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Chamaebotrys erectus sp. nov. (Rhodymeniales, Rhodophyta) from the Socotra Archipelago, Yemen

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A third species of *Chamaebotrys*, *C. erectus*, is described from an upwelling region off Socotra Island, Yemen. The new species clearly displays one of the defining features of the genus, viz. terminal tetrasporangia in nemathecial sori. The nemathecia become diffuse when mature and produce secondary tetrasporangia. Tetraspores can apparently germinate *in situ*, resulting in compound thalli with tetrasporic and cystocarpic parts. Carpogonial branches are four-celled and cystocarps are protuberant, both of which features illustrate the affinities of *Chamaebotrys* with the closely related *Coelarthrum*.

Introduction

The genus *Chamaebotrys* was recently erected by Huisman (1996) for *Coelarthrum boergesenii* Weber-van Bosse, the two features distinguishing it from the type species of *Coelarthrum*, *C. cliftonii* (Harvey) Kylin, being the terminal, rather than intercalary tetrasporangia and the nemathecial sori in which they occur (Huisman 1996). A second species of *Chamaebotrys* is *C. lomentariae* (Tanaka *et* K. Nozawa *in* Tanaka) Huisman, which is very imperfectly known only from the type collection. Both it and the type species have low-growing, decumbent thalli of small stature. It was therefore of interest when several relatively large, upright thalli referable to *Chamaebotrys* were collected from an upwelling area off Socotra (Fig. 1). These specimens are herein described as the new species *C. erectus*.

Material and Methods

Specimens were collected during two field trips to Socotra Island (Yemen; 12.47 N, 53.87 E) from 13 January–20 February 1999 and 26 March–7 May 2000, respectively. The subtidal habitats around the island were sampled while snorkelling or SCUBA diving. Specimens were pressed on herbarium sheets and preserved in a 5 % Formalin-seawater solution. Herbarium sheets, liquid-preserved specimens and microscope slides are deposited in GENT. Material for microscopical examination was stained with aniline blue. The anatomical and reproductive characteristics were observed by studying transverse sections (made by hand or with a freezing microtome set at 40 μm) and squashed preparations (whole-mounts in a mixture of corn syrup and phenol, 50:1) under a standard light microscope (Leitz Diaplan, Wetzlar, Germany). Line drawings were prepared with a camera lucida, and photographs were taken with a digital camera (Olympus DP10, Melville, U.S.A.).

Results

Chamaebotrys erectus Schils *et* Huisman, sp. nov.

Diagnosis: *Ad Chamaebotrydem boergesenii (Weber-*

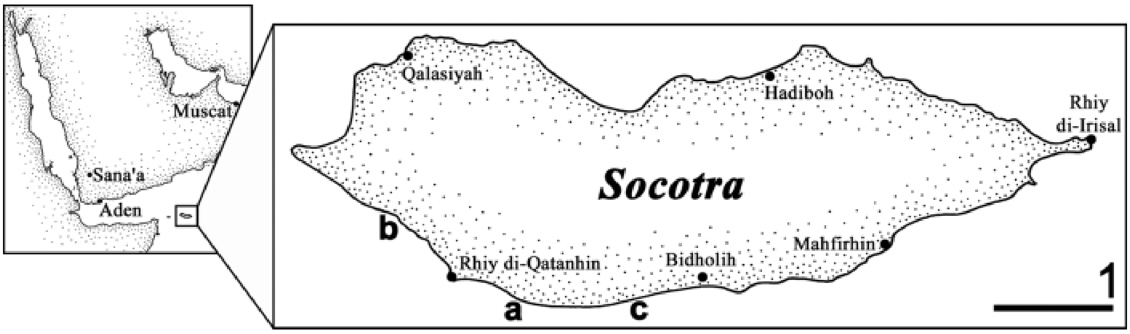
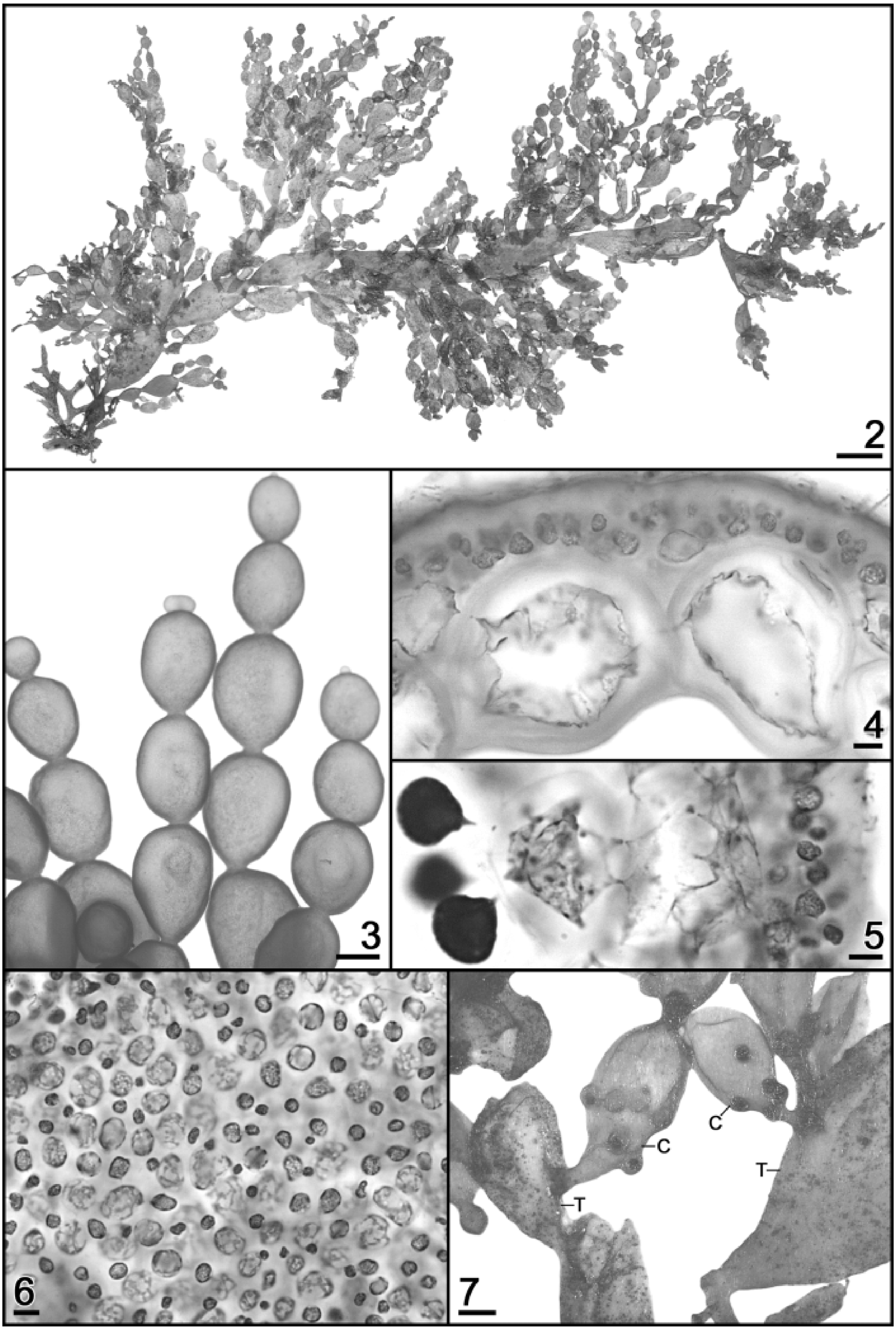


Fig. 1. Sampling stations around Socotra where *Chamaebotrys erectus* was collected: IT-059 (a); IT-103, type locality (b); Alg-40 (c). Scale bar: 20 km.



Figs 2–7. *Chamaebotrys erectus* sp. nov.
Fig. 2. Habit of holotype. Fig. 3. Apical region showing the narrow and short connections between the segments. Fig. 4. Section of cortex. Fig. 5. Cortical section showing gland cells attached to a medullary cell. Fig. 6. Surface view of cortex. Fig. 7. Compound thallus: cystocarpic axes (C) developing from tetrasporic segments (T). Scale bars: Fig. 2, 1 cm; Fig. 3, 1 mm; Figs 4–6, 10 µm; Fig. 7, 1 mm.

van Bosse) Huisman similis sed characteribus sequentibus distinguitur. Planta recta, ad 20 cm alta, sine anastomosibus inter ramos. Tetrasporangia decussate divisa, in nematheciis irregulariter formatis portata. Tetrasporae interdum in situ germinantes, thallum compositum facientes ex partis tetrasporicis gametophyticis et cystocarpicis constantes. Spermatangia ignota.

Similar to *Chamaebotrys boergesenii* (Weber-van Bosse) Huisman but with the following distinguishing characters: plants erect, to 20 cm tall, lacking anastomoses between branches. Tetrasporangia decussately divided, in irregularly shaped nemathecia. Tetraspores occasionally germinating *in situ*, resulting in a compound thallus comprised of tetrasporic, gametophytic and cystocarpic parts. Spermatangia unknown.

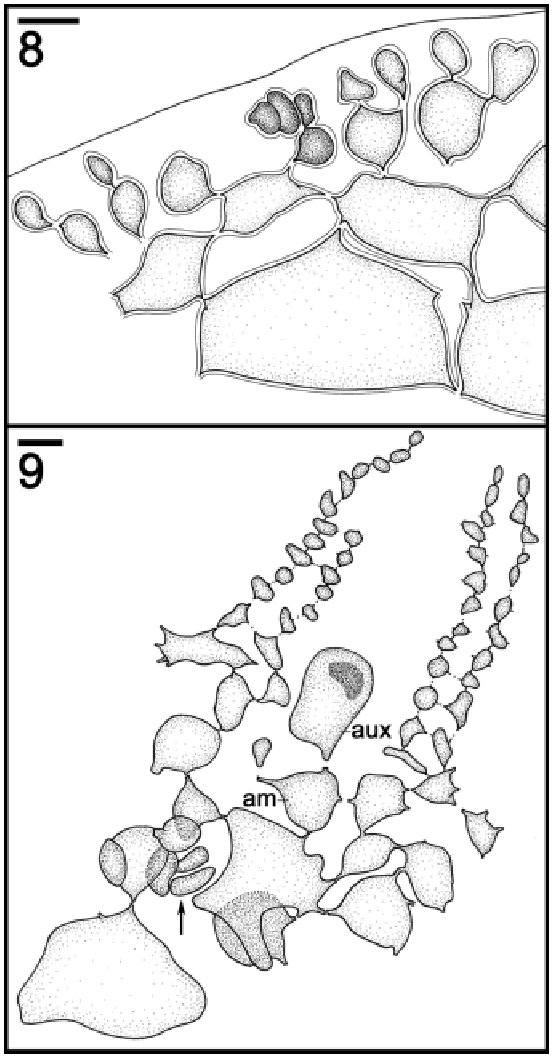
Holotype: SOC 265 (GENT).

Etymology: The specific epithet (L. *erectus* = upright) alludes to the upright habit of the species.

Type locality and specimens examined: Yemen, Socotra Island (Fig. 1): 5 February 1999, 10 km east of Rhiy di-Qatanhin (IT-059: 12.308 N, 53.658 E), shallow subtidal, leg. F. Leliaert (SOC 028: tetrasporophyte and female gametophyte); 3 March 1999, 1 km southeast of Ghubbah di-Net (IT-103: 12.425 N, 53.475 E; type locality), shallow subtidal, leg. F. Leliaert (SOC 265: tetrasporophyte and female gametophyte); 30 April 2000, west of Bidholih (ALG-40: 12.303 N, 53.843 E), subtidal: –20 m, leg. T. Schils (SMM 456: female gametophyte).

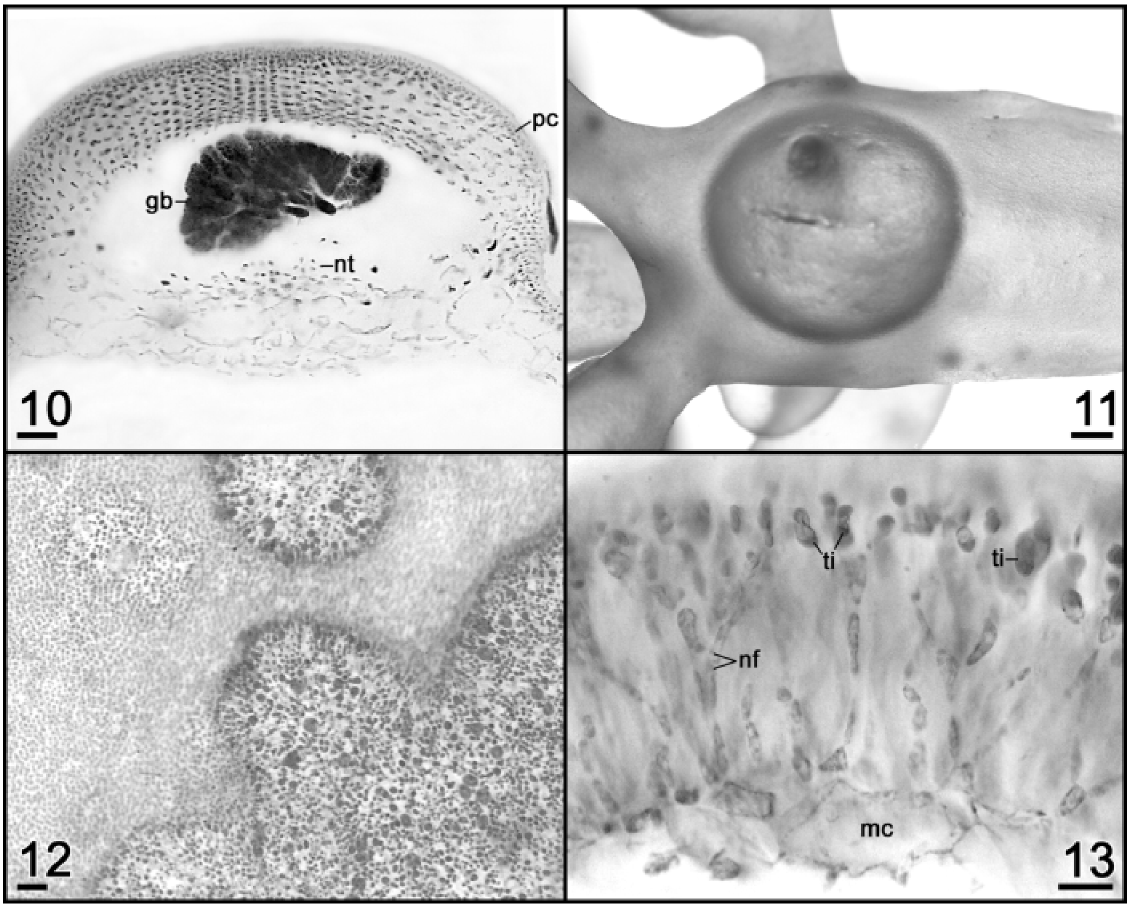
Habit and vegetative structure: Plants are upright, to 20 cm tall (Fig. 2), segmented, and branch dichotomously or have a percurrent primary axis and verticillate laterals. Several thalli, each with a short solid stipe (to 7 mm long and 1.5 mm wide), can arise from a single discoid holdfast (to 3 mm diameter). Young branches and apical regions are bright red in colour and older parts of the thallus are brownish red. Thalli are soft in texture and composed of hollow, mucus-filled segments that are joined by narrow connections (Fig. 3). The shape of the segments varies from subcylindrical near the apex to thick, elongate and barrel-shaped in older thallus parts. The inner medulla is composed of 1 or 2 layers of large, colourless cells (22.5–125 µm [l] × 27–160 µm [w]; Fig. 4). Gland cells (6.5–20.5 µm in diameter) are borne singly or in pairs on the inner surface of medullary cells (Fig. 5) or on stellate cells attached to the medullary cells. Secondary internal filaments occasionally are initiated from the medullary cells. The cortex is composed of 2–3 layers of subspherical pigmented cells (4.5–18 µm in diameter), these gradually decreasing in size towards the thallus surface. Outer cortical cells regularly bear hairs. Cortical cells in surface view are irregularly arranged (Fig. 6) and variable in diameter.

Reproductive thalli: The larger plants (e.g. SOC 265) are compound, composed of tetrasporic and gametophytic/cystocarpic individuals (Fig. 7), the latter occurring distally on the tetrasporophyte. Hence, it is suspected that the tetrasporangia germinate *in situ* and give rise to gametophytic thalli. The process of tetraspore germination, singly or syntagmatically, was not observed. Smaller, to 7 cm tall, entirely cystocarpic thalli also occur, indicating that the tetraspores can also disperse from the mother plant and produce free-living gametophytes.



Figs 8–9. *Chamaebotrys erectus* sp. nov.
Fig. 8. Four-celled carpogonial branch. Fig. 9. Initiation of a cystocarp: auxiliary mother cell (am), auxiliary cell (aux) and carpogonial branch remnants (arrow). Scale bars: 10 µm.

Carpogonial branch and cystocarps: Carpogonial branches are 4-celled and slightly curved (Fig. 8). A cortical cell, attached to the supporting cell and with secondary pit connections with adjacent cortical cells, acts as the auxiliary mother cell and initiates an obovoid auxiliary cell (Fig. 9). Immediate post-fertilisation events have not been observed. Upon presumed diploidisation of the auxiliary cell, the latter produces a stalked gonimoblast (Fig. 10). Basal to the gonimoblast, nutritive cells are formed from the cells



Figs 10–13. *Chamaebotrys erectus* sp. nov.
Fig. 10. Section of cystocarp: broken-off gonimoblast (gb), pericarp (pc), nutritive tissue (nt). Fig. 11. Protuberant cystocarp with a prominent ostiole. Fig. 12. Surface view of irregularly contoured tetrasporangial nemathecia. Fig. 13. Section of tetrasporial nemathecium showing medullary cells (mc), nemathecial filaments (nf) and tetrasporangial initials (ti). Scale bars: Fig. 10, 50 μm; Fig. 11, 0.5 mm; Fig. 12, 50 μm; Fig. 13, 20 μm.

that surround the supporting cell. Simultaneously, a protuberant pericarp surrounds the gonimoblast (Fig. 11).

Spermatangia: Not observed.

Tetrasporangia: Tetrasporangia occur in nemathecial sori (Fig. 12). During maturation the sori spread into irregular diffuse patches that can cover the greater part of the thallus. The nemathecia are composed of slender filaments (Fig. 13) that arise from outer cortical cells and cut off distal tetrasporangia. Sterile filaments occur among the tetrasporangial filaments. After releasing the first order of tetrasporangia, secondary nemathecial filaments can be produced which give rise to secondary tetrasporangia in more elevated sori. Tetrasporangia develop from darkly staining elliptical initials 13.5–25 μm [l] × 6.5–14 μm [w] (Fig. 13). The first division is transverse and oblique, with subsequent divisions splitting the two halves longitudinally at right angles to one another, resulting in decussately divided tetrasporangia 27–41 μm × 20–25 μm.

Habitat: Plants are epilithic on bare or sand inundated rocks. The associated subtidal macroalgal flora is composed of *Asteromenia peltata* (W. R. Taylor) Huisman *et* Millar, *Botryocladia leptopoda* (J. Agardh) Kylin, *Carpopeltis maillardii* (Montagne *et* Millardet) Chiang, *Champia indica* Børgesen, *Chondria armata* (Kützing) Okamura, *Dictyota cervicornis* Kützing, *Euptilota fergusonii* Cotton, *Hypnea boergesenii* Tanaka, *Lobophora variegata* (Lamouroux) Womersley *ex* Oliveira, *Sarcodia montagneana* (J. Hooker *et* Harvey) J. Agardh, *Scinaia moniliformis* J. Agardh, *Sebdenia flabellata* (J. Agardh) Parkinson, and *Udotea indica* A. Gepp *et* E. Gepp.

Discussion

Chamaebotrys erectus clearly displays the key characteristic of the genus, viz. terminal tetrasporangia in nemathecial sori. The new species has morphological and anatomical features similar to the other *Chamaebotrys* species and also to species of the closely related *Coelarthrum* (Table I). It can readily be distinguished from *Chamaebotrys boergesenii* and *C. lomentariae* by its erect thallus, large size and compound thalli comprising tetrasporic, gametophytic

Table I. Comparison of *Chamaebotrys erectus* to other *Chamaebotrys* and *Coelarthrum* species (Mshigeni and Papenfuss 1981, Huisman 1996, 2000, Wynne 2001, this paper). *Chamaebotrys lomentariae* is excluded as the species is insufficiently known (Huisman 1996).

Feature	*Chamaebotrys erectus* Schils *et* Huisman, sp. nov.	*Chamaebotrys boergesenii* (Weber-van Bosse) Huisman	*Coelarthrum cliftonii* (Harvey) Kylin	*Coelarthrum decumbens* Huisman	*Coelarthrum opuntia* (Endlicher) Børgesen
Grouping of tetrasporangia	Discrete nemathecial sori that diffuse while maturing and develop secondary tetrasporangia	Discrete nemathecial sori that remain discrete	Scattered, not in sori	Indistinct sori	Scattered, not in sori
Carpogonial branch	4-celled	?	4-celled	4-celled	4-celled
Tetrasporangia	Terminal, decussately divided	Terminal, cruciately divided	Intercalary, cruciately divided	Intercalary, cruciately divided	Intercalary, cruciately to decussately divided
Habit	Erect	Decumbent	Erect	Decumbent	Erect
Secondary lateral anastomoses	Absent	Present	Present	Present	Absent
Constrictions between the segments	Narrow	Broad	Broad	Broad	Stalk-like
Cystocarps	Protuberant	Protuberant	Immersed	Protuberant	Protuberant
Additional peculiarities	In situ germination of tetraspores: female gametophytes epiphytic on tetrasporophytes, also free-living female gametophytes	Elongate processes at apical regions of the thallus	Monostromatic septa	Outer cortex in a rosette-like formation in surface view	Cartilaginous stipe
Size (cm)	To 20	2–3	To 20	3–4	To 30
Distribution	Upwelling area of Socotra Island, Yemen	Warmer waters of the Indo-Pacific and upwelling area of Hallaniyat Islands, Oman	Indo-Pacific	Great Barrier Reef and Lord Howe Island, Australia	Indo-Pacific

and cystocarpic parts (non-compound thalli also occur). In addition, *C. erectus* produces occasional internal filaments, these being secondarily produced and not comparable to longitudinal filaments of the Champiaceae (Ricker and Kraft 1979, Huisman 1995) and Lomentariaceae (Lee 1978). Adventitious filaments have also been observed in *Coelarthrum* species and not accorded taxonomic significance (Huisman 1996). The latter feature, however, might prove to be of taxonomic importance in other Rhodymeniaceae genera, viz. the absence of internal rhizoids in *Chrysymenia* and their presence in *Cryptarachne* (generally lumped in *Chrysymenia*, e.g. Abbott and Littler 1969) might support the molecular separation of both genera (Saunders *et al.* 1999, p. 38).

In light of the recent molecular findings on the Rhodymeniales (Saunders *et al.* 1999), the observation of a 4-celled carpogonial branch in *Chamaebotrys erectus* supports maintaining the genus (which was not sequenced by Saunders *et al.* 1999) within the Rhodymeniaceae. The genus is unusual in the Rhodymeniaceae, however, in producing terminal tetrasporangia in nemathecia. This has been hypothesised as a reversion to the ancestral condition by Saunders *et al.* (1999). Further molecular studies may elucidate the phylogenetic placement of *Chamaebotrys* in relation to other Rhodymeniaceae.

Some tetrasporangia in *C. erectus* appear to be tetrahedrally divided, a result of the oblique first division in combination with the decussate arrangement of the tetraspores. Nevertheless, the divisions are always successive, a distinctive feature of cruciately (decussately) divided tetrasporangia (Guiry 1978, 1990).

In comparison to the reported sizes of the other *Chamaebotrys* species (Mshigeni and Papenfuss 1981, Huisman 1996), *C. erectus* is markedly larger. All material was collected from the south coast of Socotra, which is subject to upwelling of cold water. This phenomenon is beneficial for algal growth (constant nutrient flow and stable temperature regime), as the south coast harbours the most luxuriant and species-rich algal flora of the Island (Schils *et al.* 2001). Analogous discoveries of large representatives of certain genera from this upwelling region include *Champia gigantea* Wynne (1998), another member of the Rhodymeniales. These findings suggest that the Arabian Sea harbours a distinctive and interesting marine flora.

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