). After fertilization, the supporting cell cuts off an auxiliary cell from which 2-4 gonimoblast filaments producing large ovoid carposporangia originate. Neither a large fusion cell nor involucral filaments are present (Figs 7, 10B).

In male plants, ovoid to cylindrical spermatangial heads, 35-40 µm in diameter, are terminal on vegetative filaments (Fig. 8); spermatangial heads consist of 3-4 fertile axial cells, each of them cutting off 3-4 periaxial cells which in turn produce 2-3 spermatangia (Figs 8, 10C).

In tetrasporophytic plants, tetrahedrally divided tetrasporangia, 45-55 µm in diameter, are borne terminally on (1-)2-4-celled short pedicels arising from both erect filaments and prostrate axes (Fig. 9).

The unique combination of the above characters is not found in any other genera and leads us to propose the new genus *Woelkerlingia* for these plants (Table 1).

Table 1. Comparison of characters of genera *Woelkerlingia*, *Lomathamnion*, *Stegengaea* and *Hommersandiella*

	Woelkerlingia [a]	*Lomathamnion* [b, c]	*Stegengaea* [a, d, e]	*Hommers-andiella* [a, e, f]
Habit	epiphytic	epiphytic	epiphytic	in part endophytic
Attachment structures	digitate haptera	digitate haptera	cells of prostrate axis with a pointing process	not applicable
No. of erect filaments arising from each cell of prostrate axes	1	several	several	not applicable
Position of female fertile filaments	terminal on vegetative filaments	on short lateral branches	on short lateral branches	terminal (but later intercalary) on emergent filaments
No. of cells of the fertile female filament	2 apical and subapical cells	3 apical, subapical and hypogenous cells	3 apical, subapical and hypogenous cells	2 apical and subapical cells; epigenous and fertile axial cells, when intercalary
No. of periaxial cells borne on the fertile female subapical cell	2	2	1	1
Sterile cell produced by the supporting cell	present	present	present	absent
Foot cell	absent	absent	present	present
Spermatangia	in spermatangial heads	in spermatangial heads	in clusters umbellate	in loose penicillate tufts
Position of sper-matangial heads	terminal on vegetative filaments	on lateral unicellular pedicels	not applicable	not applicable
Mother cells of spermatangia	periaxial cells of the male fertile axis	cells cut off by periaxial cells of the male fertile axis	terminal cells of fertile erect filaments	terminal cells of fertile emergent filaments
Sporangia	tetrasporangia tetrahedrally divided	tetrasporangia tetrahedrally divided but often cruciately arranged	polysporangia	tetrasporangia tetrahedrally divided
Position of sporangia	on (1-)2-4 celled pedicels from both erect filaments and prostrate axes	on unicellular pedicel from erect filaments	on 1-2 celled pedicels from both erect filaments and prostrate axes	on 1-2 celled emergent filaments

[a] Present study. [b] Gordon (1972). [c] Womersley (1998). [d] Stegenga (1984). [e] Stegenga *et al.* (1997). [f] Stegenga (1989).

Woelkerlingia Alongi, Cormaci *et* G. Furnari gen. nov.

Thalli epiphytici axibus prostratis ex quibus filamenta erecta oriuntur. Repentia axes affixa per digitata haptera. Gametophyta dioecia. Feminea fertilia filamenta bicellularia terminalia in filamentis vegetativis. Cellula subapicalis fertilis feminei filamenti duas cellulas periaxiales ferens: unam sterilem, alteram unam sterilem cellulam atque 4 cellulis carpogonialem ramum ferentem. Carposporophytum

ex unica auxiliari cellula sine magna cellula conjunctionis, effectum. Nulla involucralia filamenta. Capitula spermatangiorum terminalia in filamentis vegetativis spermatangiis ex ipsis periaxialibus cellulis factis. Tetrasporangia tetrahedralia terminalia in pedicellis (1-)2-4 cellulis oriuntur.

Species typica: *Woelkerlingia minuta* sp. nov.

Etymology: the generic name honours Dr Wm.J. Woelkerling as a token of our esteem and friendship towards him.

Diagnosis: Thalli epiphytic consisting of prostrate axes from which erect filaments arise. Prostrate axes attached by digitate haptera. Gametophytes dioecious. Two-celled female fertile filaments terminal on vegetative filaments. The subapical cell of the fertile filament bearing two periaxial cells one of which remains sterile while the other supports a four-celled carpogonial branch and produces a sterile cell. Carposporophyte developing from one auxiliary cell without a large fusion cell. Involucral filaments absent. Spermatangial heads terminal on vegetative filaments with spermatangia produced directly by periaxial cells. Tetrasporangia, tetrahedrally divided, terminal on (1)2-4-celled pedicels.

Woelkerlingia minuta Alongi, Cormaci *et* G. Furnari sp. nov. (Figs 2-10)

Characteribus generis, thalli epiphytici axibus prostratis ex quibus filamenta erecta usque ad 1 mm alta, gradatim decrescentia apice capillacea, oriuntur. Repentia axes, 15-25 µm lata, affixa per digitata haptera. Filamenta erecta, cellulis medianis 12-22 µm latis, simplicia vel pseudodichotoma vel unilateralibus seriebus duobus ramis. Singulum erectum filamentum ex unaquaque cellula repentium axium.

Holotype: CAT 2684 (the Herbarium of the Department of Botany, University of Catania, Italy), male and female gametophytes, tetrasporophyte, collected by M. Catra on 2 June 2004 on *Cystoseira sauvageauana.*

Type locality: Scoglio Faraglione, Salina Island (The Aeolian Islands), 12 m depth.

Etymology: the specific name refers to the reduced size of the thallus.

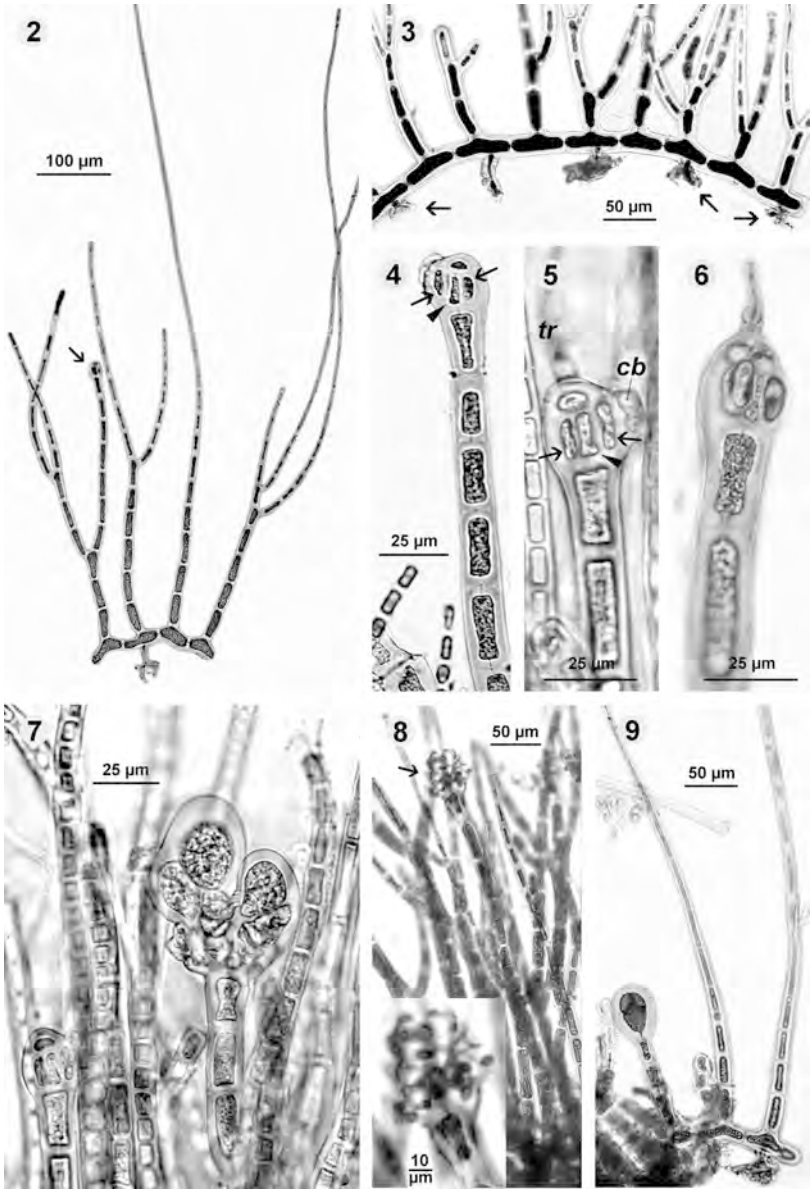
Distribution: known only from the type locality.

Diagnosis: With the characters of the genus; thalli epiphytic consisting of prostrate axes and erect filaments, to 1mm high, tapering from the base to apex becoming hair-like. Prostrate axes, 15-25 µm in diameter, attached by digitate haptera. Erect filaments, one from each cell of prostrate axes, with median cells 12-22 µm in diameter, simple to scarcely branched pseudodichotomously or with unilateral pairs of branches.

As mentioned above, *Woelkerlingia* appears to be related to *Lomathamnion* in the presence of only two periaxial cells on the subapical cell of the female fertile filament. Examination of the type material of *L. epicodii* (type species) (Figs 11-13) and the original description and illustrations (Fig. 14) confirmed its distinction from the genus *Woelkerlingia* (Table 1). Conversely, from the study of both original descriptions and illustrations of both *L. capense* (Stegenga, 1984) and *L. humile* (Stegenga, 1989) it resulted that neither of them belong to *Lomathamnion*.

"*Lomathamnion capense*" (Fig. 15A-E)

According to Stegenga (1984), *Lomathamnion capense* is a small epiphytic thallus consisting of a prostrate axis from which unbranched or once–twice forked erect filaments arise. No attachment structures are present, but cells of the prostrate axis often form a pointing process. Female fertile filaments arise



Figs 2-9. *Woelkerlingia minuta*. Holotype. **2.** Habit of a female thallus with a young procarp (arrow). **3.** Detail showing only one erect filament arising from each cell of the prostrate axis. Arrows indicate digitate haptera. **4.** Detail of a young procarp terminal on a vegetative filament. Arrowhead indicates the subapical cell; arrows indicate the two periaxial cells. **5**. Part of a female thallus showing a mature procarp; *cb* = carpogonial branch; *tr* = trichogyne. Arrowhead indicates the subapical cell. Arrows indicate the two periaxial cells. **6.** Part of a female thallus showing a mature procarp (for more details see Fig. 10A). **7.** Part of a female thallus bearing the carposporophyte (for more details see Fig. 10B). **8.** Part of a male thallus showing a compact spermatangial head (arrow) magnified in the insert (for more details see Fig. 10C). **9.** Detail showing a tetrasporangium tetrahedrally divided.

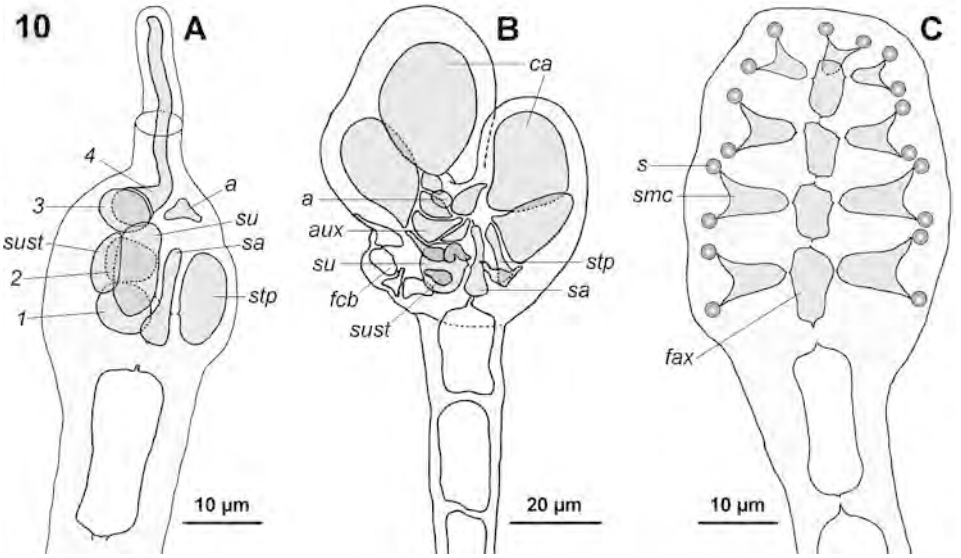
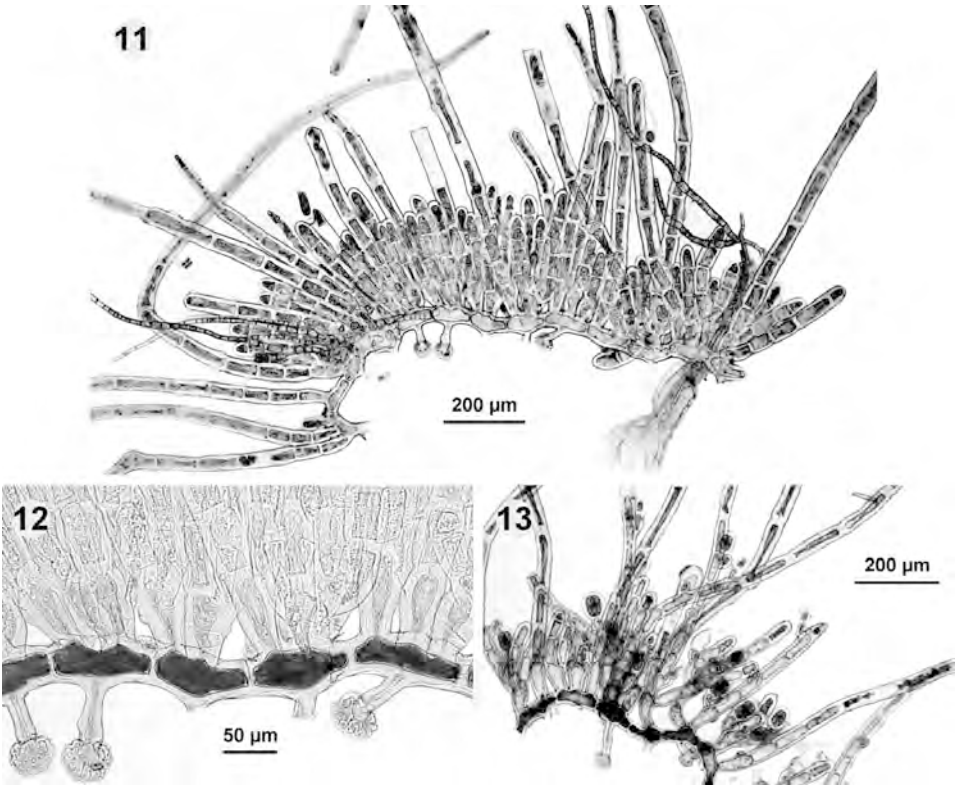


Fig. 10. *Woelkerlingia minuta*. Schematic drawings of reproductive structures. **A.** Mature procarp system. **B.** Mature carposporophyte. **C.** Optical longitudinal section of a spermatangial head. [*a* = apical cell; *aux* = auxiliary cell; *ca* = carpospore; *fax* = fertile axial cell; *fcb* = fused carpogonial branch; *s* = spermatangium; *sa* = subapical cell; *smc* = spermatangial mother cell; *stp* = sterile periaxial cell; *su* = supporting cell; *su st* = sterile cell on the supporting cell; *1, 2, 3, 4* = cells of the carpogonial branch].

on short branches, consisting of three cells (apical, subapical and hypogenous cells) smaller than other vegetative cells. The subapical cell bears only one periaxial (supporting) cell. The supporting cell produces both a sterile cell and a 4-celled carpogonial branch. After fertilization, an auxiliary cell is cut off from the supporting cell and the mature carposporophyte, without involucral filaments, consists of a few gomimoblast filaments, of which the terminal cells form carposporangia. No fusion cells have been observed. In male plants, spermatangial heads are terminal on short filaments; apical cells of spermatangial branches divide to form 5-10 spermatangium mother cells each of which bears few spermatangia. Asexual plants bear only polysporangia.

However, differently from Stegenga's interpretation, male plants bear spermatangia in umbellate clusters (Fig. 15B) and not in spermatangial heads, since a central fertile axis is lacking. Moreover, on the basis of illustrations by Stegenga [1984, fig. 3 (3-5)], we re-interpret the development of the carposporophyte as follows (Fig. 15D): the auxiliary cell divides into two cells, the proximal of which is a foot cell, labelled as "aux" (auxiliary cell) by Stegenga [1984, fig. 3 (5)], and the distal one, not labelled by Stegenga, is the gonimoblast filament initial.

Because of both the occurrence of only one pericentral cell borne on the subapical cell and of polysporangia (Stegenga, 1984), as well as both the occurrence of a foot cell forming during the development of the carposporophyte and spermatangia in umbellate clusters (this paper), *L. capense* does not fit in the circumscription of the genus *Lomathamnion* as described by Gordon (1972). Therefore, the genus *Stegengaea* is proposed to accommodate it.



Figs 11-13. *Lomathamnion epicodii*. **11.** Habit of the Holotype (AD A30961). **12.** Detail of the Holotype showing 2-3 erect filaments arising from each cell of the prostrate axis. **13.** Part of a Paratype (AD A20909) showing tetrasporangia tetrahedrally divided but cruciately arranged.

Stegengaea Alongi, Cormaci *et* G. Furnari gen. nov.

Thalli pusilli epiphytici axibus prostratis ex quibus filamenta erecta oriuntur. Feminea fertilia filamenta tricellularia in brevibus filamentis. Cellula subapicalis fertilis feminei filamenti unam cellulam sustinentem nullamque aliam periaxialem cellulam, ferens. Cellula sustinens unam sterilem cellulam atque 4 cellulis carpogonialem ramum ferens. Carposporophytum ex unica auxiliari cellula sine ulla cellula conjunctionis, effectum. Nulla involucralia filamenta. Spermatangium ferens cellula ex erecti filamenti cellula terminali, facta est. Fasciculi spermatangiorum umbellati. Asexualis reproductio polysporangiis.

Etymology: the specific name honours Dr Herre Stegenga for his contributions to the knowledge of Ceramiacean algae.

Diagnosis: Thalli small, epiphytic, with prostrate axes from which erect filaments arise. Female fertile filaments on short branches and consisting of three cells smaller than other vegetative cells. Subapical cell of the female fertile filament bearing one supporting cell but no other periaxial cells. Supporting cell bearing one sterile cell and a 4-celled carpogonial branch. Carposporophyte developing from only one auxiliary cell without fusion cell. No involucral filaments are present. Spermatangium mother cells develop from the terminal cell

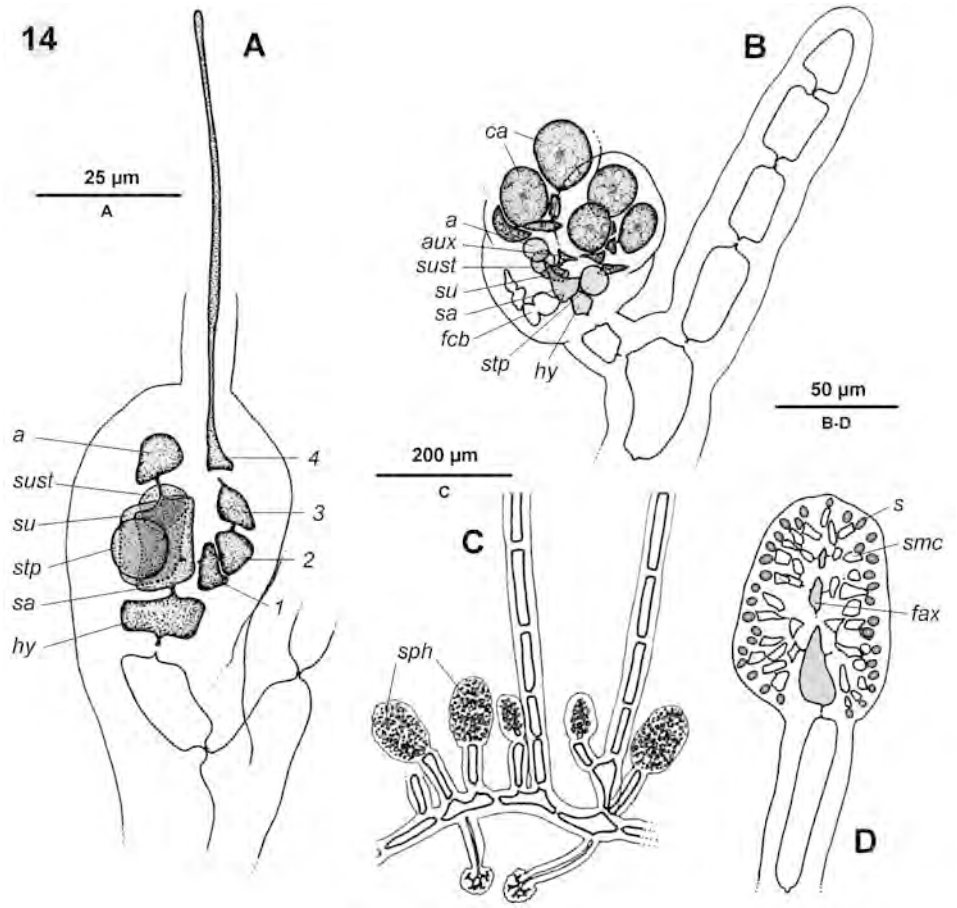


Fig. 14. *Lomathamnion epicodii*. Schematic drawings of reproductive structures. **A.** Mature procarp system. **B.** Carposporophyte. **C.** Male thallus with spermatangial heads. **D.** Optical longitudinal section of a spermatangial head [*hy* = hypogenous cell; *sph* = spermatangial head; other abbreviations as in Fig. 10]. [All from Gordon (1972) modified].

of an erect filament forming umbellate clusters. Asexual reproduction by means of polysporangia.

Monotypic genus:

Stegengaea capensis (Stegenga) Alongi, Cormaci *et* G. Furnari **comb. nov.** (*species typica*)

Basionym: *Lomathamnion capense* Stegenga 1984: 351, figs 1-3.

Distribution: South Africa: from Cape Point to Arniston (Stegenga *et al.*, 1997). The record from Natal (Stegenga, 1986) is a misidentification (Stegenga, pers. comm.).

"*Lomathamnion humile*" (Fig. 16 A-E)

According to Stegenga (1989), who transferred *Callithamnion humile* Kützing to *Lomathamnion*, this small species shows both prostrate filaments endo-

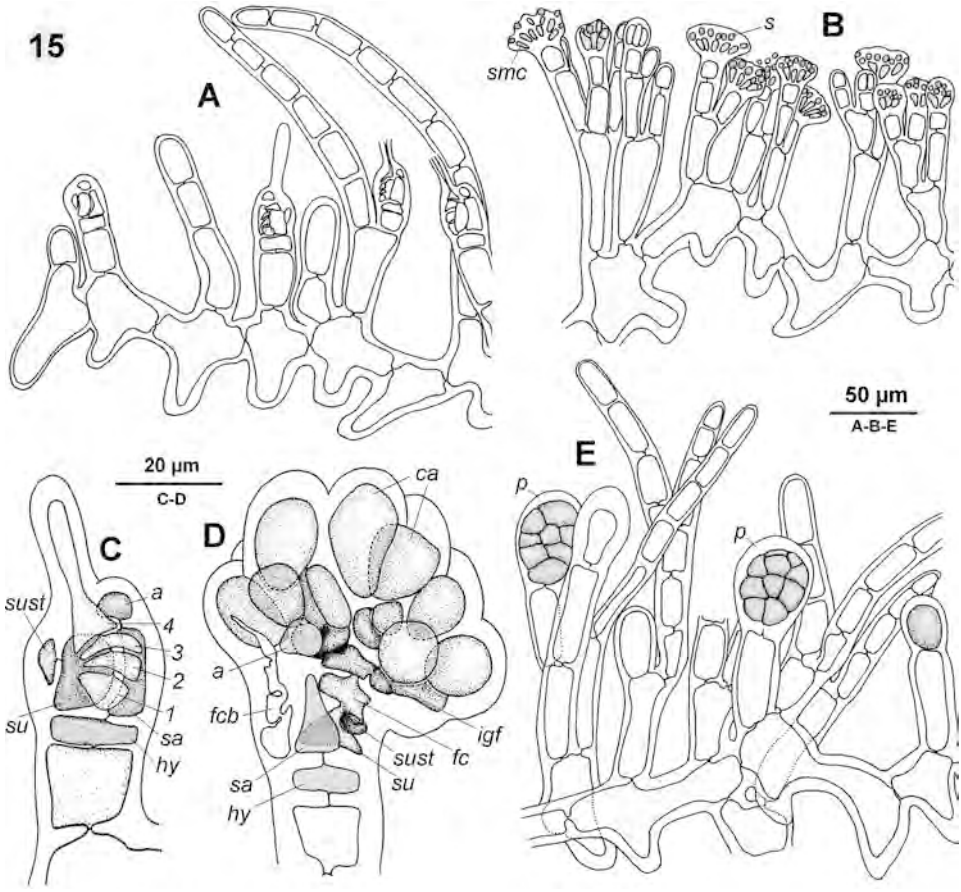


Fig. 15. *Stegengaea capensis* (= *L.capense*). Schematic drawings of reproductive structures. **A.** Female thallus with procarps. **B.** Male thallus with spermatangia terminal in clusters umbellate. **C.** Mature procarp system. **D.** Mature carposporophyte. **E.** Tetrasporophytic thallus showing polysporangia. [*hy* = hypogenous cell; *fc* = foot cell; *igf* = initial of gonimoblast filament; *p* = polysporangia; other abbreviations as in Fig. 10]. [All from Stegenga (1984, as *Lomathamnion capense*) modified and partly re-interpretated].

phytic in the cortex of the host (Halymeniaceae) and short, slightly clavate, emergent filaments rarely more than four cells. In female fertile filaments, procarps are borne on a short subapical cell, but the apical cell can continue its growth so that as a result older procarps and carposporophytes can be intercalary. The fertile axial cell bears only one periaxial cell (supporting cell), that produces only a four-celled carpogonial branch, without any associated sterile cells. After fertilization, the auxiliary cell cuts off a gonimoblast initial cell. Male fertile filaments, terminally ditrichotomously branched, are penicillate with terminal spermatangia, up to three per cell. Stegenga *et al.* (1997), on the basis of new collections, gave additional information on both mature carposporophytes, provided with one or two gonimolobes per carposporophyte and producing ovate individual carpospores, and tetrasporophytes bearing tetrahedrally divided tetrasporangia that are borne singly and terminal on one- or two-celled emergent filaments.

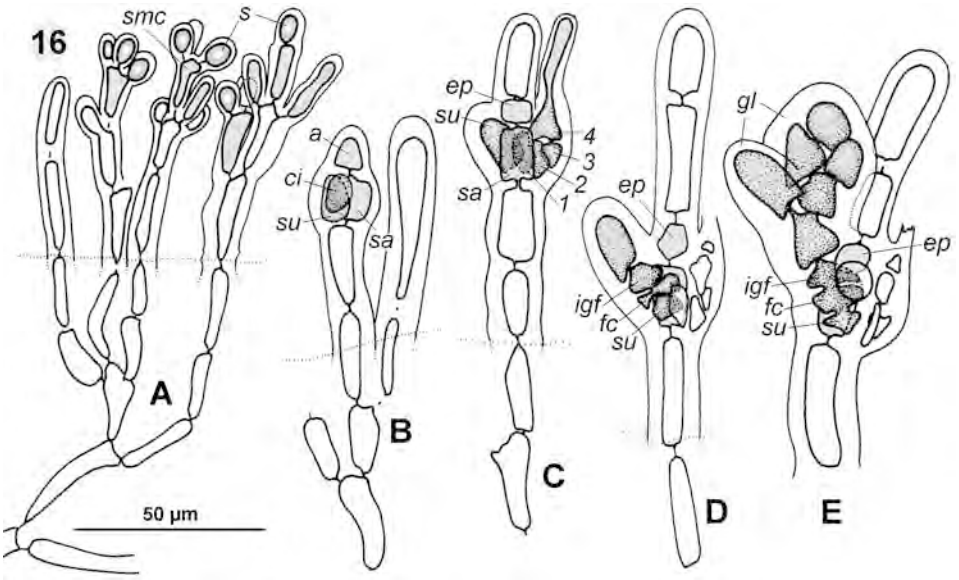


Fig. 16. *Hommersandiella humilis* (= *L. humile*). Schematic drawings of reproductive structures. **A.** Male thallus with terminal spermatangia in loose penicillate tufts. **B.** Female thallus with a young procarp. **C.** Mature procarp system. **D.** Post-fertilization stadium. **E.** Young carposporophyte. [*ci* = initial of carpogonial filament; *ep* = epigenous cell; *fc* = foot cell; *gl* = gonimolobe; *igf* = initial of gonimoblast filament; dotted line indicates surface of host seaweed; other abbreviations as in Fig. 10]. [All from Stegenga (1989, as *Lomathamnion humile*) modified and partly re-interpretated].

However, a thorough analysis of both description and illustrations of female structures reported by Stegenga (1989), led us to the following interpretation: i. when the fertile filament, after having produced the procarp from the subapical cell, continues its growth, the first division of the apical cell cuts off a cell, here named "epigenous cell", shorter than other later formed vegetative cells that arise distal to the fertile axial cell (now intercalary); ii. in female plants, the auxiliary cell divides into two cells, the proximal of which represents the foot cell, and the distal one the gonimoblast initial cell; a slight fusion occurs among supporting cell, foot cell and gonimoblast initial cell, but leaving them still distinguishable. Such a re-interpretation is illustrated in Fig. 16B-E.

Because of the occurrence of only one pericentral cell borne on the subapical cell, the intercalary position of older procarps or carposporophytes on the fertile female filaments, the absence of any sterile cells associated with the supporting cell, and penicillate terminal spermatangia (Stegenga, 1989; Stegenga *et al.*, 1997) as well as of the production of a foot cell during the development of the carposporophyte and of an "epigenous cell" forming in fertile filaments continuing their growth after the production of procarps (this paper), *L. humile* does not fit in the circumscription of the genus *Lomathamnion* as described by Gordon (1972). Therefore, the genus *Hommersandiella* is proposed to accommodate it.

Hommersandiella Alongi, Cormaci *et* G. Furnari gen. nov.

Thalli pusilli ex filamentis endophyticis brevibusque erectis filamentis emergentibus constantes. Feminea fertilia filamenta bicellularia terminalia in

filamentis emergentibus. Cellula subapicalis fertilis feminei filamenti unam cellulam sustinentem nullamque aliam periaxialem cellulam, ferens. Cellula sustinens 4 cellulis carpogonialem ramum ferens sed nullam sterilem cellulam. Femineum filamentum saepe crescens postquam sustinens cellula facta est. Carposporophytum ex unica auxiliari cellula effectum. Nulla involucralia filamenta. Masculina fertilia filamenta laxa penicillataque cum terminalibus spermatangiis. Asexualis reproductio tetrasporangiis.

Etymology: the specific name honours Dr Max Hommersand as a token of our esteem and friendship towards him.

Diagnosis: Thalli small, with endophytic filaments and short emergent filaments. Two-celled female fertile filaments terminal on emergent filaments. Subapical cell of the female fertile filament bearing one supporting cell but no other periaxial cells. Supporting cell bearing only a 4-celled carpogonial branch without any sterile cells. Female fertile filaments can continue their growth after the production of the supporting cell. Carposporophyte developing from only one auxiliary cell. No involucral filaments are present. Spermatangia terminal in rather loose penicillate tufts. Asexual reproduction by means of tetrasporangia.

In this genus the following species is here combined:

Hommersandiella humilis (Kützing) Alongi, Cormaci *et* G. Furnari **comb. nov.** (*species typica*)

Basionym: *Callithamnion humile* Kützing 1849: 639.

Homotypic synonym: *Lomathamnion humile* (Kützing) Stegenga (Stegenga, 1989: 76-78, figs 1-10)

Distribution: Namibia, South Africa (along the entire west coast and eastward to Cape Hangklip) (Stegenga *et al.*, 1997).

DISCUSSION

The genus *Lomathamnion*, described by Gordon (1972) to accomodate *L. epicodii,* is characterized by prostrate axes with digitate haptera and erect filaments 1-4 per cell of the prostrate axis; female fertile filaments borne on short lateral branches consisting of three cells (apical, subapical and hypogenous) smaller than other vegetative cells; the subapical cell bearing two periaxial cells, one of which remains sterile while the other (the supporting cell) produces a sterile cell and a four-celled lateral carpogonial branch; the carposporophyte produced by an auxiliary cell forming directly two-four gonimoblast filaments; large fusion cell or involucral filaments not present; spermatangial heads borne on lateral unicellular pedicels with spermatangia produced by cells cut off by periaxial cells; tetrasporangia, tetrahedrally divided but often almost cruciately arranged, borne on lateral unicellular pedicels.

All the above characters were confirmed by observation of the type material of *L. epicodii*.

From the comparison between the three new genera above described and the genus *Lomathamnion* (Table 1) it appears that the most closely related genus to *Lomathamnion* is *Woelkerlingia*. In fact, *Woelkerlingia* and *Lomathamnion* share the habit, the occurrence of two periaxial cells on the subapical cell of the female fertile filament and compact spermatangial heads.

However, *Woelkerlingia* differs from *Lomathamnion* in the following characters: i. the female fertile filament is terminal on vegetative filaments and consists of only two cells (apical and subapical) smaller than other vegetative cells [on short lateral branches and consisting of three cells (apical, subapical and hypogenous) smaller than other vegetative cells in *Lomathamnion*]; ii. spermatangial heads are terminal on vegetative filaments with spermatangia produced directly by periaxial cells (borne on lateral unicellular pedicels with spermatangia produced by cells cut off by periaxial cells in *Lomathamnion*); iii. tetrasporangia are tetrahedrally divided and borne terminally on (1-)2-4-celled short pedicels (tetrahedrally divided but often almost cruciately arranged and borne on lateral unicellular pedicels in *Lomathamnion*).

The genus *Stegengaea* differs from *Woelkerlingia* and *Lomathamnion* in having only one periaxial cell produced by the subapical cell of the female fertile filament (two periaxial cells borne on the subapical cell of the female fertile filament in the other two genera), in having a foot cell intercalary between the supporting cell and the gonimoblast initial filament (supporting cell cutting off no foot cells but acting as the initial cell of gonimoblast filament in the other two genera), in having spermatangia in umbellate clusters (compact spermatangial heads in the other two genera) and producing only polysporangia (tetrasporangia in the other two genera).

Moreover, *Hommersandiella* differs from *Woelkerlingia* and *Lomathamnion* in showing an inpart endophytic habit (epiphytic in the other two genera), only one periaxial cell produced by the subapical cell of the female fertile filament (two periaxial cells borne on the subapical cell of the female fertile filament in the other two genera), no sterile cells produced by the supporting cell (an apical sterile cell in the other two genera), female fertile filament that can continue its growth after the production of the supporting cell but forming an epigenous cell standing above the intercalary fertile axial cell (female fertile filament never continuing its growth in the other two genera), a foot cell intercalary between the supporting cell and the initial of gonimoblast filament (supporting cell cutting off no foot cells but acting as the initial cell of gonimoblast filament in the other two genera), and spermatangia in rather loose penicillate tufts (compact spermatangial heads in the other two genera).

Finally, *Stegengaea* differs from *Hommersandiella* in showing an epiphytic habit (in part endophytic in *Hommersandiella*), a sterile cell produced by a supporting cell (no sterile cells produced by the supporting cell in *Hommersandiella*), female fertile filament never continuing its growth (female fertile filament continuing its growth after the production of the supporting cell but forming an epigenous cell in *Hommersandiella*), spermatangia in clusters umbellate (in rather loose penicillate tufts in *Hommersandiella*), and only polysporangia (tetrasporangia in *Hommersandiella*).

In showing the above described characters, both *Woelkerlingia* and *Lomathamnion* undoubtedly belong to the tribe Spermothamnieae Schmitz and in particular in habit, spermatangia formed in compact heads, procarps on the subapical cell of the fertile filament. It should be noted that within that tribe, *Woelkerlingia* and *Lomathamnion* are the only genera showing two periaxial cells on the subapical cell of the female fertile filament while all others show three, except for *Ptilothamnion codicola* (E.Y. Dawson) I.A. Abbott and *P. rupicola* Gordon-Mills which have two (Stegenga *et al.*, 2002) but differ in producing a carposporophyte with an involucrum.

Both *L. capense* (= *Stegengaea capensis*) and *L. humile* (= *Hommersandiella humilis*) (the latter with some doubts) were included in the tribe Spermo-

thamnieae by Stegenga (1984; 1989), in spite of these algae having only one periaxial cell produced by the subapical cell of the female filament (interpreted by Stegenga as a continuation of the reductional trend started in *L. epicodii*) and the lack of compact spermatangial heads (a character which he deemed less significant). However, in our opinion, the combination of the above two reproductive characters occurring in both *Stegengaea* and *Hommersandiella* (i.e.: i. only one periaxial cell produced by the subapical cell of the female filament; ii. spermatangia not in compact heads) does not allow inclusion of the new genera in the tribe Spermothamnieae, the members of which show two-three periaxial cells borne on the subapical cell of the female filament and spermatangia only in compact heads. Nevertheless, a proposal of a new tribe to include *Stegengaea* and *Hommersandiella* does not seem opportune now, since a study on the re-definition of the diagnosis and circumscription of this tribe as well of Sphondylothamnieae, Compsothamnieae and Spongoclonieae is in progress (Hommersand, pers. comm.).

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