The taxonomy and life history of *Gloiophloea* (Galaxauraceae, Rhodophyta)

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The red algal genus *Gloiophloea* J. Agardh (Galaxauraceae, Nemaliales) includes multiaxial, dichotomously branched plants that are composed internally of a filamentous central axis, radiating dichotomously branched medullary filaments, and a loose cortex of spherical, pigmented cells. An examination of the three species presently included has shown that only the type species, *G. scinaioides* J. Agardh, should be maintained. *Gloiophloea articulata* Weber-van Bosse from Cargados Carajos, near Mauritius, is known only from a single collection of sterile plants. It differs from *G. scinaioides* in lacking an apical pit, having periclinal medullary filaments which loosely fill the internal cavity rather than being restricted to a central axis, and producing a cortex composed of files of closely appressing cells, rather than a loose matrix. *Gloiophloea articulata* appears more closely allied to the family Gymnoploeaceae of the order Gigartinales, in particular the genus *Nemastoma* J. Agardh. Sexual material needs to be examined, however, before the species can be placed without doubt. *Gloiophloea perrinae* Levring from southern Australia was distinguished from *G. scinaioides* in having a firmer texture and in minor differences in its cortical composition and cystocarp shape. Variations in these characters occur within the type species, however, and are probably due to age and growing conditions. *Gloiophloea perrinae* is therefore reduced to synonymy with *G. scinaioides*. In culture, carpospores of *G. scinaioides* give rise to a filamentous tetrasporophyte which produces cruciate tetrasporangia. Tetraspores in turn produce a filamentous protonemal gametophyte which gives rise to the fleshy gametophyte directly. The life history of *Gloiophloea* is therefore identical to that of the closely related genus *Scinaia* Bivona-Bernardi.

**INTRODUCTION**

*Gloiophloea* (Galaxauraceae, Rhodophyta) was first described by J. Agardh in 1872 for material collected by Harvey from Western Port, near Melbourne, Australia, and distributed by him as *Scinaia furcellata* Turner. The new genus included only a single species, *G. scinaioides* J. Agardh, which was said to be closely related to *Scinaia* Bivona-Bernardi but lacking the colourless cortical utricles distinctive of that genus. Since its original description, the circumscription of *Gloiophloea* has undergone a number of changes, mostly as the result of Setchell’s (1914) misidentification of the New Zealand taxon now known as *Scinaia berggrenii* (Levring) Huisman (Huisman 1985). Following Setchell’s work in 1914, eleven species were added to *Gloiophloea*. The majority of these were subsequently removed to *Pseudogloiophloea* Levring (Levring 1953 as a nom. nud., 1955; Levring in Svedelius 1956; Joly et al. 1965; Papenfuss 1968; Desikachary & Singh 1958; Chihara 1969) and even more recently to *Scinaia* (Huisman 1985). Presently, *Gloiophloea* is represented by three species: *G. scinaioides* and *G. perrinae* Levring from southern Australia and *G. articulata* Weber-van Bosse from the western Indian Ocean. The type specimen of *G. articulata* differs from *G. scinaioides* in its large size and slightly moniliform thallus. The original material is sterile, however, the species having been included in *Gloiophloea* with some doubt (Weber-van Bosse 1914; Setchell 1914). *Gloiophloea perrinae* was erected by Levring (1953) for material from Tasmania. It differed from the type species in habit, firmer texture, slightly different cortical structure and minor differences in the shape of its cystocarps. Womersley (pers. comm.) has for some time doubted the validity of *G. perrinae* as distinct from *G. scinaioides* and the results obtained in the present study confirm that doubt.

Only gametophyte plants of *Gloiophloea* have
been collected to date. Consequently, culture studies of *Gloiophloea scinaeioides* were initiated to ascertain the form of the tetrasporophyte. Studies on the closely related genus *Scinaea* (Ramus 1969 as *Pseudogloiophloea*; Boillot 1968, 1969, 1971a, 1972; van den Hoek & Cortel-Breeman 1970; Umezaki 1972; Kornmann & Sahling 1980) have revealed a triphasic, heteromorphic life history which includes a filamentous tetrasporophyte and a filamentous protonemal gametophyte from which the fleshy gametophyte develops directly. A similar life history has been found for *Gloiophloea scinaeioides* in the present study.

**MATERIALS AND METHODS**

Materials used for morphological observations were preserved either as dried herbarium specimens or in a 5% formalin/seawater solution. Sections (where possible of wet-preserved material) were cut on a freezing microtome and mounted in a 50% Karo syrup/1% aniline blue/4% 1 N HCl/45% seawater solution. Culture studies of *G. scinaeioides* were initiated from a specimen collected at Portsea Jetty, Port Phillip Bay, Victoria, and transported to the laboratory in a seawater-filled plastic bag stored on ice. Cystocarp-containing portions of the gametophyte were placed in petri dishes containing Provasoli’s enriched seawater (as described in Bold & Wynne 1978) and glass coverslips. Released carpospores were either isolated into fresh media or allowed to attach to the coverslips. In the case of the latter the coverslips were then mechanically cleaned of any contaminants and transferred to fresh media. Cultures were grown under either 16°C/45-50 μmol m⁻² s⁻¹/16 h day; 16°C/10-15 μmol m⁻² s⁻¹/16 h day; 20°C/20 μmol m⁻² s⁻¹/20 h day or 20°C/10 μmol m⁻² s⁻¹/20 h day. Media were changed every 14 days. When cultures became overcrowded, apical portions of the plants were excised and transferred to fresh media. Abbreviations for herbaria follow Holmgren *et al* (1981). Specimens examined are cited as in Huisman (1986).

**RESULTS**

*Gloiophloea scinaeioides* J. Agardh 1872, p. 29; Levring 1953, pp. 504-507, figs 35-36; Kylin 1956, p. 120.


**HOLOTYPE:** LD Herb. Agardh No. 32112 (Fig. 1).

**TYPE LOCALITY:** Western Port, Victoria, Australia (38°25'S, 145°12'E).

**DISTRIBUTION:** From Eucla (31°39'S, 128°51'E) (ADU A19377), just west of the Western Australia/South Australia border, eastward to Wilsons Promontory, Victoria (35°51'S, 146°05'E) (ADU A43243) and northern Tasmania (41°10'S, 146°22'E) (MELU 24358).

**SPECIMENS EXAMINED:** The following are representative of the 95 specimens examined.

1. **Western Port, Vic.** (LD Herb. Agardh No. 32112) (Holotype) (Fig. 1).


3. **Phillip I., Western Port, Vic.** Harvey Travelling Set Specimen No. 391. (MEL 504154) (Syntype).

4. **Western Port, Vic.** (J. Bracebridge Wilson, 1880, MEL 504163).

5. **Port Phillip Heads, Vic.** (J. Bracebridge Wilson, 1880, MEL 504163).

6. **Portsea Jetty, Vic.** On rocks at 5 m. (J. Bracebridge Wilson, 25-iii-1981, MELU 23966, 2 sheets) (Fig. 4).

7. **Aireys Inlet, Vic.** Drift. (G. T. Kraft, 21-ii-1976, MELU 23239) (Fig. 3).

8. **Tamar River, Lighthouse.** Devonport, Tas. (T. Levring, 22-ii-1948, GB un-numbered) (Holotype of *G. perrinae*) (Fig. 6).

9-10. **Low Head, Tas.** (F. Perrin & A.H.S. Lucas, March 1932, ADU A47151); (F. Perrin, Feb. 1940, MEL 504162). Two plants are mounted on the same sheet of which only the lower is *Gloiophloea*. (11) **Devonport, Tas.** -25 ft. Common on stones.
from the sand flat. (S.S. Chidgey, May, 1980, MELU 24358) (Fig. 5).


(14) Nora Creina, S.A. 4-6 m, on small stones with Ulva. (G.T. Kraft, 18-ii-1974, ADU A46012).


(16) Investigator Strait, S.A. (J.E. Watson, Station 11 at 23 m, 35°09’S, 137°31’E, 7-i-1971, ADU A38437).


(18) Vivonne Bay, Kangaroo I., S.A. Drift. (W.J. Woelkerling, 21-ii-1979, MELU 22988) (Fig. 2).


(20) Troubridge Light, (Edithburgh), St. Vincents Gulf, S.A., Station 10 in 17 m depth, on limestone. (S.A. Shepherd, 4-ii-1969, ADU A33434).

(21) Tipara Reef, Spencer Gulf, S.A. (1.3 km N.W. of Tipara Light, 5 m, S.A. Shepherd, 11-i-1978, ADU A49405).


HABITAT: The fleshy gametophyte of Gloiophloea scinaioides has been collected from depths of 2-31 m, usually growing on rocks associated with a sandy bottom. It appears to be a summer/autumn annual (December to May).

REMARKS: The morphology and reproductive development of G. scinaioides have been described earlier (Huisman 1985); the present discussion concerns only the conspecificity of G. perrinae with G. scinaioides. Levring (1953) erected G. perrinae for a specimen collected from the mouth of the Tamar River, near Devonport, Tasmania. The distinguishing features of G. perrinae were said to be its firmer texture, microscopic differences in the size of the assimilatory cells and slight differences in the size of the cystocarps (Fig. 7). This would account for its more elongated shape, as cystocarps in the genus become broader with age. Similar reasoning could also be applied to the differences in the assimilatory cell sizes. The genus Gloiophloea, therefore, is represented in Australia by the single species, G. scinaioides.

Gloiophloea (?) articulata Weber-van Bosse 1914, p. 276, figs 1, 26, 27.

HOLOTYPE: L Herb. Weber-van Bosse No. 943, 68 . . . 248 (Fig. 7).

TYPE LOCALITY: Cargados Carajos, Mascarene Group, Indian Ocean, 16°35’S, 59°40’E. Dredged from 65 m.

DISTRIBUTION: Known only from the type collection which consists of a number of unmounted, dried fragments and a wet specimen dredged from 100 m (not seen in the present survey).

SPECIMEN EXAMINED:

(1) Holotype (J.S. Gardiner, 1905, L Herb. Weber-van Bosse No. 943, 68 . . . 248) (Fig. 7), plus several dried fragments from the same collection. The plant figured as the holotype (Fig. 7) is the same as that illustrated by Weber-van Bosse (1914, pl. 16, fig. 1).

VEGETATIVE STRUCTURE: Plants are to 18 cm tall, dichotomously branched, the distance between the furcations ranging from 9 to 25 mm. Thalli are generally terete, 3-6 mm wide, somewhat flattened at the bases of the branches, with slight constrictions at the nodes. Branch apices lack the apical pit distinctive of Gloiophloea (see Weber-van Bosse 1914, fig. 26). Internally the thallus is composed of a medulla of loosely arranged pericentral filaments (cells 5-15 × 100-170 μm) from which radiate dichotomously branched subcortical filaments (cells 5-6 × 30-50 μm). Near the cortex the subcortical filaments become shorter and subtend cuboidal cortical cells, usually broader than long (5-7 μm wide by 4-5 μm long) (Fig. 8). These cortical cells are produced in files of 3-4 cells that are of a uniform size and shape. Rhizoidal filaments are produced by the subcortical cells, giving the older branches a firmer texture. Secondary pit-connections are absent throughout (Weber-van Bosse 1914, and pers. obs.).

REMARKS: The generic placement of Gloiophloea is at a younger stage of development than that illustrated for G. perrinae. This would account for its more elongated shape, as cystocarps in the genus become broader with age. Similar reasoning could also be applied to the differences in the assimilatory cell sizes. The genus Gloiophloea, therefore, is represented in Australia by the single species, G. scinaioides.
Figs 7, 8. Gloiophloea articulata Weber-van Bosse.
Fig. 7. The holotype specimen collected from Cargados Carajos (L Herb. Weber-van Bosse No. 943, 68 . . . 248).
Fig. 8. Section of cortex showing the dichotomously branched medullary filaments and compact cortical cells.

Gloiophloea articulata must remain in doubt. The holotype displays some features in common with G. scinaioides, including its dichotomously branched terete thallus, medulla of periclinal filaments and subcortex of dichotomously dividing filaments giving rise to a cortex of smaller coloured cells (Weber-van Bosse 1914). Gloiophloea articulata differs, however, in the lack of an apical pit, the periclinal medullary filaments loosely filling the internal cavity rather than being restricted to a distinct central axis, and the cortical cells being produced in files of closely appressing cells, rather than the loose matrix of G. scinaioides. These features (as well as those the species has in common with Gloiophloea) suggest the family Gymnophloeaceae of the order Ggartinales (see Kraft 1975), and in particular the genus Nemastoma J. Agardh. Sexual material needs to be examined, however, before the species can be placed without doubt.

CULTURE STUDIES
After 2–3 days in culture carpospores of Gloiophloea scinaioides were released and became attached to the glass coverslips (Fig. 10). Released carpospores were spherical with a diameter of 7–10 μm. Within 24 hours of attachment 1–2 small protrusions (Fig. 11) developed and then grew rapidly to produce an irregularly branched, filamentous plant with both prostrate and erect

Fig. 9. Wet specimen collected from Portsea, Vic., from which cultures were started (MELU 23966).

Fig. 10. Released carpospore.
axes. Cells of the filaments measured 2–8 μm × 11–50 μm. Growth appeared to be best under 16°C/15–20 μmol m⁻² s⁻¹/16 h day. After 2–3 months, the plant reached a diameter of 3–4 mm (Fig. 12). Crucially divided tetrasiomangia (15–20 × 10–11 μm) were produced either terminally or laterally and were either sessile or pedicellate (Fig. 13). They generally arose in groups of 2–5 sporangia. Sporogenesis appeared to be induced by the maturity of the plant rather than environmental cues. Released tetrasiomspores were spherical with a diameter of 5–10 μm, although they increased in size after attachment. Germination of the tetrasiomspores was identical to that of the carposporophyte and the resultant filamentous plant was indistinguishable from the tetrasiomporophyte. After 2–3 months growth this second filamentous stage (= protonemal gametophyte) produced occasional fleshy ‘buds’ with an internal structure identical to the field collected gametophytes (Fig. 15). The ‘buds’ arose initially as enlarged lateral cells of the filamentous, protonemal gametophyte (Fig. 14) so that the fleshy gametophyte was initially uniaxial but became multiaxial. The cortex of the gametophytes grown in culture was identical to that of the field collected material (Fig. 16). Fleshy gametophytes were not grown to reproductive maturity in culture, and after a few months growth the filamentous protonema appeared to lose the ability to produce buds. Transferring the cultures to long day/high temperature conditions did not induce bud formation, although this was expected considering the seasonality of the species in the field.

**DISCUSSION**

The life history of *Gloiophloea scinaoides* consists of three phases: (1) the fleshy gametophyte which, after fertilization, produces the (2) carposporophyte. Released carpospores germinate into a (3) filamentous tetrasporophyte, with meiosis presumably occurring in the formation of the tetrasiomspores. Released tetrasiomspores germinate into a filamentous protonemal gametophyte which is morphologically identical with the tetrasporophyte. The fleshy gametophyte arises directly from the filamentous protonema. Initiation of the fleshy gametophyte appears to be induced by some seasonal factor, as it is only found in the field during summer and autumn. This response could not be duplicated in culture, however. The species probably over-winters as a filamentous stage, initially as the tetrasporophyte, later as the protonemal gametophyte. The time period required for each filamentous stage to reach maturity in culture (2–3 months) corresponds to the period that the fleshy gametophyte is absent from the field.

The life history of *Gloiophloea* is therefore identical to that of the closely related genus *Scinaias* (Ramus 1969 as *Pseudogloiophloea*; Boillot 1968, 1969, 1971a, 1972; van den Hoek & Cortel-Breeman 1970; Umezaki 1972; Kornmann & Sahling 1980) and also that of the single species of *Galaxaura* [*G. oblongata* (Ellis & Solander) Lamouroux] which has been cultured (Magruder 1984). It is also identical to the life histories of many of the genera included in the Liagoraceae (e.g. *Liagora farinosa* Lamouroux (von Stosch 1965); *Helminthoclada calvadosii* (Lamouroux) Setchell (Boillot 1971b, 1974); *Helminthora divaricata* (C. Agardh) J. Agardh (Boillot 1971c, 1972)), further evidence that the family Liagoraceae and at least some of the members of the Galaxauraceae are closely related. Removing the Galaxauraceae to its own order, as has been suggested by some workers (see Huisman 1985), gains no support on the basis of life history studies.

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Fig. 11. Germinating carpospores.
Fig. 12. Filamentous tetrasporophyte arising from the carpospores.
Fig. 13. Crucially divided tetrasiomangia borne on the tetrasporophyte.
Fig. 14. Fleshy gametophyte initial arising on the filamentous protonemal gametophyte.
Fig. 15. Fleshy gametophyte.
Fig. 16. Section of the cortex of a fleshy gametophyte grown in culture.
REFERENCES


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