

Reproductive morphology and taxonomic reappraisal of *Exophyllum wentii* Weber-van Bosse (Rhodomelaceae, Rhodophyta) from Bali Island, Indonesia

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SUMMARY

The little-known and rarely collected alga *Exophyllum wentii* Weber-van Bosse is re-described in detail from the type material, as well as from new collections from Indonesia, which for the first time reveal in detail the structure of cystocarpic and spermatangial plants and the development of tetrasporangial stichidia under culture conditions. New morphological reproductive information confirms placement of the genus *Exophyllum* within the Rhodomelaceae. *Exophyllum* is distinguished from other related genera within the Rhodomelaceae by its cartilaginous, non-trichoblastic decumbent thallus with multiple holdfasts and its discoid spermatangial organs. Some Pacific material earlier attributed to *E. wentii* was found to be misidentified and re-assigned to the Dasyaceae.

Key words: culture, *Exophyllum wentii*, Indonesia, reproduction, Rhodomelaceae, taxonomy.

INTRODUCTION

The genus *Exophyllum* was erected by Weber-van Bosse (1911), based on material collected in the Philippines and Indonesia. It is a rarely collected, little-known genus (Huisman 2000) and was until the present study considered of uncertain taxonomic position (Silva *et al.* 1996). It currently consists of a single species, *Exophyllum wentii* Weber-van Bosse (1911; 1928) only known from few sporadic collections worldwide (Tanaka 1950; Kraft *et al.* 1999; Huisman 2000). Initially tentatively placed in the Rhodymeniaceae (Weber-van Bosse 1928; Tanaka 1950) based on tetrasporangial plants alone, its placement in that family was deemed unlikely by Kylin (1956) and Papenfuss (1962). Indeed, fertile gametophytes of *E. wentii* from the type locality were unknown at the time of the original description of tetrasporangial plants by Weber-van Bosse (1911). Huisman (2000) reports spermatangial plants from the Montebello Islands, Western Australia,

but these are not described in detail or illustrated. Fertile male and for the first time female plants were discovered at Padangbai, Bali, Indonesia in December 2004 and May 2005, and the results of the study of this material are reported here.

MATERIALS AND METHODS

Collection of material

Mature female and male gametophytes and tetrasporophytes of *E. wentii* Weber-van Bosse were collected by SCUBA diving in the subtidal zone from depths of 7–20 m at Padangbai (8°52'23.9"S, 115°51'20.9"E) Bali Island, Indonesia (Fig. 1). Female and tetrasporophytes were identified from preliminary samples at depths of 16.5–20 m on 23.xii.2004. During later random sampling, male gametophytes and tetrasporophytes were collected at depths of 7–15 m on 6.v.2005. Female gametophytes and tetrasporophytes were not collected at that time, but because sampling was not systematic, it can be assumed that they are more rare, and coexist with male plants. Some live tetrasporophytes were transported for culture purposes to the Breeding Science Laboratory, Graduate School of Fisheries Sciences, Hokkaido University, Hakodate, Japan.

Measurements of physical parameters

Seawater temperatures and depth were determined using a SCUBAPRO Xtender V3 dive computer. Seawater salinity was measured using a SEKISUI Model SS-31 A salinometer.

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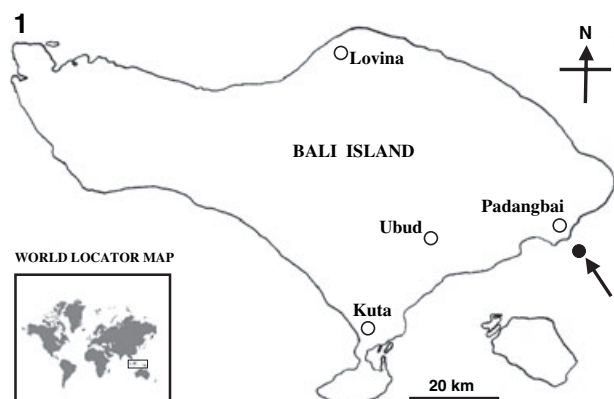


Fig. 1. Map of collecting site (arrow) off the coast of Bali Island, Indonesia.

Photography

Underwater photographs were taken using an OLYMPUS C-4040 camera with fisheye housing Fix 4040. Mature habit photographs of gametophytes were taken using a CANON Powershot A-80 (Canon, Japan) and a ZEISS standard microscope with a camera attached. Developmental stages were photographed using a LEICA DMIL stereomicroscope (Leica, Germany) with a NIKON CN150 camera (Nikon, Japan) attached. Photomicrographs were taken on a LEICA DMLS microscope (Leica, Germany) with an OLYMPUS Camedia C-5050 camera attached (Olympus, Japan).

Culture methods

Tetraspores were initially cultured under different conditions (15, 20 and 25°C), 12:12 h LD, in microplates (diameter 16 mm) with a slightly modified Provasoli's Enriched Seawater medium (Provasoli 1966). However, it was observed that at 20 and 25°C, with 35 practical salinity units (PSU), tetraspores were damaged by bacteria and died after 5 days. At 15°C, tetraspores were still alive after 3 months.

Slide preparation

Permanent slides of selected material were made using a LEICA SM 2000 R (Leica, Germany) sliding microtome, cutting sections 30–35 µm thick, which were stained using a modified aniline blue solution. Air-dried spermatangial stichidia were squashed on a glass slide, covered with a glass coverslip pretreated with Wittmann's aceto-iron-hematoxylin-chloral hydrate (Wittmann 1965). Microscope slides and voucher specimens have been deposited in the Herbarium, Graduate School of Sciences, Sapporo (SAP) Japan.

RESULTS

Exophyllum wentii Weber-van Bosse (1911), 29 (syntype localities: North Ubian Island, Sulu Archipelago, Philippine Islands; Borneo Bank and Sawu, Indonesia)

Material examined

Exophyllum wentii: Lectotype: Sulu, Indonesia, 1900, leg. A. Weber-van Bosse (L 0061135; Siboga-Expedition NR 375, dry; sterile; Isotype L 0109994, spirit); Syntype: Sawu Island Reef, leg. A. Weber-van Bosse (L 0109993, spirit, tetrasporic); Tanegasima, Southern Japan, 10.vi.1948, leg. T. Tanaka (Graduate School of Science, Hokkaido University, Sapporo (SAP) 026390; dry, tetrasporic); Tokunoshima Island, Ryukyu Islands, Japan, 20.vi.1990, leg. H. Ohba, The Natural History Museum, London (BM) 00519774; Padangbai, Bali Island, Indonesia, leg. T. Tani and A. Oogane, 23.xii.2004, cystocarpic; tetrasporic; 6.v.2005, spermatangial (all in SAP).

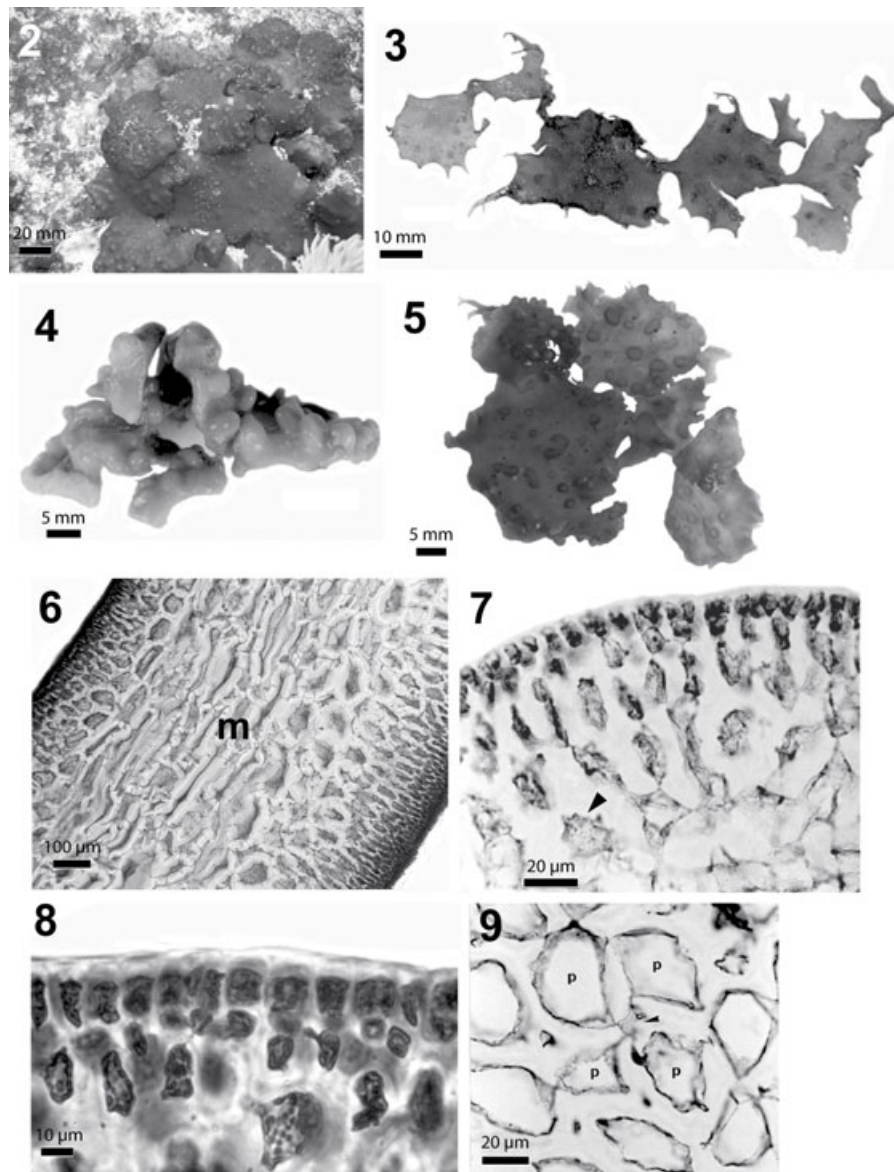
Misapplied name '*E. wentii*': Waikiki, Hawaii: 1.xii.1954, leg. J. Newhouse (Bishop Museum, Honolulu (BISH) 474629, spirit, spermatangial); Palolo Deep, Samoa, 18.ix.1998, leg. P. A. Skelton (Phycological Herbarium, The University of the South Pacific, Suva (SUVA) 5477L, spermatangial); Namada, Viti Levu, Fiji, 14.iii.1998, leg. P. A. Skelton and G. R. South (SUVA-A 5478L, spermatangial); Afaahiti, Tahiti: 7.vi.1997, leg. A. D. R. N'Yeurt (Phycological Herbarium, Université de la Polynésie française, Punaauia (UPF) 379, 380, 381, 712L); 10.vi.1997, leg. A. D. R. N'Yeurt (UPF 713L tetrasporic).

Habitat

Indonesian plants collected for the present study were cartilaginous and of a reddish-brown to greenish color, closely adhering to the substratum in clear water at a depth of 7–20 m, associated with hard corals and coralline algae (Fig. 2). The sampled population only occupied a small isolated area of approximately 6 × 4 m on the gentle reef slope, but plants densely covered most of this space, being attached to each other and the substratum through strap-like haptera. Water temperature was 28.3°C, with relatively high water salinity (36–39 PSU).

Vegetative features (Figs 3–9)

Thalli consist of dorsiventral, coriaceous, decumbent blades 31–(68)–97 mm long, 96–(103)–110 mm wide and 1.5–(2.4)–2.9 mm thick, attached by several short cylindrical to strap-shaped ventral holdfasts 0.5–0.7 mm in diameter and 1.2–1.5 mm long (Figs 3–5).



Figs 2–9. *Exophyllum wentii*. Habit and vegetative morphology. 2. In-situ photograph of male *E. wentii* growing at 10 m depth, Bali, Indonesia. 3. *E. wentii*: habit of pressed Lectotype specimen (L 0061135) from Sulu, Indonesia, showing dentate margins in younger blades. 4. Habit of tetrasporic, spirit-preserved Syntype (L 0109993) from shallow-water habitat in Sawu Island, showing highly convoluted thallus. 5. Habit of cystocarpic female gametophyte from Bali, Indonesia (Graduate School of Science, Hokkaido University, Sapporo (SAP) 100613a). 6. Transverse section of thallus of male Bali plant (SAP 100613a) showing compact medulla (m) grading into smaller-celled cortex. 7. Cortical region of Syntype (L0109993), showing cuboid to elongate cortical cells and stellate outer medullary cell (arrowhead). 8. Transverse region of the cortex of female Bali plant (SAP 100612a). Compare with Figure 7. 9. Detail of axial ring of Syntype (L0109993), showing axial cell (arrowhead) surrounded by four pericentral cells (p).

Structure is uniaxial, but this feature is quickly obscured by secondary cortication. Young thalli are reniform with toothed margins, becoming mostly smooth and irregular in shape when older (Weber-van Bosse 1928). The ventral surface is uniform, whereas the dorsal surface is generally blotchy and develops numerous rounded protuberances that sometimes extend into long haptera that make contact with the substratum and develop into new blades. Trichoblasts are absent. Internal structure is pseudoparenchymatous, with a large-celled medulla consisting of ovoid cells 56–(81)–161 µm long and 179–(206)–304 µm wide (Fig. 6), giving way to progressively smaller cells and reaching a dense cortical layer consisting of cuboid-rectangular cells 5–15 µm long and 3–12 µm broad (Figs 7,8). The axial cell is surrounded by four pericentral cells (Fig. 9). Secondary pit-connections are

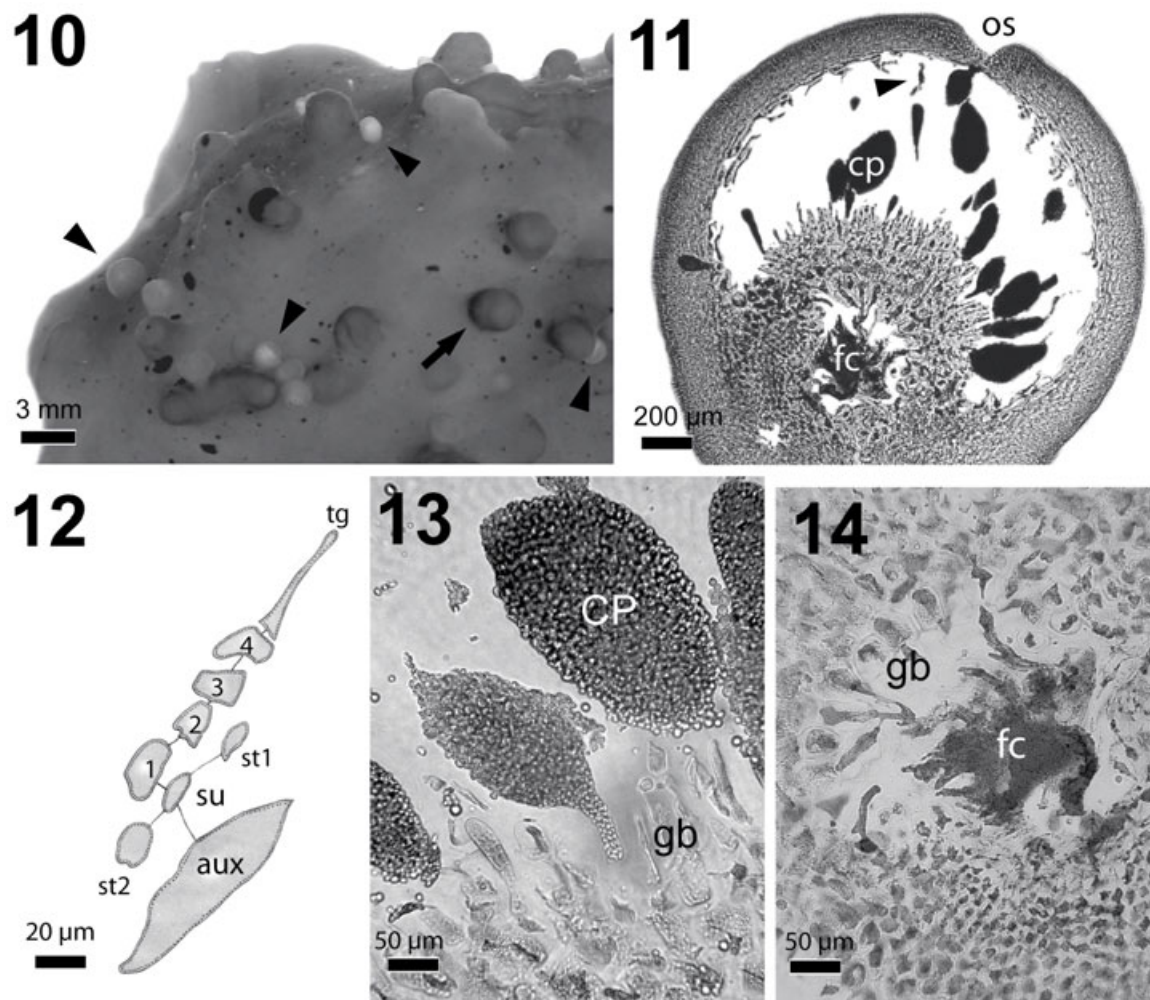
abundant among often stellate inner cortical cells 20–50 µm in diameter.

Reproduction

The reproductive cycle of *Exophyllum* consists of an isomorphic alternation of generations. Gametophytes are dioecious, with protuberant, pedicellate reproductive organs formed directly on the dorsal thallus surface, but also in marginal and ventral areas in the case of male spermatangial stichidia only. Pedicels are pluri-siphonous. Tetrasporophytes are isomorphic with gametophytes and bear stalked tetrasporangial stichidia on the dorsal surface of the thallus.

Female plant (Figs 10–14)

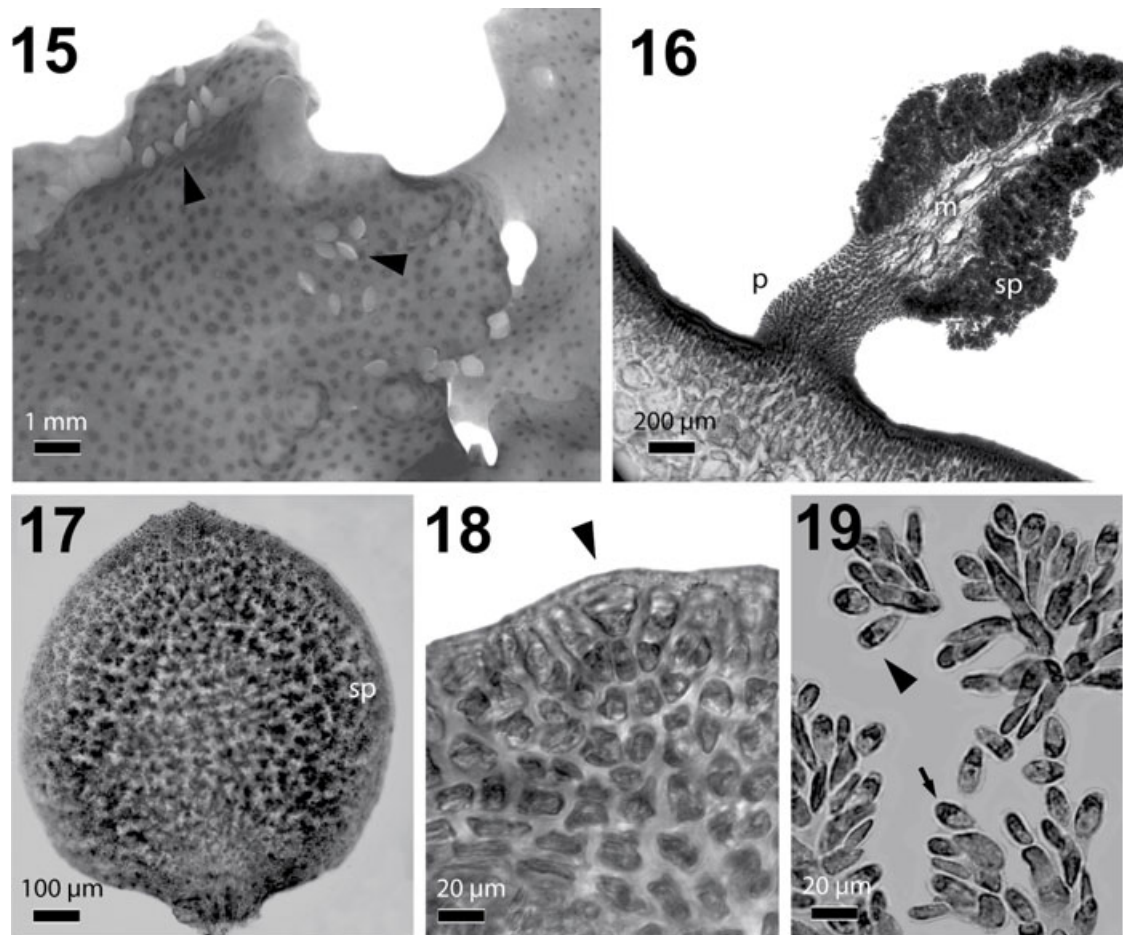
Procarys are located in the upper cortical region of fertile thalli, and consist of an auxiliary cell derived



Figs 10–14. *Exophyllum wentii*. Female reproductive morphology. 10. Detail of fertile female thallus surface of Bali plant (Graduate School of Science, Hokkaido University, Sapporo (SAP) 100612a) showing scattered globose cystocarps (arrowheads) with whitish carposporangia, which could be mistaken for darker-colored vegetative knobby outgrowths (arrow). 11. Transverse section of mature cystocarp of female thallus (SAP 100612b) showing basal fusion cell (fc), single terminal clavate carposporangia (cp) on gonimoblast filaments, and ostiole (os). Remnants of sterile traversing filaments can also be seen (arrowhead) in the cystocarp cavity. 12. Camera lucida drawing of procarp complex of female plant (SAP 100612c) showing four celled carpogonial branch (1–4) with outwardly directed trichogyne (tg), supporting cell (su) with sterile cell groups (st1, st2) and auxiliary cell (aux) derived from a fertile axial cell. 13. Detail of carposporophyte (SAP 100612e) showing mature carposporangia (cp) occurring singly at the end of gonimoblast filaments (gb). 14. Detail of dense basal fusion cell (fc) of carposporophyte of female plant from Bali (SAP 100612d) showing non-divided, sympodially branched radiating gonimoblast filaments (gb).

from a fertile axial cell, a supporting cell with lateral sterile groups, and an outwardly directed four celled carpogonial branch terminating into a moderately long trichogyne (Fig. 12). After presumed fertilization, the supporting cell cuts off from the axial cell, and the auxiliary and nearby sterile cells unite to form a basal fusion cell bearing much-branched gonimoblast initials of the developing carposporophyte. Cystocarps are sessile, globose with a small ostiole, developing irregularly among the papillae only on the dorsal surface of the blade, up to five per thallus (Fig. 10). Young cystocarps are transparent to greenish; the mature carposporophyte is whitish to pale pink, 1.9–(2.0)–

2.4 mm long and 1.1–(2.4)–2.8 mm in diameter. The mature cystocarp (Fig. 11) has a pericarp up to 200 μ m thick, consisting of seven to nine layers of oval to spherical cells arranged in straight lines. Sterile traversing gonimoblast filaments are present in the cystocarp cavity. The carposporophyte has a basal, erect fusion cell 148–(215)–282 μ m long and 145–(156)–167 μ m in diameter (Fig. 14), supporting chains of much-branched gonimoblast filaments 63–(76)–102 μ m long. Carposporangia are 180–(228)–280 μ m long and 54–(87)–137 μ m in diameter, usually elliptical or nearly cylindrical with a stalk cell, occurring singly at the end of gonimoblast filaments (Fig. 13).



Figs 15–19. *Exophyllum wentii*. Male reproductive morphology. 15. Detail of fertile male thallus surface (Graduate School of Science, Hokkaido University, Sapporo (SAP) 100611) showing discoid, erect spermatangial organs (arrowheads). Note blotchy texture of thallus. 16. Longitudinal section of spermatangial organ (SAP 100613a), showing multiaxial pedicel (p), and central sterile multiaxial region (m) surrounded by spermatangial tissue (sp.). 17. Surface view of spermatangial disc (SAP 100613a), consisting of a fertile region of spermatangial initials (sp.) and central and marginal sterile areas. 18. Detail of sterile apical region of spermatangial disc (SAP 100613a) showing distinct apical cell (arrowhead). 19. Detail of branched spermatangial initials bearing terminal elongate ovoid spermatia (arrowhead) with confluent cell walls (arrow). Note absence of cover cells (SAP 100613a).

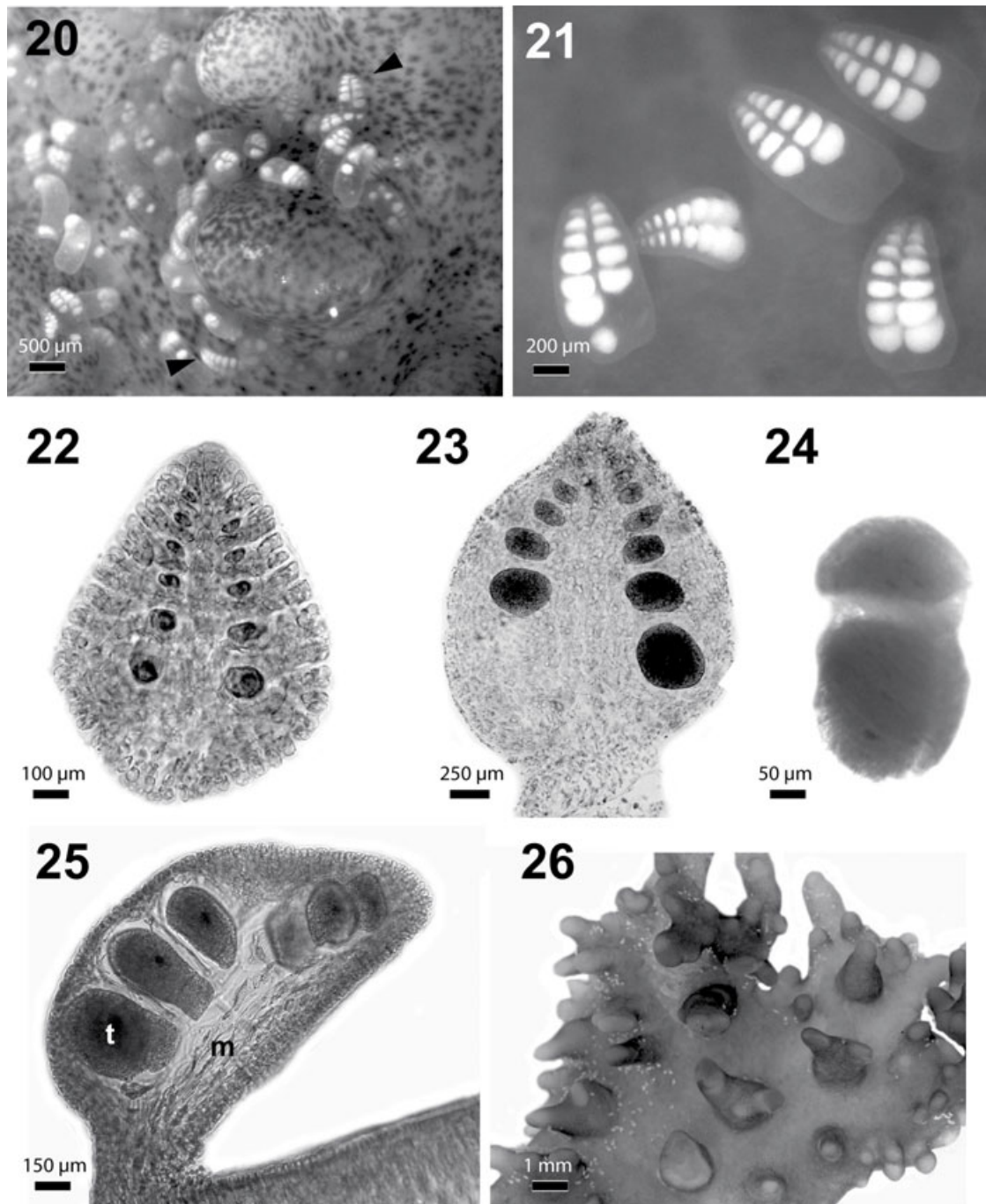
Male plant (Figs 15–19)

Pedicellate male spermatangial organs are discoid, erect, straight to slightly curved and randomly scattered predominantly over the dorsal thallus surface (Fig. 15), but also occur on the ventral surface and marginal areas of the thallus. Individual spermatangial discs (Figs 16,17) are oval, transparent, 410–(856)–1290 μm long and 350–(720)–930 μm wide, with sterile central and marginal cells and a distinct apical cell (Fig. 18); The alae or wing cells cut off small initials, forming horizontal plates whose cells in turn cut off one to four elongate spermatangial cells 12–(15)–18 μm long (Fig. 19).

Tetrasporic plant (Figs 20–26)

Fertile tetrasporangial plants can be easily recognized by the presence of whitish transparent to pink tet-

rasporangial stichidia that occur densely on the thallus dorsal surface (Fig. 20). Club-shaped to globose-conical and distinctly curved tetrasporangial stichidia are 893–(1067)–1342 μm long and 359–(452)–580 μm in diameter, with a plurisiphonous stalk, 57–(127)–217 μm long and 147–(196)–259 μm in diameter, scattered randomly on the dorsal thallus surface (Fig. 21). Each mature stichidium is somewhat compressed, having up to nine rows of strictly paired tetrahedrally divided tetrasporangia 107–(238)–347 μm long and 187–(271)–362 μm in diameter (Figs 22,23). The central region of the stichidium is composed of longitudinal filaments, giving rise at regular intervals to perpendicular filaments whose innermost cell bear a single sporangium (Fig. 25). Specialized cover cells were not seen, the tetrasporangia being regularly covered with small



Figs 20–26. *Exophyllum wentii*. Tetrasporophyte reproductive morphology. 20. Close-up view of tetrasporic thallus (Graduate School of Science, Hokkaido University, Sapporo (SAP) 100610) showing numerous curved tetrasporangial stichidia (arrowheads). 21. Detail of tetrasporangial stichidia, showing white paired tetrasporangia in distinct rows (SAP 100610). 22. Young tetrasporangial stichidium (Isotype, L 0109993) showing early arrangement of tetrasporangia in strict pairs. 23. Mature tetrasporangial stichidium with multi-axial pedicel (Isotype, L 0109993). Note absence of specialized cover cells over tetrasporangia. 24. Single tetrahedrally divided tetrasporangium grown under culture conditions from Bali stock. 25. Longitudinal section of mature tetrasporangial stichidium (SAP 100610), showing individual tetrasporangia (t) nested between filaments perpendicularly issued from multi-axial central region (m). 26. Detail of tetrasporic plant from Bali (SAP 100610) showing morphological plasticity in the form of a convoluted thallus with long, variously branched knobby proliferations. Compare with Figure 4.

cortical cells issued from the surrounding filaments (Fig. 23). In other Rhodomelaceous algae, such as *Bostrychia arbuscula* Harvey, a fertile pericentral cell of the developing tetrasporangial stichidium at first cuts off two specialized plate-like cover cell initials, and a third cover cell is produced from a residual stalk cell derived from the fertile pericentral cell (Hommersand 1963). The developmental stages of the tetrasporangia could be observed by plants maintained in culture, showing that the division of the sporangium is tetrahedral (Fig. 24). Tetrasporic plants are sometimes more convoluted and have longer, branched knobby protuberances on the thallus (Figs 4,26).

Comparison with the type material of Exophyllum wentii

An examination of the tetrasporic dried and spirit-preserved lectotype and syntype specimens of *E. wentii* Weber-van Bosse housed in L (lectotype locality: North Ubian Island, Sulu Archipelago, Philippines) show a coriaceous, flattened (in deepwater specimens) to convoluted (in intertidal specimens) plant, with a dorsiventral and prostrate habit (Figs 3,4). Although these have been already described in French by Weber-van Bosse (1928), some important features are confirmed here from new examination of the material, and careful translation of the original description. The thalli consist of irregularly ovoid blades, which are in part broadly scalloped and attached to each other through strap-like haptera. Rounded protuberances are present on the dorsal surface (Fig. 4). The specimens in Leiden (L0061135, L0109993, L0109994) are in all respects identical to the illustrations on plate VI (figs 5,6) of Weber-van Bosse's 1928 description of the species from the Siboga collections, and one specimen (L0061135) was designated as the lectotype by H. Ohba on 15 July 1998, as labeled on the herbarium sheet. The sterile lectotype (L 0061135; Siboga-Expedition NR 375, Fig. 3) has a thallus that is hardly dissected or branched, but a tetrasporic syntype Indonesian specimen from Sawu Island Reef from shallower water (pl. VI, Fig. 6 in Weber-van Bosse 1928) has a more imbricate and dissected habit, while still having mostly smooth margins and undersurface. Similarly, a tetrasporic specimen identified as *E. wentii* from Tanegasima, southern Japan (Tanaka 1950, 176, pl. II Fig. 3, SAP 026390), Tokunoshima Island, Ryukyu Islands (BM 00519774) and new material collected for the present study from Bali, Indonesia were examined and found to be conspecific and to share generally identical characteristics with the type material of the species, including a flattened, broadly dentate to smooth thallus that is not strongly dissected or irregularly branched, the presence of four pericentral cells, and tetrasporangia occurring in strict pairs.

Although the lectotype, syntypes and Bali Island material were collected from different localities, depth and seasons and differ in gross morphology, their conspecificity is clear from an examination of their similar internal anatomy, and similar reproductive structures where present.

DISCUSSION

Familial placement of *Exophyllum wentii*

The family Rhodomelaceae is usually characterized by dioecious plants with a predominantly four (sometimes three) celled carpogonial branch. The female reproductive system is remarkably uniform within the family (Scagel 1953). The fertile pericentral cell of the procarp initially cuts off the first sterile group initial, followed by the carpogonial branch initial at a right-angle to the first sterile group initial (Kylin 1956). Carposporophytes develop from the fusion of the auxiliary cell and nearby sterile cells into a basal fusion cell, which does not divide into gonimoblast initials, but becomes sympodially branched into gonimoblast filaments bearing terminal, clavate carposporangia. Spermatangia are confluent and held within a pectic wall, occurring in terete or flat organs borne on a monosiphonous stalk. Tetrasporangia are tetrahedrally divided, develop directly from pericentral cells, occur singly or in groups of two to six per segment of stichidial branches, and are mostly protected by several specialized cover cells derived from the fertile pericentral cell of the stichidium (Scagel 1953; Hommersand 1963; Womersley 2003). Comparing *E. wentii* with other selected flattened, mostly cartilaginous members of the Rhodomelaceae (Table 1), it can be seen that although generally following trends within the family, *E. wentii* stands out by the following unique combination of characters: a coriaceous, convoluted decumbent habit, attachment through multiple holdfasts, and discoid, non-trichothallic spermatangial organs. The curved tetrasporangial stichidia are also more markedly dorsiventral than in other genera. According to Van Den Hoek *et al.* (1995), based on Feldmann (1978), there are four types of tetrasporangia: cruciate, cruciate-decussate, zonate and tetrahedral. The type of tetrasporangium present can be used to characterize taxa within the red algae (Guiry 1978). Our culture experiments on tetrasporangia of *E. wentii* showed that the final developmental stage is tetrahedral and the tetrasporangia occur strictly in pairs (Figs 21,24), which agrees with the concept of the family Rhodomelaceae as described in Abbott (1999) and Womersley (2003). It would be highly desirable to obtain molecular data for the species, to compare with other members of the Rhodomelaceae and to confirm the current familial placement. Unfortunately, samples

Table 1. Comparison of selected characters between *Exophyllum* and other selected flattened Rhodomelaceae genera

	<i>Exophyllum</i> [†]	<i>Lenormandiopsis</i> [‡]	<i>Osmundaria</i> [§]	<i>Placophora</i> [¶]	<i>Heterocladia</i> ^{††}
Habit	Decumbent, coriaceous, convoluted, blade-like	Erect lobed blade	Erect, cartilaginous, long flat axes	Deeply lobed, dorsiventral, with an apical margin	Erect, paddle-shaped cartilaginous axes
Holdfast	Multiple, ventral	Single, basal	Single, conical	Monosiphonous ventral rhizoids	Single, basal, discoid
Trichoblasts	Absent	Present	Absent	Present	Present
Carpogonial branch	Four celled	Four celled	? Four celled	Three celled	Four celled
Sterile traversing filaments in cystocarp	Single, terminal	Single, terminal	Single, terminal	Single, terminal	Single, terminal
Spermatangia	Present	Present	Present	Present	Present
Tetrasporangia	In discoid, oval plates	On terete, branched curved axes	In ovoid to spheroid heads	In terete, erect reproductive branches	On trichoblasts
	In paired straight rows in curved stichidia	In paired straight rows in curved stichidia	In paired straight rows in flattened stichidia	Occurring singly in dorsal longitudinal series, in terete reproductive branches	Helically arranged in terete stichidia

Sources: [†]this study; [‡]Norris (1987); [§]Abbott (1999), Womersley (2003); [¶]Scagel (1953); ^{††}Phillips *et al.* (2000).

for such a study could not be obtained for the present study.

'*Exophyllum wentii*' from the North and South Pacific

This study has also enabled the clarification of an earlier misidentification of Pacific material attributed to *E. wentii*: Hollenberg (1968), based on earlier Hawaiian collections by J. Newhouse, discovered spermatangial plants of an alga that he thought was *E. wentii*, and placed it within the Rhodomelaceae. Abbott (1999), based on the discovery of tetrasporangial plants of the same alga found earlier by Hollenberg, argues that the whorled nature of the tetrasporangia in stichidia and the absence of cover cells totally covering mature tetrasporangia warrants placement of what she considers to be *Exophyllum* within the Dasyaceae, although the absence of female material precluded a firmer classification of that species. The second author has examined the Hawaiian material studied by Hollenberg (BISH 474629) and other collections from Fiji (*In Herb.* SUVA-A), Samoa (Skelton and South 2002) and French Polynesia (Payri *et al.* 2000) whose nomenclature is based on Hollenberg's and Abbott's publications, and we conclude that they represent a very different genus and species from *E. wentii* as described by Weber-van Bosse (1911) and vouched for by specimens in L (Table 2). From Table 2, the most notable features distinguishing the Indonesian *E. wentii* and the Pacific material are the number of pericentral cells (four in *E. wentii* and five in the Pacific material), the nature of the spermatangial stichidia (disc-like in *E. wentii*, elongate cylindrical in the Pacific material) and the disposition of the tetrasporangia (strictly in pairs in *E. wentii*, whorled in the Pacific material). The Hawaiian and other Pacific material belongs in the Dasyaceae and not in the Rhodomelaceae, and its exact identity will be reported elsewhere.

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Table 2. Comparison of selected characters between Indonesian *Exophylum wentii* and Pacific material identified in the published literature as *Exophylum wentii*

	<i>Exophylum wentii</i> (Indonesia)†	' <i>Exophylum wentii</i> ' (Hawaii, Pacific)‡
Habit	Dorsiventral, irregularly branched on margins only; upper surface with rounded protuberances; lower surface smooth.	Dorsiventral, irregularly branched, keeled under surface with smooth upper surface.
Pericentral cells	Four	Five
Pseudolaterals	Absent	Present, abundant
Cortical layer	Three to eight cells thick; outermost cells 5–6 µm long and 2–3 µm broad.	Two to three cells thick; outermost cells 20–32 µm long and 7–9 µm broad.
Spermatangia	Outermost cells not exerted from thallus surface. In discoid, oval plates on surface of thallus	Outermost cells usually exerted from thallus surface. In curved, stichidia-like cylindrical bodies on thallus surface
Tetrasporangia	Occurring on thallus surface in curved club-like stichidia, up to nine pairs of sporangia to 200 µm in diameter in planar rows. Sporangia and plurisiphonous stichidia pedicel wholly covered by non-specialized cortical cells.	Occurring on surface of thallus in straight stichidia; up to four whorled sporangia per segment, with two cover cells per sporangium to 46 µm in diameter; stichidia attached by monosiphonous one- to two-celled pedicel.

Sources: †this study; ‡Hollenberg (1968), Abbott (1999), this study.

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