**Struvea thoracica** sp. nov. (Cladophorophyceae), a new deep-water chlorophyte from the Great Barrier Reef and New Caledonia

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*Struvea thoracica* Kraft & Millar, sp. nov., is described from deep-water habitats along the mid-north to southern Great Barrier Reef and in New Caledonia. Plants reach 26 cm in length and at maturity consist of coarse fibrous blades to 2 mm in thickness, 18 cm in length, and 12 cm in width borne on simple to ramified stalks 8–18 cm in length and 2.5 mm in diameter. Organization of the blades is dorsiventral, with first-order laterals arising oppositely on axial bearing cells, the laterals in turn producing a further order of branches that are strongly curved ‘ventrally’. This results in a ‘dorsal’ surface on which the primary laterals are evenly spaced, coarse, and prominently exposed, imparting the ‘ribcaged’ appearance for which the alga is named. Cell division in all branch orders is segregative, as evidenced by the rounded cytoplasts that form distally within the walls of axial cells as they undergo their first cell divisions, as well as by the gaps left between the end walls of daughter cells and the lateral walls of the parent cells following cell divisions in higher branch orders, a feature also of the tenacula that occasionally form apically on second- and higher-order laterals. The new species is distinguished from the other two members of the genus (the type, *S. plumosa* Sonder, and *S. elegans* Børjesen) by its greater blade thickness, dorsiventrality of blade construction, and relatively few tenacular cells.

**INTRODUCTION**

The genus *Struvea* Sonder has recently undergone major revision, with the bulk of its 10 species transferred by Kraft & Wynne (1996) to *Phyllodictyon* J.E. Gray because of differences in cell-division processes. Kraft & Wynne demonstrated that divisions in the former are ‘segregative’ (in the sense of Børjesen 1912, 1913), whereas those of the latter are the ‘normal’ desmoschizus (*sensu* Bold & Wynne 1985, p. 149) that typifies most filamentous chlorophytes. Only the type species, *S. plumosa* Sonder from Western Australia, and a second, *S. elegans* Børjesen, from the Caribbean Sea, Indian and Pacific Oceans, appear to form their reticulate blade networks by segregative processes.

For some years we have known of a distinctive struveoid species growing on the floors of deep channels separating reefs in the Capricorn Group of mostly coral cays at the southern end of the Great Barrier Reef, as well as some of the outer ribbon reefs of north-central Queensland (Fig. 1). Because of the size and especially the thickness and dorsiventrality of its blades, we at first suspected that the species might represent a new genus (which we provisionally christened ‘Struvedendron’), but recent collections of the same entity by the second author in New Caledonia have led us to re-examine the material more critically, with the result that we now recognize its strong alliances to *Struvea sensu stricto*. *Struvea*, besides displaying segregative division, is characterized by net-like blades that form distally on clavate primary axes, opposite branching of several orders, and laterals that commonly form specialized terminal cells (‘tenaculae’) that adhere to contiguous cells by narrow, apically-spreading processes. These features characterize our material, which nevertheless differs from the other *Struvea* species by the much greater thickness of the blades and the unique dorsiventrality that is imparted to them by the directed growth of the first- and higher-order laterals. Although our attempts to confirm placement of the new species in *Struvea* by molecular means based on the recent New Caledonia collections have been unsuccessful (W. Freshwater, personal communication), we do not wish to delay the naming of this unusual alga further and now place it in *Struvea* with some confidence based on the anatomical features it displays.

**MATERIAL AND METHODS**

All collections were obtained using SCUBA and either preserved in 4% formalin-seawater, pressed as herbarium vouchers or air dried and placed in silica gel crystals for DNA extraction. Voucher herbarium specimens are housed at the School of Botany, University of Melbourne (MELU) and at the National Herbarium of New South Wales (NSW). Herbarium abbreviations are designated as given in Holmgren *et al.* (1990).

Photographs were taken on either a Wild Photomakroskop M400 or a Wild Leitz MPS51 Ortholux II system with Kodak EPY (Ektachrome 64T Professional) positive film. All images were either scanned (at 350 dpi) directly from 35 mm film using a Nikon LS-2000 slide scanner, or by flat-bed scanner (at 1500 dpi). The photographic plates were produced electronically and digitally using Adobe® Photoshop 6.0, then transferred to a CD ROM.
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**Fig. 1.** The Great Barrier Reef and New Caledonia region of the Coral Sea from which *Struvea thoracica* has been collected. (A) The north-central localities of Ribbon Reefs nos. 2 and 4. (B) The Capricornia Section showing Wistari Reef, Wilson Island, and One Tree Island.

**OBSERVATIONS**

**Diagnosis**

*Struvea thoracica* Kraft & Millar, sp. nov.

Planta singulae vel 2–4 aggregatae, 3–26 cm longae, erectae ex haptéro fibroso digitato, constantes e caulisibus simplicibus vel sparse ramosis parum annulatid ad 18 cm longis productivibus frondes singulas spongias ad 2 mm crassas, 18 cm longas, 12 cm latas. Frondes maturae constantes e reticulo denso ex ordinibus usque ad 4 ramorum laterialium facto, ramis lateraliis oppositis in cellulis sustinentibus costarum et ramorum ordinum priorum, eis ordinis primi secundique fluentibus ad paginam solam (‘ventralem’) et dense expansendae super eam, cellulis terminalibus raro terminantibus in tenaculis affixas ad paginas laterales cellularum contiguarum, tenaculis interdum lateraliibus factis elongatione perpetua subapicalibus cellulis sustententibus. Rami laterales primi ordinis in paginis ‘dorsalibus’ non tecti ramis lateraliibus ordinum secundariorum, quasi costae prominentes aequiliter distantes. Cellularum divisiones in axibus primariis et totis ramorum ordinibus segregativae.

Plantae singulae vel in aggregatis 2–4, ranging from 3 to 26 cm in length, erect from a digitate, fibrous holdfast, and composed of simple to sparingly ramified, slightly annulate stalks to 18 cm in length and 2.5 mm in width giving rise distally to single blades of spongy consistency to 2 mm in thickness, 18 cm in length, and 12 cm in width. Mature blades consisting of a dense reticulum composed of up to four orders of laterals, the laterals arising oppositely on successive bearing cells of costae and lower-order branches, those of the first and second orders distally curving toward and densely spreading over just one (the ‘ventral’) surface, terminal cells infrequently terminating in tenaculaceae that attach to lateral surfaces of contiguous cells, the tenacular cells at times becoming laterally po-

sitioned due to continued subapical elongation of the bearing cell. First-order laterals on ‘dorsal’ surfaces not covered by higher-order laterals, appearing as evenly spaced, prominent costae. Cell divisions in primary axes and all branch orders segregative.

**ETYMOLOGY:** ‘The thoracic *Struvea*’, named for the rib-caged construction of the fronds, with their dorsally exposed primary-axial ‘vertebrae’ and regularly spaced series of paired costae (‘ribs’) that curve ventrally to enclose the ‘visceral’ higher orders of branching.

**HOLOTYPE:** MELU, A41911 (Fig. 2).

**TYPE LOCALITY (Fig. 1):** Wistari Channel, Capricorn Group, southern Great Barrier Reef (23°25’S; 151°55’E).

**DISTRIBUTION (Fig. 1):** Southern Great Barrier Reef; north-central Great Barrier Reef; Noumea (22°16’S, 166°26’E), New Caledonia.

**SPECIMENS EXAMINED:** Great Barrier Reef (1) Ribbon Reef no. 2, plants from the lee side of the reef crest at −32 m (*Siotas*, 17 November 1985, MELU, A41731, 41733); (2) Ribbon Reef no. 4, plants from the lee side of the reef crest from 31 to 32 m (*Siotas*, 20 November 1985, A41732, 41771); (3) Wistari Channel, plants from the base of the reef wall at 23–24 m (*O’Brien, Siotas, Gabrielsson & Millar*, 23 November 1982, MELU, A41911–13, 41915), −30 m (*O’Brien, Gabrielsson & Ricker*, 24 November 1982, MELU, A41910, 41914), 26–30 m (*Kraft, Ricker & O’Brien*, 14 November 1983, MELU, A41916–24, 41926–28 = (GRB 15571, 15582)), −24 m (*O’Brien & Robins*, 15 November 1983, MELU, A41925), 25–30 m (*O’Brien & McConville*, 20 November 1983, MELU, A41931–33); (4) Wilson Island, 15–18 m (*O’Brien & Withell*, 21 November 1983, MELU, A41929); and (5) One Tree Island, 25–27 m off the south-central reef face (*Ricker & Kraft*, 19 November 1983, MELU, GRB 15750). New Caledonia, Noumea, Anse Vata, Ile aux Canards, 22 m on shore- or NW side of island (*Millar, Freshwater and Menou*, 13 September 2002, NSW 610014, NSW 610015, NSW 610920).

**HABITAT:** *Struvea thoracica* occurs in similar habitats throughout its known range and appears to be confined to waters below 15–18 m, where it grows primarily in shellgrit- and coral-debris-floored channels or reef flats subject to substantial tidal currents. Because collections have only come from the austral spring months of November on the Great Barrier Reef and September from New Caledonia, the seasonality and longevity of plants is unknown. What is known is that plants from 4 cm high to 26 cm high are found growing together in the same grove at the same time. They may be fast growing but short lived austral spring annuals.

**HABIT AND ANATOMY:** Plants grow erect and singly, in pairs (Fig. 3), or in aggregates of up to four, each anchored by holdfast filaments that issue along the basal 1–4 mm of the virtually unbranched, only slightly annulate stalks (Figs 4–7). Anchoring filaments are 150–350 μm in diameter, contorted in outline, simple or sparingly subdichotomously branched, and are usually septate just above the points where the tips flare out into coralloid digitations. Nonseptate stalks 2.5–18 cm in length by 1–2.5 mm in diameter make an abrupt transition to a single spongy, multicellular blade (Figs 2–5) that in mature plants reaches 2 mm in thickness and differs in surface appearance depending on whether seen in ventral or dorsal view (Fig. 4), the ventral surface having a uniformly fibrous texture whereas the dorsal side shows a regular series of paired, evenly spaced coarse ‘ribs’ formed by the exposed cells of the first-order laterals or ‘spine’ (Fig. 4).

Primary axes are unbranched or once or twice medially divided (Figs 3, 5) and initially clavate (Fig. 3), becoming acutely tapering distally before the onset of primary segmentation, which appears as a series of bead-like units resulting from segregative division of the cytoplasm (Fig. 5). Two opposite first-order laterals arise distichously on every primary-segment, become septate by segregative divisions, reach 250–800 μm in diameter, and each issue opposite pairs of second-order laterals 100–200 μm in diameter (Fig. 6) that in their turn produce a further order of branching, the apical cells ranging from 60 to 110 μm in diameter. First-order laterals and the next-order branches that they bear curve sharply distally (Figs 8, 9) and initiate the dorsiventrality of the blades that is maintained by the growth of all subsequent branch orders. Evidence for segregative cell division
is manifest by the complete lack of intercalary divisions throughout the plants (Fig. 8), which means that the number of cell units in the axes is set at the time of initial septation. This process also results in an elongated basal segment below in which no further cross-wall formation or production of laterals occurs (Fig. 10). Also indicative of segregative division is the regular positioning of all laterals at the distal poles of bearing cells (Figs 8, 10) and the triangular gaps formed at the peripheries of the horizontal boundaries between adjacent cells and the lateral walls of the parent cell (Figs 11, 12, 15). The elaboration of second- and higher-order filaments and their curvature toward the ventral surface (Fig. 12) ultimately produces the thickly meshed blades in which ventral (Fig. 13) and dorsal (Fig. 14) surfaces are differently structured.

Cells of the thalli are filled peripherally by either randomly aggregated (Fig. 15) or reticulate (Fig. 16) arrays of chloroplasts, each plastid 3–5 μm in diameter and containing a single small pyrenoid. Because apical cells of second- and higher-order laterals approach cells of the same or lower-level branch orders, an additional cell is sometimes, although not often, segregated at the tip of the filament (Fig. 17), makes contact with the contiguous cell, and splays out

Figs 2–7. *Struvea thoracica* Kraft & Millar, sp. nov. Habit and early development.

Fig. 2. The pressed holotype specimen (MELU, A41911).

Fig. 3. Habit of *in situ* plants from 30 m depth at Wistari Reef (14 November 1983; GBR 15571). Photo by Robert W. Ricker.

Fig. 4. Two fronds that have overlapped and partly anastomosed, one displaying its undifferentiated ‘ventral’ surface, the other its strongly costate ‘dorsal side’ (MELU, A41771).

Fig. 5. A divided stalk, one branch at an early, open-meshed stage of blade differentiation, the other showing the distal bead-like products of segregative cell division (MELU, A41928).

Fig. 6. Early development of primary laterals, initiation of second-order branches, and distal curving of laterals toward the ‘ventral’ surface (MELU, GBR 15571).

Fig. 7. Anchoring filaments at the base of a virtually untapered, nonannulate stalk (MELU, GBR 15571).
Figs 8–14. *Struvea thoracica* Kraft & Millar, *sp. nov.* Blade structure (8–12, NSW 610920; 13, 14, MELU, A41913).

**Fig. 8.** Early growth of first- and second-order laterals in dorsal view. Note complete lack of intercalary cell divisions that characterizes species undergoing segregative division.

**Fig. 9.** Same apex as Fig. 8, viewed from the ‘ventral’ surface toward which the first- and second-order laterals are curving.

**Fig. 10.** The base of the blade of Figs 8 and 9, the basal segment typically (for *Struvea*) elongate and bearing the lowermost pair of opposite primary laterals.

**Fig. 11.** Second-order laterals in which segregative cleavage of cytoplasts has recently occurred, as evidenced by the gaps between horizontal and lateral walls.

**Fig. 12.** Dense overlapping of unsegmented second-order laterals on septate primary branch filaments, none of which has formed tenaculae.

**Figs 13, 14.** Ventral (Fig. 13) and dorsal (Fig. 14) views of the base of a mature isotype frond, the costae of the latter visible because not covered by the dense weft of ventrally-positioned blade filaments.

apically (Fig. 18) into a branched attachment pad. Such ‘tenacular’ cells normally range from 40 to 50 μm in width by 30–70 μm in length, but occasionally extend to 150–350 μm in length. Tenaculae may remain terminal (Fig. 18), but often the bearing cell protrudes to one side (Fig. 19) and elongates further from that site, thereby progressively shifting the tenacular cell (Figs 20, 21) to a lateral position. This constitutes a true ‘cellulisympodium’ in the sense that Norris *et al.* (1984) coined the term. In a few rare instances, the new apex of the bearing cell abuts and apparently forms a light adhesion to a contiguous cell, but does not produce a further tenaculum (Fig. 22). Tenaculae adhere by irregularly subdichotomous narrow processes that issue around the circumference of the apex (Figs 22, 23).

A feature of cells in most specimens is an abundance of narrow, needle-like cytoplasmic inclusions (Fig. 24), most being less than a micron at the widest girth, 20–30 μm in length, and acutely attenuate to both ends. When thicker (to 2–3 μm diameter medially), which occurs very occasionally, usually only one end is tapered, the other being squared off or variously chisel-shaped.
Fig. 15. Gaps (arrows) between horizontal and lateral walls that result from segregative division.

Fig. 16. The peripheral, reticulate arrangement of chloroplasts, many showing central pyrenoids.

Fig. 17. The apical primordium of a tenacular cell, the triangular gaps at the cross-wall (arrows) indicative that it too arises by a segregative division.

Fig. 18. The apical flaring and adhesion of a tenaculum to an adjacent blade cell.

Fig. 19. Protrusion of a tenacular bearing cell (arrow) at the start of renewed elongation.

Fig. 20. Shunting of the tenacular cell (arrow) to a lateral position with apical elongation of the bearing cell.

Fig. 21. A completely lateral tenaculum.

Fig. 22. A lateral tenacular cell and contact (arrows) between the unmodified tip of the bearing cell and the lateral surface of a contiguous cell.

Fig. 23. The digitate, subdichotomous anchoring processes at the apices of tenacular cells.

Fig. 24. Needle-like cell inclusions.

DISCUSSION

The new species differs in a number of ways from the type, *Struvea plumosa*, and *S. elegans*, in both of which the blades form basically monostromatic, open reticula and the apices of primary and secondary laterals regularly form tenacular cells, the ends of tertiary filaments either becoming tenacular or remaining unconnected to lower-order cells (Womersley 1984, figs 73B, C; Kraft & Wynne 1996, figs 8, 13–15). Secondary and tertiary laterals not lying strictly in the plane of the frond appear to make their slight deflections in roughly equal numbers toward either surface (Womersley 1984, fig. 73C; Kraft & Wynne 1996, figs 12, 14). *Struvea plumosa* more often grows in aggregates than singly (Womersley 1984, fig. 73B), probably because its bases can become somewhat stoloniferous (Kraft & Wynne 1996, fig. 2), and stalks are strongly annulate both at the base (Kraft & Wynne 1996, fig. 2) and where they immediately subtend the blades (Kraft & Wynne 1996, fig. 1).

Although segregative divisions in *S. thoracica* have not been seen as unequivocally as they were in *S. plumosa* (Kraft & Wynne 1996, figs 3, 4, 14, 15), they are nevertheless strong-
ly implied by the one instance we observed (Fig. 5) in which cytoplasmic processes were observed at the distal end of a stalk, as was shown to be present in *S. plumosa* (Kraft & Wynne 1996, figs 3, 4). Where adjacent cells in *S. plumosa* appear to be separated by horizontal cross-walls that superficially look as though cladophoroid septation has occurred, it was shown (Kraft & Wynne 1996, fig. 5) that a triangular gap occurs between the cross-walls of adjacent cytoplasmic processes and the lateral wall of the parent cell that is continuous across the junction, indicating that segregatively divided cytoplasmic processes have formed walls within the parent wall that have been applied to its interior lateral surface. This phenomenon equally characterizes cell division in the new species (Figs 11, 15) and, along with the presence of tenacular cells and strong habit similarities between *S. plumosa* and *S. thoracica* at the latter’s early stages of blade development (Figs 5, 6), strongly indicates that the new species should be placed in the genus *Stru-*

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