The red algal genus *Coelarthrum* Børgesen (Rhodymeniaceae, Rhodymeniales) in Australian seas, including the description of *Chamaebotrys* gen. nov.

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The genus *Coelarthrum* presently includes eight species world-wide, of which three (*C. muelleri* (Sonder) Børgesen, *C. cliftonii* (Harvey) Kylin and *C. boergesenii* Weber-van Bosse) have been recorded from Australian seas. An examination of type and recent collections of these and several non-Australian species has resulted in several nomenclatural and taxonomic changes. The type of the genus, *C. albertisii* (Piccone) Børgesen from the Canary Islands, is considered to be conspecific with the earlier Australian taxon *C. cliftonii. Coelarthrum muelleri* is conspecific with the Indian Ocean taxon *C. opuntia* (Endlicher) Børgesen. A new species, *Coelarthrum decumbens*, has been recognized in collections from eastern Australia, differing in its decumbent habit and production of tetrasporangia in sori. Tetrasporangial development in *Coelarthrum boergesenii* differs substantially from that occurring in the other species, and the genus *Chamaebotrys* is erected to accommodate this taxon. The new genus is vegetatively similar to *Coelarthrum* but tetrasporangia are terminal and produced in nemathecia, whereas in *Coelarthrum* the sporangia are modified intercalary cortical cells.

INTRODUCTION

In 1910, Børgesen created the genus Coelarthrum to receive Chylocladia albertisii Piccone, a species originally described from the Canary Islands (Piccone 1884) but also found to occur in the West Indies (Børgesen 1910). Since its inception, seven additional species have been attributed to the genus: C. boergesenii Weber-van Bosse, C. muelleri (Sonder) Børgesen, C. cliftonii (Harvey) Kylin, C. opuntia (Endlicher) Børgesen, C. mortensenii Børgesen, C. lomentariae Tanaka et Nozawa in Tanaka, and C. coactum Okamura et Segawa in Segawa. The last-mentioned species was included under C. boergesenii by Abbott & Littler (1969). At present the genus includes those members of the Rhodymeniaceae that have mucilagefilled, vesicular branches with regular constrictions and septa and lack internal filaments (although rhizoidal filaments are known in C. cliftonii). Species distinctions are based on habit, the morphology of the constrictions, and cortical features. During the course of my studies of the Australian algal flora four species of Coelarthrum were found to occur, three of which were referable to C. boergesenii, C. muelleri and C. cliftonii, the fourth representing a new species. A critical comparison between these species and several non-Australian taxa has shown C. muelleri to be conspecific with the earlier C. opuntia and C. cliftonii to be conspecific with the type of the genus C. albertisii (which also includes C. mortensenii from Mauritius). An examination of tetrasporangial initiation has shown that in C. boergesenii the sporangia are produced terminally on cortical filaments in nemathecia, whereas those of the other species are intercalary. It is therefore proposed that C. boergesenii be placed in the segregate genus Chamaebotrys.

MATERIALS AND METHODS

All specimens examined were preserved in 5% Formalin/seawater. Most sections were cut with a freezing microtome set at 30–50 μ m. Sections were stained with 1% aniline blue and mounted in 50% corn syrup.

Abbreviations for herbaria follow Holmgren et al. (1990).

Key to the Species of Coelarthrum and Chamaebotrys

- (1) Plants with terminal tetrasporangia produced in distinct nemathecia *Chamaebotrys* (2)
- (1) Plants with intercalary tetrasporangia arising as modifications of mid-cortical cells, scattered throughout
 - the cortex or in vague sori Coelarthrum (3)
 (2) Plants mostly upright, without secondary lateral attachments Chamaebotrys lomentariae
 - (Tanaka et K. Nozawa in Tanaka) comb. nov.
 (2) Plants largely decumbent, secondary lateral attachments common ... Chamaebotrys boergesenii
- - (4) Plants largely decumbent, segments small [2–2.5
 (B) × 3–4 mm (L)], with tetrasporangia in sori, cystocarps protuberant .. *Coelarthrum decumbens* sp. nov.

(4) Plants upright, segments generally larger [to 5–7
 (B) × 19 mm (L)], with scattered sporangia, cystocarps mostly immersed ... Coelarthrum cliftonii (Harvey) Kylin

SYSTEMATIC ACCOUNT

Genus Coelarthrum Børgesen 1910, p. 192

Plants upright or decumbent, attached to the substratum by a single discoid holdfast and occasionally several secondary holdfasts. Axes regularly segmented, dichotomously to polychotomously branched at the distal end of each segment, occasionally with secondary anastomoses. Joints between segments broad or stalk-like. Segments composed of an outer cellular layer encasing a mucilage-filled cavity. Cellular layer derived from a diffuse apical meristematic region, when mature of three to several layers, the innermost (medulla) of large, hyaline cells, grading outwardly into a cortex of several layers of smaller, pigmented cells. Septa associated with joints one to several cells thick. Hair cells occasionally present on outer cortical cells, usually near apical regions. Internal rhizoidal filaments occasionally present. Spherical gland cells borne either directly on the inner surface of the medullary cells, on rhizoids or (more commonly) in clusters on specialized stellate cells projecting into the cavity. Tetrasporangia scattered throughout the cortex or grouped into sori, with cruciately/decussately arranged spores (rarely tetrahedral), arising as modifications of intercalary mid-cortical cells. Spermatangia borne on outer cortical cells. Carpogonial branches four-celled, borne on mid-cortical supporting cells, retaining the shape of the branch initial. Auxiliary cell borne on an intercalary cortical cell attached to the supporting cell; after presumed diploidization producing a gonimoblast initial via a transverse division. Mature gonimoblast clavate or subspherical, composed almost entirely of carposporangia, with an obscure, poorly developed fusion cell. Cystocarp cavity formed by periclinal separation of the medullary and cortical layers, the latter thickened by renewed growth, with a prominent ostiole. Mature cystocarps protuberant or partially immersed in the thallus.

TYPE SPECIES: *Coelarthrum albertisii* (Piccone) Børgesen 1910, p. 192 [= *Coelarthrum cliftonii* (Harvey) Kylin].

Australian species

Coelarthrum cliftonii (Harvey) Kylin 1931, p. 15

Figs 1-15

BASIONYM: *Chylocladia cliftonii* Harvey 1855, p. 556. 1858, pl. LVII.

HOMOTYPIC SYNONYM: *Erythrocolon cliftonii* J. Agardh 1896, p. 91.

HETEROTYPIC SYNONYMS: Chylocladia albertisii Piccone 1884, p. 37 (Type locality: Canary Islands). Coelarthrum albertisii (Piccone) Børgesen 1910, p. 192. Chylocladia tenera J. Agardh 1896, p. 87, nom. nudum. Coelarthrum mortensenii Børgesen 1944, p. 19 (Type locality: Mauritius).

LECTOTYPE: TCD (Fig. 1).

TYPE LOCALITY: Fremantle, Western Australia.

DISTRIBUTION: Australia: Known from the Montebello Islands (north-western Australia) south and east to Troubridge and Kangaroo islands (South Australia). Ex-Australia: Canary Islands (Piccone 1884; as *Chylocladia albertisii*); Natal, southern Africa (Norris 1986); Mauritius (Børgesen 1944; as *Coelarthrum mortensenii*); West Indies (Børgesen 1910); Hawaii (Abbott & Littler 1969); Indonesia (Weber-van Bosse 1928).

SELECTED SPECIMENS EXAMINED: Western Australia: Off Cape Bouvard (J.M. Huisman, 11.v.1994; MURU, JH 559). Fremantle (G. Clifton, TCD) (Lectotype of Chylocladia cliftonii) (Fig. 1). Fremantle (G. Clifton, AD, A18250) (Isotype). Parker Point, Rottnest Island (J.M. Huisman, 18,x,1989; MURU, JH 595). Roe Reef, Rottnest Island. Epilithic at 20 m depth (J.M. Huisman, 10.xi.1990; MURU, JH 588). Coronation Island Pelsaert Group, Houtman Abrolhos (J.M. Huisman, 24.ix.1994; MURU, HA 911). Snowy's Island, Pelsaert Group, Houtman Abrolhos (J.M. Huisman & T.H. Rose, 29.ix.1991; MURU, HA 910). Goss Passage, Wallabi Group, Houtman Abrolhos, 30 m depth (J.M. Huisman, 31.ix.1994; MURU, HA 397). West of south tip of Hermite Island, Montebello Islands, 12 m depth (J.M. Huisman, 10.vii.1992; MURU, JH 593, 594). South Australia: Egg Island, Isles of St Francis, 35 m depth (S.A. Shepherd, 7.i.1971; AD, A38099). Pearson I., 30-35 m depth (S.A. Shepherd, 7.i.1969; AD, A33692). Troubridge Light, 23 m depth (S.A. Shepherd, 4.ii.1969; AD, A33812). Vivonne Bay, Kangaroo I. On jetty piles at 0-3 m depth (G.T. Kraft & U. Min-Thein, 4.xii.1971; AD, A41412). West Indies: St Jan, off America Hill west of Tortola, 27 m depth (C, Herb. Børgesen 2033). South Africa: Black Rock, in drift (J. Phelan, 19.i.1986; NAT, 3734). Canary Islands: Isola di Lanzarote, Canary Islands (A. Piccone, 14-16.viii.1882; Slide preparation in C) (Holotype of Chylocladia albertisii) (Fig. 3). Mauritius: Between Gunner's Quoin and Flat Island, dredged from 46 m depth (T. Mortensen, 15.x.1929; C) (Holotype of Coelarthrum mortensenii) (Fig. 2). HABITAT: Plants are generally found attached to rock or cor-

al at depths to 35 m.

HABIT AND VEGETATIVE STRUCTURE: Mature plants 5-20 cm in height, light pink to red, soft and pliable. Specimens from colder waters attain a greater height with larger and more elongate segments. Attachment to substratum by a single small discoid holdfast and occasionally several secondary attachment points. Branching profuse, with two to many segments arising dichotomously or radially from the distal ends of parent segments. Main axes often percurrent. Anastomoses between branches common (Fig. 5). Axes segmented throughout (Figs 1-5), the segments terete (to 5-7 mm diam.) and elongate near the base (to 19 mm in length), becoming spherical near the apices (1-2 mm diam.). Lower segments generally broader towards their distal end. Constrictions between segments 0.5-2 mm in diam. Anatomically the thallus is multiaxial, with a diffuse growing point giving rise to a membranous cellular layer encasing a cell-free cavity. The former composed of 3-4 cell layers, the inner medulla of large, equidimensional to elongate, hyaline cells (70–250 \times 50–100 μ m in surface view) supporting the cortical 1 or 2 layers of progressively smaller, pigmented cells (surface cells 4-8 µm diam.) (Fig. 6), secondary pit-connections common. Monodistromatic septa occur between segments and are formed from the medullary layer subtending the site of branch initi-



Figs 1-7. Coelarthrum cliftonii (Harvey) Kylin.

- Fig. 1. Lectotype of Chylocladia cliftonii Harvey from Fremantle, Western Australia (TCD).
- Fig. 2. Holotype of Coelarthrum mortensenii Børgesen from Mauritius (C).
- Fig. 3. Holotype of Chylocladia albertisii Piccone from the Canary Islands (PAD).
- Fig. 4. Specimen from the West Indies included by Børgesen in Coelarthrum albertisii (C).
- Fig. 5. Branch apices showing the initiation of new segments, the broad connections between segments (large arrows) and secondary lateral anastomoses (small arrows) (MURU, HA 910).
- Fig. 6. Cortex in surface view (MURU, JH 595).
- Fig. 7. Surface view of developing tetrasporangium with connections to several adjacent cells (arrows) (MURU, JH588).



Figs 8-9. Coelarthrum cliftonii (Harvey) Kylin.

Fig. 8. Portion of cystocarpic plant with largely immersed cystocarps (MURU, JH 588).

Fig. 9. Section of cystocarp with the medullary layer of hyaline cells invaginating and the pericarp remaining at the level of the outer cortex. (MURU, HA 910).

ation. Hair cells occasionally borne on the outer cortical cells. Internal rhizoidal filaments occasionally present. Spherical to ovoid gland cells (10–30 μ m diam.) borne (generally in groups of 2 or 3 but 1–7 can occur) on stellate cells projecting into the inner cavity (Fig. 10), directly on the medullary cells or on internal rhizoids.

TETRASPORANGIA: Tetrasporangia (20–40 μ m diam.) are scattered throughout the cortex, derived from a mid-cortical cell in an intercalary position (Figs 7, 11). Sporangia are generally subspherical with cruciately/decussately arranged spores, although occasionally sporangia with tetrahedrally arranged spores occur.

SPERMATANGIA: Spermatangia arise from outer cortical cells (Fig. 12). The cortical filaments proliferate laterally along the surface of the thallus, and their cells produce spherical spermatangia (2–3 μ m diam.).

CARPOGONIAL BRANCH AND CYSTOCARP: Carpogonial branches arise on mid-cortical cells and are composed of four cells that retain the shape of the branch initial (Fig. 13). One of the inner cortical cells attached to the supporting cell acts as the auxiliary mother cell and produces a terminal auxiliary cell (Fig. 14). Following presumed fertilization a connection is made between the carpogonium and the base of the auxiliary cell, although the exact mode of this connection was not observed. Several small cells of unknown function are cut off from the cells of the carpogonal branch (Fig. 15). During the process of carpogonial branch formation and auxiliary cell production the supporting cell greatly increases in size and eventually occupies a position between the hyaline medullary cells. The gonimoblast initial is cut off from the auxiliary cell via a transverse division and forms a clavate cluster of carposporangia (Fig. 15). Localized renewed growth of the outer cortex above the developing carposporophyte results in a thickened pericarp that projects only slightly above the level of the cortex (Figs 8, 9). The cystocarp cavity is formed by the splitting of the medullary and cortical layers, with the medulla invaginating somewhat to accommodate the carposporophyte (Fig. 9). The connections between the medulla and cortical layers stretch and eventually break, although remnants can often be seen in the cystocarp cavity. A region of nutritive tissue surrounds the base of the carposporophyte. Mature cystocarps are 700–800 μm in diameter (including the pericarp) with angular carposporangia (15-20 µm diam.).

REMARKS: Several collections were mentioned by Børgesen (1910) when erecting the genus *Coelarthrum*. Of these, the type specimen of *Chylocladia albertisii* Piccone (the basionym and therefore the type of the genus) is housed in Padova. Unfortunately, this specimen is sterile and unavailable for loan. The species has not been collected again from the type locality or nearby (Afonso-Carillo, personal communication). Thus the information on which to base a concept of this species is severely limited. I have been able to examine a photograph of the type specimen (Fig. 3) to ascertain the habit, and in Copenhagen (C) there is a slide preparation that Bør-

Figs 10-15. Coelarthrum cliftonii (Harvey) Kylin.

- Fig. 11. Tetrasporangia in transverse view showing the intercalary nature of the sporangia (MURU, JH 588).
- Fig. 12. Spermatangia borne on cells of the outer cortex (MURU, HA 911).
- Fig. 13. Four-celled carpogonial branch (MURU, HA 910).

Fig. 10. Section of cortex (MURU, JH 595).

Fig. 14. Auxiliary cell borne on an inner cortical cell. The carpogonium is in close proximity but it is not known if the diploid nucleus has been transferred (MURU, JH 595).

Fig. 15. Young clavate gonimoblast arising from an initially transverse division of the auxiliary cell. The remnants of the carpogonial branch persist (MURU, JH 595).

Abbreviations. a.m., auxiliary mother cell; aux, auxiliary cell; c.b., carpogonial branch; gb, gonimoblast; gl, gland cell; sp, spermatangia; su, supporting cell; t.i., tetrasporangial initial; tr, trichogyne.











10-12 13-15



gesen made of Piccone's material. Although the material is poorly prepared, it is possible to ascertain the surface view of the cortex. The outer cortex is composed of loosely arranged, somewhat spherical cells that do not form a coherent layer. This material also shows the broad connections between segments that were illustrated by Børgesen (1910: fig. 11) and are evident in the type specimen (Fig. 3). Also included in the protologue (of *Coelarthrum*) was a collection from St Jan, West Indies, of which several plants are in the Copenhagen collection (C, Herb. Børgesen 2033, Fig. 4). Børgesen suggested that these plants differed slightly from those of Piccone but concluded that they belonged to the same species. As far as can be ascertained from the limited type material available. his conclusion appears well founded. The West Indian material is tetrasporic with intercalary sporangia and, as noted by Børgesen (1910, p. 192), they are 'dispersed over the whole thallus'.

Examination of the type and recent collections of Coelarthrum cliftonii (Harvey) Kylin from western and southern Australia indicates conspecificity with Coelarthrum albertisii. A variety of habits are displayed, from sparsely branched with elongate segments to densely branched with shorter segments. In addition, many plants show secondary anastomoses between segments, a feature also found in Coelarthrum albertisii (Børgesen 1944, p. 18). Plants collected from the colder waters of southern Australia are generally more robust with larger segments than those collected from warmer waters in Western Australia. This characteristic was also noted in C. opuntia and suggests that the variability in segment size could be due to temperature. In habit, then, the range presented by C. cliftonii from or near the type locality includes that of C. albertisii. Both have a similar cortical arrangement and morphology of septa. Piccone himself felt that Chylocladia albertisii was similar to Harvey's Chylocladia cliftonii (Piccone 1884). Kylin (1931, p. 15, fig. 4C) noted that Coelarthrum cliftonii differed from all other species of the genus in the production of filaments from the stellate cells and medullary cells. In recent western Australian collections these filaments are secondarily produced and lacking in younger portions of the plants. In addition, filaments are absent or rare in some plants from near the type locality, as was also the case for material from South Africa (Norris 1986, p. 538, and pers. obs. on NAT, 3734). From this I can only conclude that the production of internal filaments is a variable feature and should not be used as a specific character. In all other features C. cliftonii appears identical to C. albertisii. Since Chylocladia cliftonii Harvey (1855, p. 556) predates Chylocladia albertisii Piccone (1884, p. 37) the correct name for the taxon is *Coelarthrum cliftonii*, a combination first proposed by Kylin (1931, p. 15).

Coelarthrum mortensenii was described by Børgesen (1944, p. 19) from Mauritius. An examination of the type collection has shown it to include plants that are identical to several Western Australian specimens. The cortex (as described by Børgesen 1944) is identical to that of *C. cliftonii*. As such *C.* mortensenii is also reduced to synonymy with *C. cliftonii*. Børgesen compared his new species to *C. opuntia* and noted many of the differences found in the present study.

Coelarthrum cliftonii is similar to *C. opuntia* in gross habit, with both species forming upright thalli attached (generally) by a single holdfast. It differs in its broad connections and monostromatic septa between segments and cystocarps partially immersed in the thallus (see also Weber-van Bosse 1928, fig. 206). *Coelarthrum opuntia* has stalk-like connections and protuberant cystocarps.

Coelarthrum opuntia (Endlicher) Børgesen 1937, p. 333

Figs 16-25

BASIONYM: Chrysymenia opuntia Endlicher 1843, p. 42.

HOMOTYPIC SYNONYMS: Chondria opuntia J. Agardh 1841, p. 21 non (Goodenough et Woodward) C. Agardh 1817, p. XVIII. Gastroclonium opuntia (Endlicher) Kützing 1849, p. 866. Lomentaria(?) opuntia (Endlicher) J. Agardh 1852 [1851–1863], pp. 737--738. Sedoidea ?opuntia (Endlicher) Kuntze 1891, p. 921.

HETEROTYPIC SYNONYMS: Lomentaria muelleri Sonder 1853, p. 693 (Type locality: Lefevre Peninsula, South Australia). Chylocladia muelleri (Sonder) Harvey 1860, pl. CXXXVIII. Erythrocolon muelleri (Sonder) DeToni 1900, p. 585. Coelarthrum muelleri (Sonder) Børgesen 1931, p. 9–11, figs 6, 7. Lomentaria valida Kützing 1865, p. 30, table 85a, b. [Type locality: supposedly Tasmania, however Womersley (personal communication) has examined what appears to be the type specimen in L and it was collected from Lefevre Pen., South Australia.]

LECTOTYPE: LD, Herb. Agardh 36065 (Fig. 16).

TYPE LOCALITY: Indian Ocean.

DISTRIBUTION: Australia: from Darwin, Northern Territory, around Western Australia to Wilson's Promontory, Victoria, and northern Tasmania. A single drift specimen has been collected from Queensland (NSW, Herb V. May 2199) but it is in poor condition and the species does not seem to be a regular part of the eastern Australian flora. Ex-Australia: Indian Ocean (Type locality & Børgesen 1937); Pakistan (Børgesen 1931, 1934; as *Coelarthrum muelleri*); Indonesia (Weber-van Bosse 1928; as *Chrysymenia opuntia*); Japan? (Segawa 1978, p. 97, fig. 453; as *Coelarthrum muelleri*).

SELECTED SPECIMENS EXAMINED: Western Australia: Esperance, drift (J. Firman, xii.1952; AD, A18947). South of Parker Point, Rottnest Island, 10 m depth (J.M. Huisman, 29.xi.1991; MURU, JH 192). Map Reef, off Yanchep, 10-12 m depth (J.M. Huisman, 13.xi.1994; MURU, JH 377). Port Denison, drift (G.T. Kraft, 14.xii.1971; MELU, K4162; AD, A41792). Monkey Mia, Shark Bay (J.M. Huisman & A. Couté, 25.vii.1988; MURU, JH 590). West of the south tip of Hermite Island, Montebello Islands, 12 m depth (J.M. Huisman, 10.vii.1992; MURU, JH 244). Dampier Archipelago (W. Wood, 29.xi.1983; MURU, DA119). Cable Beach, Broome, in rock pools at low tide (J.M. Huisman, MURU, JH 591). South Australia: Lefevre Peninsula (16.xii.1847; MEL 502099) (Holotype of Lomentaria muelleri Sonder) (Fig. 17) also MEL 502100 (Isotype). Gulf St Vincent (AD, A1234a, b). Vivonne Bay, Kangaroo Island, on jetty pilings at 3-4 m depth (P. Latz, 22.xi.1968; MEL 696683; AD, A33018). Stenhouse Bay, Yorke Peninsula, on jetty pilings at 3-7 m depth (G.T. Kraft, 18.ix.1973; MELU, GK4681). Cape Jaffa, drift at the jetty (G.T. Kraft, 28.xii.1976; MELU, GK6104). Outer Harbour, trawled from 3-5 m depth (P. Loan, 9.viii.1963; AD, A26649). Outside Tapley Shoal, Gulf St Vincent, 15 m depth (S.A. Shepherd, 2.ii.1969; AD, A33539-40). Elliston, Eyre Peninsula, 7 m depth (S.A. Shepherd, 21.x.1970; AD,



Figs 16-22. Coelarthrum opuntia (Endlicher) Børgesen.

- Fig. 16. Lectotype of Chondria opuntia J. Agardh (= Chrysymenia opuntia Endlicher) (LD).
- Fig. 17. Holotype of Lomentaria muelleri Sonder (MEL 502099).
- Fig. 18. Branch apices showing the stalk-like connections between segments (MELU, GK 4103).
- Fig. 19. Cortex in surface view (MELU, GK 4103).
- Fig. 20. Surface view of developing tetrasporangium with connections to several adjacent cells (arrows) (MURU, JH 592).
- **Fig. 21.** Portion of cystocarpic plant with protuberant cystocarps and prominent ostioles (MELU, GK 4103). **Fig. 22.** Section of cystocarp (MELU, GK 4103).

















A37431). Egg Island, Isles of St Francis, 32–38 m depth (S.A. Shepherd, 11.i.1971; AD, A38040, A38098). Investigator Strait, 27 m depth (J.E. Watson, 9.i.1971; AD, A38445). Point Lowly, Spencer Gulf, dredged from 22-24 m depth (S.A. Shepherd, 22.vii.1971; AD, A39288). Marino, drift (H.B.S Womersley, 26.x.1975; AD, A46643). Wallaroo, on jetty piles at 0.5-2.5 m depth (S. Gill, 9.xi.1980; AD, A51898). Victoria: Point Lonsdale (MEL 45322). Waratah Bay, North Walkerville, drift (D. Sinkora, xi.1990; MEL 696705). Western Port (J. Bracebridge Wilson, 8.i.1892; MEL 502105). Port Phillip Heads (J. Bracebridge Wilson, 11.i.1888; MEL 502104). Tasmania: Currie River (F. Perrin, iv.1935; AD, A49704). North Point (J.M. Huisman, 10.ii.1991; MURU, JH 592). Queensland: Port Newry, Mackay, drift (V. May, i.1943; NSW, V. MAY Herb. no. 2199). Northern Territory: Middle Arm, Darwin, 3 m depth (S. Chidgev, vii.1982; MELU A36264-7). Indian Ocean: 'ex libra orientali'? Lectotype of Chondria opuntia (LD, Herb. Agardh 36065). Sri Lanka: South Coast (A.B. Kibwal, C). Pakistan: Cape Monte, Karachi (A.B. Kotwal, C). Japan: Honshu, Shizuoka Prefecture, Shimoda-shi, Tohii, On rocks in subtidal (J. Tanaka, 21.iii.1986; C).

HABITAT: Plants collected *in situ* have been invariably attached to rock or some other firm substratum (such as jetty pilings) at depths ranging from shallow rock pools to 38 m.

HABIT AND VEGETATIVE STRUCTURE: Plants to 30 cm in height, dark-red to purple, arising from a discoid holdfast, generally with a cartilaginous stipe from which several axes can arise. Axes dichotomously to polychotomously branched, often with even-topped branches of similar height (indicating synchronous growth), conspicuously segmented (Fig. 18). Segments variable in shape, elongate $20-30 \times 2-6$ mm, or ovoid 5-7 \times 2–3 mm. Plants from warmer waters tend to have more ovoid segments. Constricted region between segments narrow and stalk-like (Figs 18, 21), many cells thick. Internally the thallus is multiaxial, with the meristematic apical region recognizable as a diffuse cluster of smaller cells subtended by a network of stellate cells. As the cellular layer matures, cells of the medulla increase in size and become hyaline. The increase in girth of the hyaline medullary cells results in the surface view of the thallus appearing as rosettes, but continued growth of the outer cortical cells can obscure this pattern (Fig. 19). When mature, the cellular layer (Fig. 23) is composed of 1 or 2 inner layers of large, elongate, hvaline medullary cells $(180-360 \times 70-110 \ \mu m \text{ in surface view})$ subtending 2 or 3 layers of progressively smaller, pigmented cortical cells (surface cells 6-8 µm diam.). On rare occasions internal rhizoids arise from the medullary cells, although they are often present below cystocarps (Fig. 22). Stellate cells bearing 1-4 spherical to ovoid gland cells (10-35 µm diam.) are borne on the inner

surface of the medullary layer (Fig. 23). Hair cells common near the apices.

TETRASPORANGIA: Tetrasporangia (35–60 μ m diam.) are scattered throughout the cortex, derived from a mid-cortical cell in an intercalary position (Figs 20, 24). Sporangia are generally subspherical with cruciately/decussately arranged spores.

SPERMATANGIA: Spermatangia (2–3 μm diam.) arise on outer cortical cells (Fig. 25).

CARPOGONIAL BRANCH AND CYSTOCARP: Carpogonial branches arise from an inner cortical cell. Developing carpogonial branches were not observed, but, from the arrangement of post-fertilization stages, they would appear to arise in an identical manner to Coelarthrum cliftonii. Carpogonial branches are four celled and retain the outline of the original cortical cell. An inner cortical cell attached to the supporting cell acts as the auxiliary mother cell and produces the auxiliary cell. During this development the cortical cells undergo localized renewed growth and form the pericarp. Cells adjacent to the supporting cell and auxiliary mother cell become slightly stellate and stain darkly with aniline blue, indicating a nutritive function. The diploid nucleus is apparently transferred to the proximal end of the auxiliary cell. The first division of the auxiliary cell is transverse, followed by two distal oblique divisions. Subsequent development of the gonimoblast results in a spherical cluster of carposporangia. As the gonimoblast matures, the pericarp and medulla split apart along a periclinal plane at approximately the level of the auxiliary mother cell. This process results in the arms of the stellate cells stretching to accommodate the newly formed cavity. They eventually break, but their remnants can often be seen in mature cystocarps. Nutritive tissue surrounds the base of the carposporophyte. As the cystocarp matures the cells lining the inner surface of pericarp become stellate and form a poorly developed tela arachnoidea. Mature cystocarps are hemispherical, mostly protuberant (Figs 21, 22) and with an obvious ostiole (Fig. 21). They measure $1100-1400 \ \mu m$ in diameter with angular carposporangia (C. 30 µm diam).

REMARKS: Examination of numerous specimens has shown the Australian taxon *Coelarthrum muelleri* to be conspecific with the Indian Ocean *Coelarthrum opuntia*. The intended basionym of the latter (*Chondria opuntia* J. Agardh 1841) is a later homonym of *Chondria opuntia* (Goodenough et Woodward) C. Agardh (1817, p. XVIII) and consequently illegitimate. *Chrysymenia opuntia* Endlicher (1843) is therefore treated as a nomen novum [Article 58.3, ICBN (Tokyo Code)]. Because *Chrysymenia opuntia* Endlicher predates *Chylocladia muelleri* Sonder (1853), the correct name for the taxon is *Coelarthrum opuntia*, a combination first proposed by Børgesen (1937).

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Figs 23–25. Coelarthrum opuntia (Endlicher) Børgesen.

Fig. 23. Section of cortex with gland cells (AD, A33018).

Fig. 24. Tetrasporangia, with cruciately arranged spores, borne in an intercalary position (MURU, JH 592).

Fig. 25. Spermatangia borne on outer cortical cells (AD, A46643).

Figs 26–29. Coelarthrum decumbens sp. nov.

Fig. 26. Section of cortex with gland cells (MELU, GK9934).

Fig. 27. Tetrasporangia borne in an intercalary position (MELU, GK9934).

Fig. 28. Spermatangia on outer cortical cells (MELU, K10831).

Fig. 29. Four-celled carpogonial branch (MELU).



Figs 30-34. Coelarthrum decumbens sp. nov.

Fig. 30. The holotype specimen from Lord Howe Island (MELU, GK 9566).

Fig. 31. Cortex in surface view (MELU, GK 9934).

Fig. 32. Surface view of developing tetrasporangium with connections (arrows) to several adjacent cells (MELU, GK 9934).

Fig. 33. Portion of thallus with numerous secondary anastomoses and protuberant cystocarps (MELU).

Fig. 34. Section of cystocarp (MELU).

Coelarthrum opuntia is an easily recognized species due to the stalk-like connections between segments and, commonly, the presence of a cartilaginous stipe. Segment shape is variable and can be elongate/cylindrical or ovoid. The lectotype specimen of Chondria opuntia (Fig. 16) has ovoid segments, whereas many of those of the holotype of Chylocladia muelleri are elongate (Fig. 17). Most specimens, however, fall somewhere between the two and often have elongate lower segments and spherical upper segments. Specimens from colder waters tend to be larger with elongate segments, whereas those from warmer waters have spherical segments. The protuberant cystocarps of fertile specimens enable easy separation from Coelarthrum cliftonii, in which the cystocarps are immersed (compare Figs 8 and 21). Similar cystocarps were illustrated for Indonesian material by Weber-van Bosse (1928, fig. 201). Coelarthrum muelleri has been also been recorded from Japan (Segawa 1978, p. 97, fig. 453). Material examined during the present study shows the general features of C. opuntia (including the stalk-like connections), but the habit shows a percurrent main axis and some rhizoidal filaments lining the inner surface of the medullary cells. Neither of these features has been observed in Australian material. While this might suggest an independent species, a similar

variability has been observed in the closely related *C. cliftonii*, and without access to a range of specimens from Japan I am reluctant to pass judgement.

Coelarthrum decumbens Huisman sp. nov.

Figs 26–34

DIAGNOSIS: Plantae diluto-roseae usque ad rubras, 3-4 cm altae, haptero primario singulari, decumbentes postreme, ramis lateralibus saepe ad substratum secondarie affixae. Axes irregulariter dichotome ramosi segmentis ovoideis ad obovoideis, 2-2.5 mm latis et 3-4 mm longis, segmentis apicalibus sphaericis et 1-2 mm diametro. Inter segmentia articuli lati. Processi elongati et anastomoses secondariae aliquando formati. Segmenta strato celluloso externo et cavite centrali; stratum cellulosum tristratum ad quadristratum, medulla cellularum magnarum hyalinarum fabricata, hoc cum 2 vel 3 stratis cellularum corticalium pigmentiferarum. Cellulae glandulosae in cellulis stellatis portatae et in cavitem interiorem procurrentem. Tetrasporangia in soros aggregata sporis cruciate dispositis, a cellulis medi-corticalibus intercalaribus oriundia. Spermatangia in cellulis externis corticalibus portata. Rami carpogoniales quadricellulares, a cellula interiore corticali orienti. Cystocarpia protuberantia.

Plants light pink to red, 3–4 cm in height, with a single primary holdfast, becoming decumbent, lateral branches often

secondarily attached to the substratum. Axes irregularly dichotomously branched, with ovoid to obovoid segments 2–2.5 (B) \times 3–4 (L) mm, apical segments spherical, 1–2 mm in diameter. Joints between segments broad. Elongate processes and secondary anastomoses occasionally formed. Segments with an outer cellular layer and central cavity; the cellular layer composed of 3 or 4 cell layers, the medulla of large, hyaline cells bearing 2 or 3 layers of pigmented cortical cells. Gland cells borne on stellate cells projecting into the inner cavity. Tetrasporangia grouped into sori, with cruciately arranged spores, derived from intercalary mid-cortical cells. Spermatangia borne on outer cortical cells. Carpogonial branches four-celled, arising from an inner cortical cell. Cystocarps protuberant.

TYPE LOCALITY AND SPECIMEN: Ned's Beach, Lord Howe Island, New South Wales, Australia. At 1.5–2 m depth, on undercut coral mounds (*G. T. Kraft & R. Ricker*, 10.xii.1978; MELU, GK9566) (Fig. 30).

ETYMOLOGY: Named for the decumbent habit.

DISTRIBUTION: Known from the eastern Australian localities of Lord Howe Island, New South Wales, and the Great Barrier Reef, Queensland.

SPECIMENS EXAMINED: New South Wales: (all Lord Howe Island). Erskotts Passage, on reef (G.T. Kraft & A.J.K. Millar, 13.xii.1986; MELU, K10,692); 7-10 m depth (G.T. Kraft & C. O'Brien, 30.ix.1976; MELU, GK9934). North West Roach Island, 21-24 m depth (G.T. Kraft & A.J.K. Millar, 17.xii.1986; MELU, K10,937); (G.T. Kraft, 12.xii.1978; MELU). North Passage, 5-6 m depth on vertical rock face (G.T. Kraft & R. Ricker, 4.xii.1978; MELU, GK9459). North Channel, 6-12 m depth (G.T. Kraft, 4.xii.1978; MELU). Ned's Beach, 1.5-2 m depth, on undercut coral mounds (G.T. Kraft & R. Ricker, 10.xii.1978; MELU, GK9566); 6-7 m depth (G.T. Kraft & R. Ricker, 10.xii.1978; MELU, GK9513). 'The Wall', South Island, 27 m depth, on sand-covered rock (A.J.K. Millar & G.T. Kraft, 16.xii.1986; MELU, K10,831). Queensland: Keyhole, One Tree Island, Capricorn Group, Great Barrier Reef, 27 m depth (D. Hill & L. Darling, 17.xi.1982; MELU, A41874); (C. O'Brien & A. Siotas, 17.xi.1982; MELU, A41871-3). Wistari Reef, adjacent to Heron Island, Capricorn Group, Great Barrier Reef, 6 m depth (M.A. Borowitzka, 18.iii.1974; MELU, A41866).

HABITAT: Plants appear to be exclusively epilithic and have been collected at depths ranging from 1.5 to 27 m.

HABIT AND VEGETATIVE STRUCTURE: Plants with a single primary holdfast but with axes spreading laterally and becoming decumbent (Fig. 30). Lateral branches often become secondarily attached to the substratum and to adjacent branches (Fig. 33). Constrictions between segments are broad and associated septa are mono-distromatic. All axes have a cell-free internal cavity filled with mucilage. The outer cellular layer is composed of an inner medullary layer of large, hyaline cells (70– 180 × 70–100 μ m diam. in surface view), bearing 2 or 3 layers of pigmented cortical cells (surface cells 3–5 μ m diam.) (Fig. 26). Spherical gland cells (5–20 μ m diam.) are borne singly or in pairs on stellate cells arising from the medullary layer and project into the inner cavity (Fig. 26). The mature cortex appears rosette-like in surface view (Fig. 31).

TETRASPORANGIA: Tetrasporangia (15–25 μ m diam.) arise in vaguely defined sori and are derived from an inner cortical cell in an intercalary position (Figs 27, 32). The increase in

size of the sporangium causes some distortion of nearby outer cortical cells, but a distinct nemathecium with paraphyses is not formed. Sporangia are generally spherical to elliptical with cruciately arranged spores (Fig. 27).

SPERMATANGIA: Spermatangia (1–2 μ m diam.) arise on outer cortical cells (Fig. 28).

CARPOGONIAL BRANCH AND CYSTOCARP: Carpogonial branches are four-celled (Fig. 29) and arise on an inner cortical cell. Stages of the cystocarp development were not observed but appear to be similar to those of *Coelarthrum cliftonii*. Mature cystocarps are protuberant, 500–700 μ m in diameter, with angular carpospores (*C.* 15 μ m diam.) (Figs 33, 34).

REMARKS: Coelarthrum decumbens differs from the other species of Coelarthrum in its semi-prostrate habit, small size and in the production of sporangia in vaguely defined sori. In Coelarthrum cliftonii and Coelarthrum opuntia the sporangia are dispersed throughout the thallus. In addition, C. decumbens can be separated from C. cliftonii on the basis of its protuberant cystocarps, those of C. cliftonii being largely immersed. Coelarthrum opuntia produces protuberant cystocarps, but its upright habit and stalk-like joints between segments separate it from the new species. Coelarthrum decumbens appears vegetatively similar to Chamaebotrys boergesenii, and sterile specimens are difficult to separate. Coelarthrum decumbens has the outer cortex arranged in a rosette-like formation when viewed from the surface (see Fig. 31). The outer cortex of Chamaebotrys boergesenii is less regular (Fig. 37), although in some portions the arrangement can approach that found in Coelarthrum decumbens. In addition, the septa of C. decumbens are generally mono-distromatic, while those of Chamaebotrys boergesenii are often several cells thick. Sporangial material is required for positive identification (see discussion under Chamaebotrys).

Genus Chamaebotrys Huisman gen. nov.

DIAGNOSIS: Plantae decumbentes ad substratum ad locos aliquot affixae. Axes segmentati dichotome vel trichotome irregulariterque ramosi, saepe axibus contiguis anastamoses secondarios formati. Segmenta sphaerica ad ovoidea, stratii cellulosi externi composita et cavitatem mucicompletam includens. Stratum cellulosum tristratum ad pluristratum, medulla distrata cellulis grandibus hyalinisque et cortice unistrato ad tristrato cellulis parvioribus pigmentosis fabricata. Cellulae glandulosae cellularum hyalinorum in pagina interiore directe exorientes vel in cellulis stellatis in cellulis portatis et in soros nematheciales aggregata. Cystocarpia protuberantia.

Plants decumbent, attached to the substratum at several points. Axes segmented, dichotomously to trichotomously and irregularly branched, often with secondary anastomoses to adjacent axes. Segments spherical to ovoid, composed of an outer cellular layer encasing a mucilage-filled cavity. Cellular layer of three to several cell layers, with the medulla of 1 or 2 layers of large, hyaline cells and the cortex of 1–3 layers of smaller, pigmented cells. Gland cells arise directly on the inner surface of the medullary cells or on stellate cells borne on them. Tetrasporangia with cruciately arranged spores, arising terminally, and grouped into nemathecial sori. Cystocarps protuberant.

TYPE SPECIES: *Chamaebotrys boergesenii* (Weber-van Bosse) Huisman comb. nov.



Figs 35-38. Chamaebotrys boergesenii (Weber-van Bosse) gen. et comb. nov.

Fig. 35. The lectotype specimen from 'Sailus Besar, Iles Paternoster' [(L 8811(2)].

Fig. 36. Apical region of specimen from Rottnest Island, Western Australia, showing elongate processes (MURU, JH 194).

Fig. 37. Surface view of cortex (MURU, JH 194).

Fig. 38. Developing sporangia in surface view showing only a single connection (arrows) to an adjacent cell (MURU, JH 194).

Fig. 39. Chamaebotrys lomentariae (Tanaka et K. Nozawa in Tanaka) comb. nov. Holotype specimen (SAP 052169).

BASIONYM: Coelarthrum boergesenii Weber-van Bosse 1928, p. 473, figs 207, 208.

ETYMOLOGY: The generic name is derived from the Greek 'chamae' (low lying) and 'botrys' (grapes) and refers to the habit and form of the thallus.

Chamaebotrys boergesenii (Weber-van Bosse) Huisman comb. nov.

Figs 35-38, 40-42

BASIONYM: Coelarthrum boergesenii Weber-van Bosse 1928, p. 473, figs 207, 208.

SYNONYM: *Coelarthrum coactum* Okamura et Segawa in Segawa 1936, p. 186 (synonymy proposed by Abbott & Littler 1969).

LECTOTYPE: Several specimens are included in the type collection housed in Leiden. Of these, the material from Borneo Bank (Makassar Strait) (L 8811-1) was designated as the lectotype by I.A. Abbott (17.iii.1969). This material consists of two specimens, one sterile and one tetrasporic. In Abbott & Littler (1969) the specimen from Saleyer Reef (L8811-3) was designated the lectotype. This specimen is sterile. As Webervan Bosse described and illustrated (1928, fig. 207) a cysto-

Figs 40-42. Chamaebotrys boergesenii (Weber-van Bosse) gen. et comb. nov.

Fig. 40. Section of cortex (MURU, JH 194).

Fig. 41. Section of tetrasporangial nemathecium showing terminal sporangia (MURU, JH 194).

Fig. 42. Diagrammatic representation of a cystocarp in section [L8811(2)].







carpic plant, neither of the specimens from Saleyer Reef (L8811-3) or Borneo Bank (L 8811-1) are representative of the protologue. Also included in the collection is a cystocarpic specimen (L8811-2) from Sailus-Besar, Isles Paternoster, that is more representative of the protologue and should be regarded as the lectotype (Fig. 35).

DISTRIBUTION: Australia: Isolated records from Rottnest Island, Western Australia; Lord Howe Island, New South Wales, and the Great Barrier Reef, Queensland (Cribb 1983 and present study). Ex-Australia: Apparently widespread in warmer waters. Reported from Indonesia (Weber-van Bosse 1928); Hawaii (Abbott & Littler 1969); Japan (Segawa 1936); Marshall Islands (Dawson 1956); Bougainville Island (Taylor 1977); Tanzania (Mshigeni & Papenfuss 1981), Kwazulu, Zanzibar, Kenya (Norris 1986). Many records need to be reexamined in the light of the present results. Børgesen's record from Mauritius (1944, p. 18, fig. 12) was later found to represent *Erythrocolon podagricum* J. Agardh (Børgesen 1952, p. 38–39).

SPECIMENS EXAMINED: Western Australia: Cathedral Rocks, Rottnest Island, forming a prostrate mat on the undersurface of a rock ledge at 15 m depth (J.M. Huisman, 13.i.1990; MURU, JH 194). New South Wales: (all Lord Howe Island). Far Rocks, Signal Point, 1–1.5 m depth (G.T. Kraft & J. Lewis, 4.iii.1976; MELU, GK 9303). South Passage, 7-10 m depth (G.T. Kraft & C. O'Brien, 1.x.1976; MELU, GK 10114). Neds Beach, 6-7 m depth (G.T. Kraft & R. Ricker, 10.xii.1978; MELU, GK 9513). Queensland: One Tree Island, Capricorn Group, Great Barrier Reef. On bryozoan Pleurotoichus sp., 27 m depth (P. Gabrielson & J. Hauser, 17.xi.1982; MELU, A41875). Indonesia: Borneo Bank, 40-50 m depth [L8811 (1)] Siboga Exp. No. 306, 307. Sailus Besar, Iles Paternoster, 27 m depth [L 8811(2)] Siboga Exp. (Fig. 35). Ile Saleyer, recif. [L 8811(3)] Siboga Exp. Solomon Islands: Guadalcanal, Rove. Under table Acropora, upper sublittoral (H.B.S. Womersley & A. Bailey, 24.viii.1965; AD, A37111). In reef pool, shaded (A. Bailey, 2.xi.1965; AD, A37112).

HABITAT: Chamaebotrys boergesenii has been collected growing in protected positions on and under rock and coral ledges. It is occasionally found growing epizoically. Specimens have been collected from the upper sublittoral to 40–50 m depths.

HABIT AND VEGETATIVE STRUCTURE: Plants form a prostrate mat of entangled axes attached to the substratum by short, solid stipes. Axes dichotomously to trichotomously branched (Fig. 36), irregularly moniliform with spherical to ovoid segments $[2-6 (L) \times 2-5 \text{ mm} (B)]$ with broad constrictions between the segments and numerous adventitious branches that can form secondary holdfasts or fusions between adjacent segments. Septa between segments several cells thick. Segments composed of an outer cellular layer encasing a mucilage-filled cavity. Outer cellular layer with a medulla of large hyaline cells (70–180 \times 70–110 μ m in surface view) subtending 2 or 3 layers of progressively smaller, pigmented cortical cells (6-8 μm diam.). Cortical cells in surface view (Fig. 37) appear closely abutted. Spherical gland cells (20-25 µm diam.) borne singly or in pairs, either on stellate cells arising from the inner surface of the medullary layer or directly on the medullary cells (Fig. 40).

TETRASPORANGIA: Spherical to elliptical, cruciately divided tetrasporangia (20–30 \times 35–40 μ m) are borne in nemathecial

sori. Elongate sporangial mother cells arise from outer cortical cells and produce sporangia both laterally and apically. Sporangia are terminal (Fig. 38). Additional elongate sterile cells are interspersed between the sporangia (Fig. 41).

SPERMATANGIA: Not seen.

CARPOGONIAL BRANCH AND CYSTOCARP: Early stages of carpogonial branch formation and cystocarp development not observed. Mature cystocarps protuberant, with a well-developed pericarp (Fig. 42). Their arrangement suggests a developmental pattern similar to that of *Coelarthrum opuntia*.

REMARKS: The genus *Chamaebotrys* is proposed to accommodate species similar in morphology to *Coelarthrum* but differing in tetrasporangial initiation. In *Coelarthrum* the sporangia are intercalary and either scattered over the segments or aggregated into poorly defined sori. Sporangia in *Chamaebotrys*, however, are terminal and produced in nemathecial sori. Very rarely an intercalary sporangium will be observed, and in such cases the sporangium will only be connected to a single additional cell. The intercalary nature of the sporangia in *Coelarthrum* is best observed by microscopical examination of fertile regions of the thallus in surface view, and can be seen clearly in developing sporangia (compare Figs 20 and 38). Several pit-connections can generally be seen per sporangium.

The type species of Chamaebotrys is C. boergesenii (Weber-van Bosse) Huisman comb. nov., based on Coelarthrum boergesenii Weber-van Bosse. At the time of description (Weber-van Bosse 1928) tetrasporangia were apparently unknown in Coelarthrum boergesenii and, although the range of the species has been apparently greatly extended by subsequent collections, all have included only sterile (e.g. Dawson 1956; Abbott & Littler 1969; Mshigeni & Papenfuss 1981; Cribb 1983; Norris 1986) or cystocarpic material (Segawa 1936; as Coelarthrum coactum). Included in the type collection, however, is a specimen (L8811-1) bearing tetrasporangia that Weber-van Bosse apparently overlooked. The sporangia are borne in nemathecia and are terminal, both features found in the more recent Western Australian collections. Tetrasporangial specimens are therefore readily identified, but there remains some difficulty in naming sterile plants with any confidence.

Coelarthrum boer gesenii was originally distinguished from C. albertisii on a number of features including its small size, the presence of anastomoses between the branches, the nature of the outer cortex (1 or 2 layers of smaller cells forming a coherent outer layer as opposed to more loosely arranged filaments through which the subcortical layer of larger cells is visible; see Weber-van Bosse 1928, fig. 205) and its spherical gland cells (Weber-van Bosse 1928). Børgesen (1944, p. 18) suggested that 'anastomoses are surely also present in Coelarthrum albertisii' and additionally that Weber-van Bosse had misinterpreted his (i.e. Børgesen's) description of the gland cells, which, in fact, were spherical in both species. He concluded that 'of these characters it is especially the cortical layer which makes the difference' (Børgesen 1944, p. 18). Examination of the type specimens of both C. albertisii and C. boergesenii shows the former to have an outer cortex composed of loosely arranged, somewhat spherical cells. They do not form a coherent outer layer, but neither are they arranged into distinct rosettes. In C. boergesenii the outer cortical layer is composed of more angular cells (in surface view), forming a coherent layer. This type of cortex was also found in the

care must be taken, however, if this character is used to distinguish species. While the outer cortex appears to provide a readily observed feature, it must also be recognized that its arrangement can be variable and undergoes several changes as the cortex matures.

Abbott & Littler (1969) suggested that a consistent and significant difference between the two species can be found in the habit. *Coelarthrum albertisii* has 'clearly erect thalli' whereas those of *C. boergesenii* are 'creeping . . . and when best developed, matlike' (Abbott & Littler 1969, p. 168). This habit is also the case in Australian specimens, and this feature separates *C. boergesenii* from the majority of species of *Coelarthrum.* The semi-prostrate *Coelarthrum decumbens*, however, poses some difficulty, as it is similar to *C. boergesenii* in both habit and vegetative structure. As discussed under *C. decumbens*, it differs from *C. boergesenii* in the rosette-like appearance of the outer cortex in surface view and in features of the internal septa. Tetrasporangial specimens are readily identified.

Weber-van Bosse (1928, p. 474) also described *Coelar-thrum boer gesenii* f. *minima*, based on a sterile plant of smaller dimensions than the type form. Authentic material of f. *minima* has not been examined during the present study and without fertile specimens its generic placement cannot be assessed. Plants from Lord Howe Island of similar dimensions to those reported by Weber-van Bosse (1928) have been examined and they conform with *Chamaebotrys* in all respects. Based on the variation in size seen in those specimens, there seems little value in maintaining *C. boergesenii* f. *minima*.

Coelarthrum lomentariae was described by Tanaka & Nozawa (in Tanaka 1964) for Japanese plants with tetrasporangia in nemathecial sori, and an examination of the type specimen (SAP 052169; Fig. 39) has shown that the sporangia are terminal. The species therefore displays all the features of Chamaebotrys and the combination Chamaebotrys lomentariae (Tanaka et K. Nozawa in Tanaka) Huisman comb. nov. is proposed (Basionym: Coelarthrum lomentariae Tanaka et K. Nozawa in Tanaka 1964, p. 79-81, figs 6, 7, pl. IIIA). Chamaebotrys lomentariae is similar to C. boergesenii and may prove to be conspecific. The original description indicates that it differs in possessing broad constrictions between segments and in its erect habit, although the illustration (Tanaka, 1964, fig. 6A) suggests a decumbent habit similar to C. boergesenii. Chamaebotrys lomentariae is a rare plant that appears to be known only from the type collection. At present it seems best to maintain C. lomentariae until more collections become available and an assessment of its defining characters can be made.

DISCUSSION

As presently constituted, three families—the Rhodymeniaceae, the Lomentariaceae and the Champiaceae—are recognized in the order Rhodymeniales. Following the currently accepted criteria (Huisman 1995), *Chamaebotrys* is clearly a member of the Rhodymeniaceae as the apical cells are not in an obvious cluster and the gland cells are borne on the inner surface of the cortex and not on medullary filaments. *Chamaebotrys* is the tenth genus to be included in the family that produces (at least in part) some axes, segments or vesicles with an internal cavity. Others are *Botryocladia* (J. Agardh) Kylin, *Gloiosaccion* Harvey, *Chrysymenia* J. Agardh, *Cenacrum* Ricker et Kraft, *Coelarthrum* Børgesen, *Erythrocolon* J. Agardh, *Fryeella* Kylin, *Hymenocladiopsis* Moe and *Webervanbossea* DeToni. All display hollow,¹ sometimes mucilage-

vanbossea DeToni. All display hollow,¹ sometimes mucilagefilled, portions that are lined internally by large hyaline cells that bear gland cells either directly or on specialized cells or filaments. Features useful in separating the genera are summarized in Table 1. In the past it was often believed that the genera of the Phodymaniacean displayed a monotoney uniformity in their

Rhodymeniaceae displayed a monotonous uniformity in their reproductive development, a feature that has resulted in the use of vegetative characters to separate taxa. Criteria used in the past to separate the hollow genera include the presence of substantial solid axes (*Botryocladia*), internal rhizoidal filaments (*Cryptarachne*, a genus now included in *Chrysymenia*) and the presence of constrictions or diaphragms. The significance of these features has often been debated, with the various combinations accepted in the past reflecting their relative importance at the time. The present study attempts to define the hollow genera on reproductive as well as vegetative features; those considered to be of significance follow.

Reproductive features

TETRASPORANGIA: Of the reproductive characters, the origin and disposition of the tetrasporangia provide readily recognizable features that have proved most useful. Sporangia can be tetrahedral or cruciate/decussate, scattered throughout the cortex or grouped in sori, associated in nemathecia or without any noticeable modification of the cortex, and arise in an intercalary or terminal position. These features are consistent within genera and have been used in the past to establish taxa.

SPERMATANGIA: Spermatangia invariably arise on outer cortical cells.

CARPOGONIAL BRANCH AND CYSTOCARP: Published descriptions and the present observations indicate that, between genera, the carpogonial branch varies only in the number of constituent cells. Three- or four-celled carpogonial branches have been described (rarely '3-4' as in Cenacrum Ricker et Kraft 1979). This feature is useful (if difficult to observe) and may be of use at a higher level of classification (see below). In contrast, the features of the mature cystocarp seem of less importance (certainly in the hollow genera). Cystocarps are either strongly protuberant or immersed in the cortex, but this feature (in Coelarthrum at least) does not correspond with any major change in the development of the cystocarp. The immersed cystocarp of Coelarthum cliftonii is the result of the invagination of the medullary layer, whereas in Coelarthum opuntia the layer remains at the same level. While this feature is useful in separating species, it does not appear to be of generic importance.

Cystocarps in the 'solid' genera are more varied. One of the more controversial characters used in the past is the presence of a *tela arachnoidea* (a layer of stellate or slender cells surrounding the carposporophyte), which has often been used in separating genera and was a defining feature of Kylin's 'Fauchea' Group (Kylin 1956). These stellate cells are formed

¹ The term 'hollow' is used here to describe thalli with cell-free central cavities that are mostly mucilage-filled.

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Genus	Habit	Tetrasporangia	Carpogonial branch	Distinguishing features	Literature
Botryocladia (J. Agardh) Kylin	Vesicles borne termi- nally and laterally on solid axes	Cruciate, intercalary in cortex	Four-celled	Sympodial branching	Brodie & Guiry 1988; Millar 1990
<i>Cenacrum</i> Ricker et Kraft	Flattened, branched thallus with some hollow portions; un- segmented	Cruciate, terminal in nemathecia	(Three-) four- celled	Habit	Ricker & Kraft 1979
Chamaebotrys Huis- man	Terete, regularly seg- mented hollow axes	Cruciate, terminal in nemathecia	Not known	Habit and terminal sporangia	This paper
Chrysymenia J. Agardh	Flattened or terete, seg- mented or unseg- mented, branched thallus, entirely hol- low	Cruciate, intercalary in cortex	Four-celled	Absence of regular constrictions	Lee 1978
Coelarthrum Børge- sen	Terete, regularly seg- mented hollow axes	Cruciate, intercalary in cortex	Four-celled	Habit and intercalary sporangia	This paper
Erythrocolon (J. Agardh) J. Agardh	Terete, regularly seg- mented hollow axes	Cruciate, intercalary in cortex	Not known	Layer of smaller cells lining the inner sur- face of the hyaline cells	Pers. obs.
Fryeella Kylin	Flattened, branched thallus with internal septa	Cruciate, terminal in nemathecia	Not known	Septa without associ- ated constrictions	Hawkes & Scagel 1986
Gloiosaccion Harvey	Saccate	Cruciate, intercalary in nemathecia	Four-celled	Scattered sporangia with nemathecial filaments	Pers. obs.
Hymenocladiopsis Moe	Flattened, branched thallus; partially hol- low	Tetrahedral, terminal in cortex	Three-celled	Tetrahedral sporangia	Moe 1986
Webervanbossea DeToni f.	Terete, regularly seg- mented hollow axes	Cruciate, terminal in nemathecia	Three-celled	Sporangia in nemathe- cial sori	Huisman 1995

during the periclinal separation of the cortical layers during the creation of the cystocarp cavity. Where the cells undergo further divisions a noticeable layer is produced. This feature contrasts with the situation in most taxa, where the cortical cells 'stretch' and eventually break, and remnants can often be seen traversing the cystocarp cavity. Irvine & Guiry (1980) have suggested that a group of closely related taxa (their 'Group 1') can be recognized in which well-developed tela arachnoidea occur. The included genera all have a soft consistency, a feature that Irvine & Guiry felt was associated with the production of the tela arachnoidea. They agreed with Sparling (1957), however, who did not recognize Kylin's 'Fauchea Group' (which included many of the same genera), arguing correctly that Kylin's group included other taxa with seemingly unrelated vegetative features. Kylin's group appears more coherent, however, with the removal of Webervanbossea, a genus recently examined by Huisman (1995) and found to lack a persistent tela arachnoidea. Studies of the 'Fauchea Group' are underway (Townsend & Huisman, in prep.) and indicate a well-defined assemblage.

Vegetative features

MORPHOLOGY: Plants are either regularly divided and segmented (e.g. *Coelarthrum*), composed of vesicles on solid stalks (e.g. *Botryocladia*), palmately flattened (e.g. *Cenacrum*) or of single saccate vesicles (e.g. *Gloiosaccion*). *Botryocladia* is regarded as being sympodially branched, a feature seen clearly in the majority of species with an extensive solid axis (e.g. *Botryocladia ebriosa* Millar 1990). Several of the constituent species, however, are composed of single vesicles on a short stalk and their sympodial nature can only be inferred. The single species of *Gloiosaccion* (*G. brownii* Harvey) is also composed of single vesicles borne on short stalks, and some authors consider this species to be better placed in *Botryocladia* (Feldmann & Bodard 1965). *Gloiosaccion*, however, has a number of features that support its recognition, most notably the production of tetrasporangia associated with nemathecial filaments (unpublished observations). Tetrasporangia in *Botryocladia* are not associated with a modification of the cortex.

THE CELLULAR LAYER AND GLAND CELLS: The outer cellular layer varies only slightly in the majority of the hollow genera. Most have a medulla of 1 or 2 layers of large hyaline cells supporting a cortex of several layers of pigmented cells. Some differences can be seen in *Erythrocolon*, which produces an inner layer of smaller cells that lines the surface of the hyaline cells (pers. obs.). The construction of this layer is unique and bears no resemblance to the rhizoidal filaments occasionally produced in other genera. It serves as a defining feature of the genus. In most genera gland cells are found either directly on the inner surface of the medullary cells or on specialized stellate cells. In *Webervanbossea, Cenacrum* and occasionally *Coelarthrum*, gland cells are associated with internal filaments (see Huisman 1995).

CONSTRICTIONS AND/OR SEPTA: The presence of constrictions (and the associated septa) between segments is a feature of many of the hollow genera. The septa are one to several cells thick and are composed of the remains of the medullary layer subtending the site of branch initiation. The regular septa in *Coelarthrum* and others are not homologous with those found in the Champiaceae, which are formed from inwardly directed filaments arising from the longitudinal filaments (Lee 1978). The septa in the Rhodymeniaceae invariably result from the initiation of new branches or segments. In several genera septa are always present at branch bases (e.g. *Coelarthrum, Chamaebotrys, Erythrocolon* and *Webervanbossea*), whereas in others branches can arise without the formation of septa (some species of *Botryocladia* with branched vesicles, e.g. *B. adreana* Brodie et Guiry 1988). *Chrysymenia* includes some species with septa [e.g. *Chrysymenia wrightii* (Harvey) Yamada (Lee 1978)] and others without [e.g. *Chrysymenia ornata* Ky-lin (Millar 1990)]

Familial classification

As discussed by Huisman (1995), the Lomentariaceae and Champiaceae are clearly defined on both vegetative and reproductive grounds and would appear to be of monophyletic origin. The Rhodymeniaceae, however, includes taxa displaying a variety of features and lacks the single defining character found in the other families. Difficulties in clearly circumscribing the family are well documented (Ricker & Kraft 1979; Huisman 1995) and are suggestive of a need for further subdivision. Recently Saunders & Kraft (1994), Hommersand (1994), and Strachan et al. (1995) have reported preliminary nucleotide sequence data that indicates a polyphyletic origin to the Rhodymeniaceae. These studies have suggested that Gloiocladia (Saunders & Kraft 1994), Ceratodictyon (Hommersand 1994) and Webervanbossea (Strachan et al. 1995) are more closely aligned with the Lomentariaceae than the Rhodymeniaceae. Huisman et al. (1993) pointed out some vegetative and reproductive similarities between Semnocarpa (of the Lomentariaceae) and Webervanbossea and Ceratodictyon (of the Rhodymeniaceae) and suggested that there might be a close affinity between the two families. Thus it would appear that the Rhodymeniaceae, as presently constituted, is untenable, although further morphological and molecular studies of the many poorly known genera are required before the boundaries of any revision can be drawn. If the family is to be divided, one possible indication of where the division might fall is seen in the close correlation between the site of tetrasporangial initiation and the number of cells in the carpogonial branch. Of the 20 genera of the Rhodymeniaceae in which both of these features are known, eight produce fourcelled carpogonial branches and intercalary sporangia, whereas nine have three-celled carpogonial branches and terminal sporangia. Three genera (Cenacrum, Rhodymenia Greville and Maripelta Dawson) are reported to produce three- or fourcelled carpogonial branches. These features are also largely consistent with traditional groupings within the Rhodymeniacae. Of the genera known to have three-celled carpogonial branches and terminal sporangia, the majority (of those recognized at the time) were included by Kylin (1956) in his 'Fauchea-Gruppe'. The one exception is Halichrysis (Schousboe ex J. Agardh) Schmitz, which was poorly known. The three genera mentioned earlier as being more closely aligned with the Lomentariaceae than the Rhodymeniaceae (Webervanbossea, Gloiocladia and Ceratodictyon) all display threecelled carpogonial branches and terminal sporangia.

Thus it would appear that these features could indicate a fundamental division of the family. The same characters have already been recognized as important in familial placement in the order, as they (partly) formed the basis for separating the Lomentariaceae from the Champiaceae (Lee 1978). The Champiaceae includes genera with four-celled carpogonial branches and intercalary sporangia, while the Lomentariaceae includes genera with three-celled carpogonial branches and terminal sporangia (Lee 1978). If the Rhodymeniaceae is to be also divided along these lines, the hollow genera will be distributed between the two subsequent groups, indicating they are not as closely related as is often suggested (e.g. Guiry & Irvine 1981). Given that the three families of the Rhodymeniales presently recognized include hollow members (the Champiaceae and Lomentariaceae exclusively so), such a vegetative structure might represent the primitive condition in the Rhodymeniales. If such is the case, separating the morphologically similar hollow taxa into disparate groups is less disagreeable than one might expect from initial impressions. Following this, at least some of the parenchymatous genera will have evolved from hollow ancestors, a not unlikely scenario given that many of the genera have both parenchymatous and hollow portions. Further morphological and molecular studies are necessary, however, before phylogenetic schemes can be proposed with confidence.

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