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Taxonomic Notes on Marine Algae from Malaysia. VII. Five Species of Rhodophyceae, with the Description of *Lomentaria gracillima* sp. nov.

S. Kawaguchi[a], A. Kato[b], M. Masuda[b]*, K. Kogame[b] and S. M. Phang[c]

[a] Division of Bioresources, Faculty of Agriculture, Kyushu University, Fukuoka 812-8581, Japan
[b] Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan
[c] Institute of Biological Sciences, University of Malaya, Kuala Lumpur 50603, Malaysia

* Corresponding author: mmasuda@sci.hokudai.ac.jp

The presence of three species of *Halymenia* (Halymeniaceae), *H. durvillei* Bory de Saint-Vincent, *H. dilatata* Zanardini and *H. maculata* J. Agardh in Malaysia is confirmed by their gross morphology and anatomical features. The reproductive details of *H. durvillei* including the *Halymenia*-type auxiliary-cell ampullae are described for the first time. *Peyssonnelia inamoena* Pilger (Peyssonneliaceae) is reported from Malaysia for the first time, and its monoecious gametophytes and its *P. harveyana*-type spermatangial development are confirmed. A small-statured new species of *Lomentaria* (Lomentariaceae), *L. gracillima* Masuda *et* Kogame, is described on the basis of such characteristic features as very short and slender axes (up to 8 mm long by 200–250 µm wide) and the production of tetrasporangial sori in fairly wide regions of ascending axes and erect branches: the subapical or middle portions of the axes; and the proximal to middle portions of the branches.

Introduction

Knowledge of the species composition of the marine algal flora in Malaysian waters is important in assessing relationships between the flora of the Pacific Ocean and that of the Indian Ocean. In the present paper we report five species of red algae. These include confirmed records of three species of *Halymenia* (Halymeniaceae), *H. durvillei* Bory de Saint-Vincent, *H. dilatata* Zanardini and *H. maculata* J. Agardh, and a new record of *Peyssonnelia inamoena* Pilger (Peyssonneliaceae). Furthermore, a new species of *Lomentaria* (Lomentariaceae), *L. gracillima* Masuda *et* Kogame, is proposed to accommodate the alga with diminutive thalli.

Material and Methods

Specimens examined were collected at various localities in Malaysia by snorkelling. The specimens were fixed in 10% Formalin in seawater (some *Peyssonnelia* specimens were fixed and preserved in 100% ethyl alcohol), and later some were dried as voucher herbarium specimens or mounted in 30% Karo® on microscope slides and deposited in the Herbarium of the Graduate School of Science, Hokkaido University (SAP), or in the Seaweed Herbarium, Institute of Biological Sciences, University of Malaya (KLU). Methods for microscopic examination were as described by Masuda *et al.* (1999).

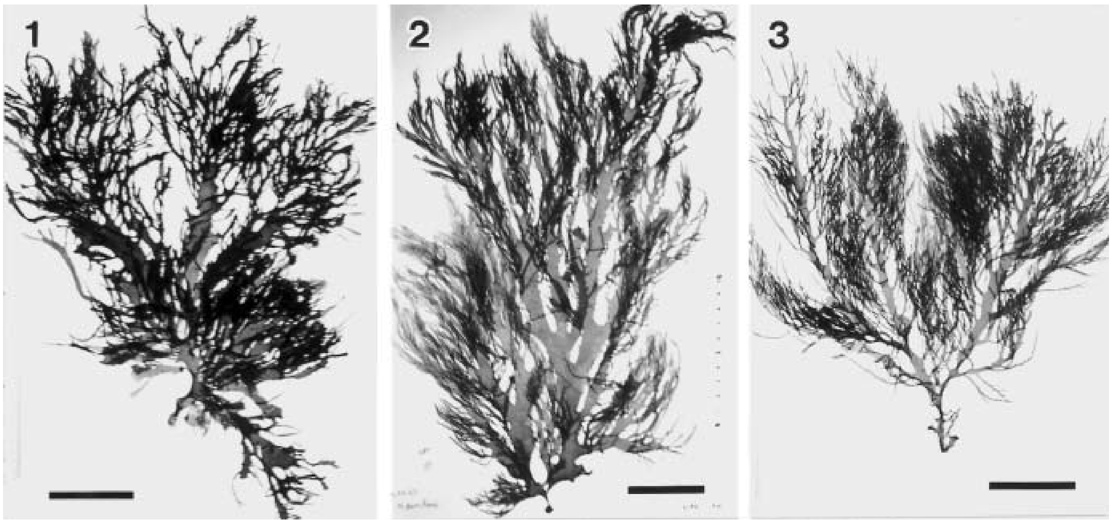
Observations and Discussion

Halymenia durvillei Bory de Saint-Vincent 1828: 180–181, pl. 15 (Figs 1–11)

Distribution: Tropical regions in the Pacific Ocean (Silva *et al.* 1987, present paper) and the Indian Ocean (Silva *et al.* 1996, present paper).

Specimens examined: Kedah: Teluk Genting (6°10'57''N, 99°43'41''E; 22.xii.1997; cystocarpic SAP 090438 and tetrasporangial SAP 090439), Pulau Genting, Langkawi. Sabah: Pulau Gulisaan (6°07'24''N, 118°02'49''E; 16.v.1998; cystocarpic SAP 090440), Sandakan; Pulau Nunuyan Laut (5°56'00''N, 118°06'36''E; 18.v.1998; cystocarpic SAP 090441), Sandakan; Pulau Ruskan Kecil (5°11'22''N, 115°08'30''E; 31.v.1998; vegetative SAP 090443), Labuan; Tanjung Kaitan (6°07'00''N, 116°05'49''E; 3.vi.1998; spermatangial SAP 090444), Kota Kinabalu; Pulau Gaya (6°02'27''N, 116°01'02''E; 4.vi.1998; cystocarpic SAP 090445), Kota Kinabalu; Pulau Dinawan (5°51'05''N, 115°59'28''E; 5.vi.1998; vegetative SAP 090446 and tetrasporangial SAP 090447), Kota Kinabalu. Johor: Tanjung Data (2°26'21''N, 103°59'25''E; 6.vi.1999; cystocarpic SAP 090448), Pulau Babi Besar; Pulau Babi Tengah (2°28'45''N, 103°57'49''E; 6.vi.1999; cystocarpic SAP 090449 and tetrasporangial SAP 090450).

Thalli grow solitarily or gregariously on bedrock or dead coral in the upper subtidal zone of reef flats. The thalli are deep to dark red in colour with lustre but without maculation on the surfaces and are compara-



Figs 1–3. *Halymenia durvillei* Bory de Saint-Vincent. Herbarium specimens deposited in SAP.
Fig. 1. Cystocarpic thallus from Teluk Genting, Pulau Genting, Langkawi (SAP 090438), which shows a very similar habit to the type illustration (Bory de Saint-Vincent 1828, pl. 15) (scale bar = 5 cm). Fig. 2. Tetrasporangial thallus with a wide axis (Teluk Genting, Pulau Genting, SAP 090439) (scale bar = 5 cm). Fig. 3. Cystocarpic thallus with a percurrent axis from Pulau Gaya, Kota Kinabalu (SAP 090445) (scale bar = 5 cm).

tively firm in texture. The thalli are shortly stipitate, gradually expanding into branched blades up to 80 cm long. These blades are variable in gross morphology: in some individuals the blades lack percurrent axes and are repeatedly dichotomously or subdichotomously (or trichotomously) branched with narrow axils, forming irregularly pinnately arranged laterals (Figs 1, 2); in others, percurrent axes are obvious and beset with dense or sparse laterals similar in morphology to the axes (Fig. 3). In both types of blades short spine-like proliferations are produced from the margins and sometimes on the surfaces. The breadth of the axes also varies greatly according to individual plants, being from 0.8 cm to 5 cm in the widest portion.

The blades internally consist of a comparatively dense filamentous medulla and a compact cortex (Fig. 4) and are 420–550 µm thick. The medullary filaments are mostly simple, running anticlinally or obliquely from cortex to cortex, or sometimes periclinally oriented (Fig. 4). Large, slightly refractive ganglionic cells are sporadically present among the medullary filaments (Fig. 4). The cortex consists of 6–8 cells with the outermost ones being usually highly elongated.

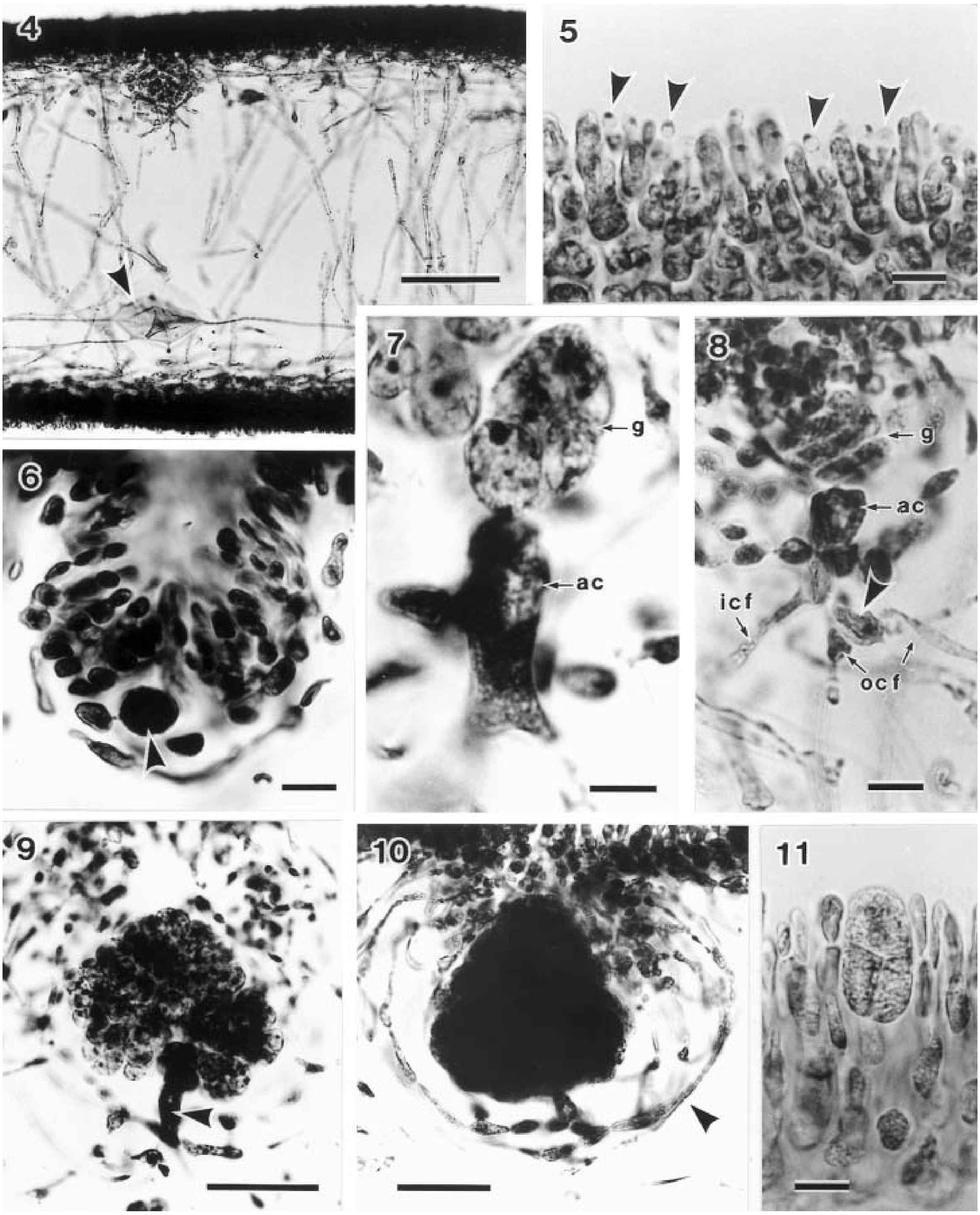
Gametophytes are dioecious. Spermatangia are scattered over male blades except for the basal portions and are formed from the outermost cortical cells (Fig. 5). Female reproductive structures are also scattered over female blades except for the basal portions. Carpogonial branches were not studied. Auxiliary cells are formed in the bottom of cup-shaped ampullae branched to the third order (Fig. 6). The auxiliary cells in contact with connecting filaments produce gonimoblasts towards the blade surface (Figs 7–9). After contact with an incoming connecting filament, the auxiliary cell also produces a cell inwardly from which several outgoing connecting filaments are cut off (Fig. 8). During the gonimoblast development, ampullary cells become conspicuously elongated and remain as a loose network of filaments surrounding the developing carposporophyte. Mature cystocarps are spherical to pear-shaped (Fig. 10), 180–230 µm in diameter and are deeply submerged in the medulla.

Tetrasporangia are cut off from the cortical cells in the third or fourth layer from the surface (Fig. 11). Mature cruciately divided tetrasporangia are broadly ellipsoidal, 17–20 µm wide by 28–32 µm high and are immersed in the outer cortex.

Halymenia durvillei was first described by Bory de Saint-Vincent (1828) based on material from New Ireland, Papua New Guinea. According to Weber-van Bosse (1921) who observed type material of *H. durvillei*, the species is characterised by its comparatively dark red colour, robust blades with non-gelatinous texture and toothed margins as well as repeatedly branched axes. Our Malaysian specimens have these features in common, although a wide range of gross morphological variations was noticed. Overall reproductive features of this species, including the *Halymenia*-type auxiliary-cell ampullae (Chiang 1970), are reported for the first time. Our observations of Malaysian specimens show that anticlinal medullary filaments are sometimes very conspicuous, although Abbott (1999) stated that *H. durvillei* had no such filaments in the medulla.

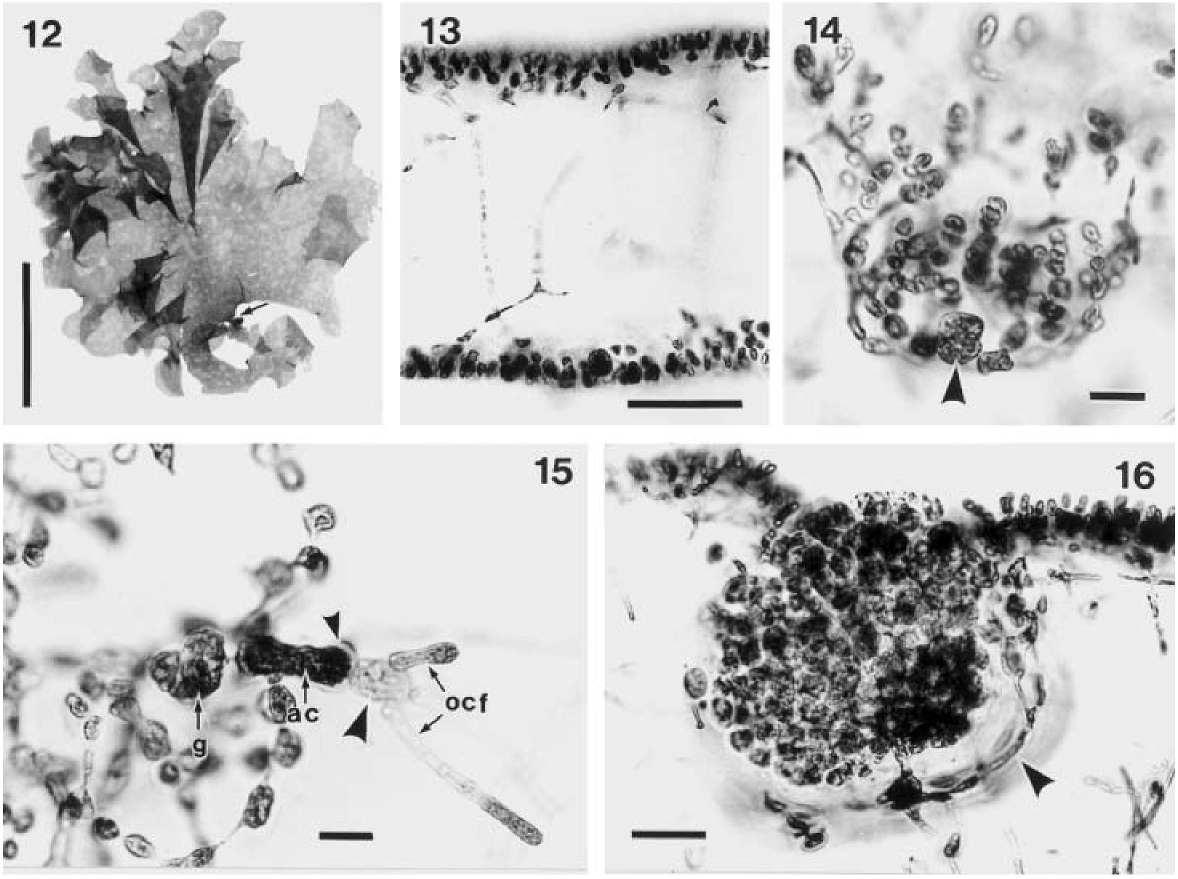
Halymenia dilatata Zanardini 1851: 35 (Figs 12–16)

Distribution: Tropical and subtropical regions in the Pacific Ocean and the Indian Ocean (Kawaguchi and Lewmanomont 1999 and references therein).



Figs 4–11. *Halymenia durvillei* Bory de Saint-Vincent. Transverse sections of Formalin/seawater-preserved specimens stained with cotton blue.
Fig. 4. Internal structure of a blade: arrowhead shows a refractive ganglionic cell (scale bar = 100 μm). Fig. 5. Spermatangia (arrowheads) produced from the outermost cortical cells (scale bar = 10 μm). Fig. 6. Auxiliary-cell ampulla: arrowhead shows an auxiliary cell (scale bar = 10 μm). Figs 7, 8. Early stages of the gonimoblast development: arrowhead indicates a cell producing outgoing connecting filaments. ac, auxiliary cell; g, gonimoblast; icf, incoming connecting filament; ocf, outgoing connecting filament (each scale bar = 10 μm). Fig. 9. More advanced stage of the gonimoblast development: arrowhead indicates an auxiliary cell (scale bar = 50 μm). Fig. 10. Mature cystocarp surrounded by a loose network of filaments (arrowhead) (scale bar = 50 μm). Fig. 11. Tetrasporangium embedded in the outer cortex (scale bar = 10 μm).

Specimens examined: Sabah: Pulau Bankawan (6°04'56''N, 117°59'50''E; 17.v.1998; spermatangial/cystocarpic SAP 090427 and tetrasporangial SAP 090428), Sandakan; Pulau Burong (5°14'13''N, 115°11'29''E; 31.v.1998; tetrasporangial SAP 090429), Labuan; Pulau Sulug (5°57'35''N, 115°59'41''E;



Figs 12–16. *Halymenia dilatata* Zanardini. Transverse sections of Formalin/seawater-preserved specimens stained with cotton blue unless otherwise indicated.
Fig. 12. Herbarium tetrasporangial specimen with a short stipe (arrow) from Pulau Burong, Labuan (SAP 090429) (scale bar = 5 cm). Fig. 13. Internal structure of a blade (scale bar = 100 µm). Fig. 14. Auxiliary-cell ampulla: arrowhead shows an auxiliary cell (scale bar = 10 µm). Fig. 15. Early stage of the gonimoblast development: large arrowhead indicates a cell producing outgoing connecting filaments; small arrowhead indicates the fusion point between an auxiliary cell and an incoming connecting filament, the latter of which is out of focus. ac, auxiliary cell; g, gonimoblast; ocf, outgoing connecting filament (scale bar = 10 µm). Fig. 16. Mature cystocarp surrounded by a loose network of filaments (arrowhead) (scale bar = 50 µm).

5.vi.1998; cystocarpic SAP 090430), Kota Kinabalu. Terengganu: Pulau Paku Besar (5 °46'38''N, 103 °02' 29''E; 24.v.1999; cystocarpic SAP 090431).

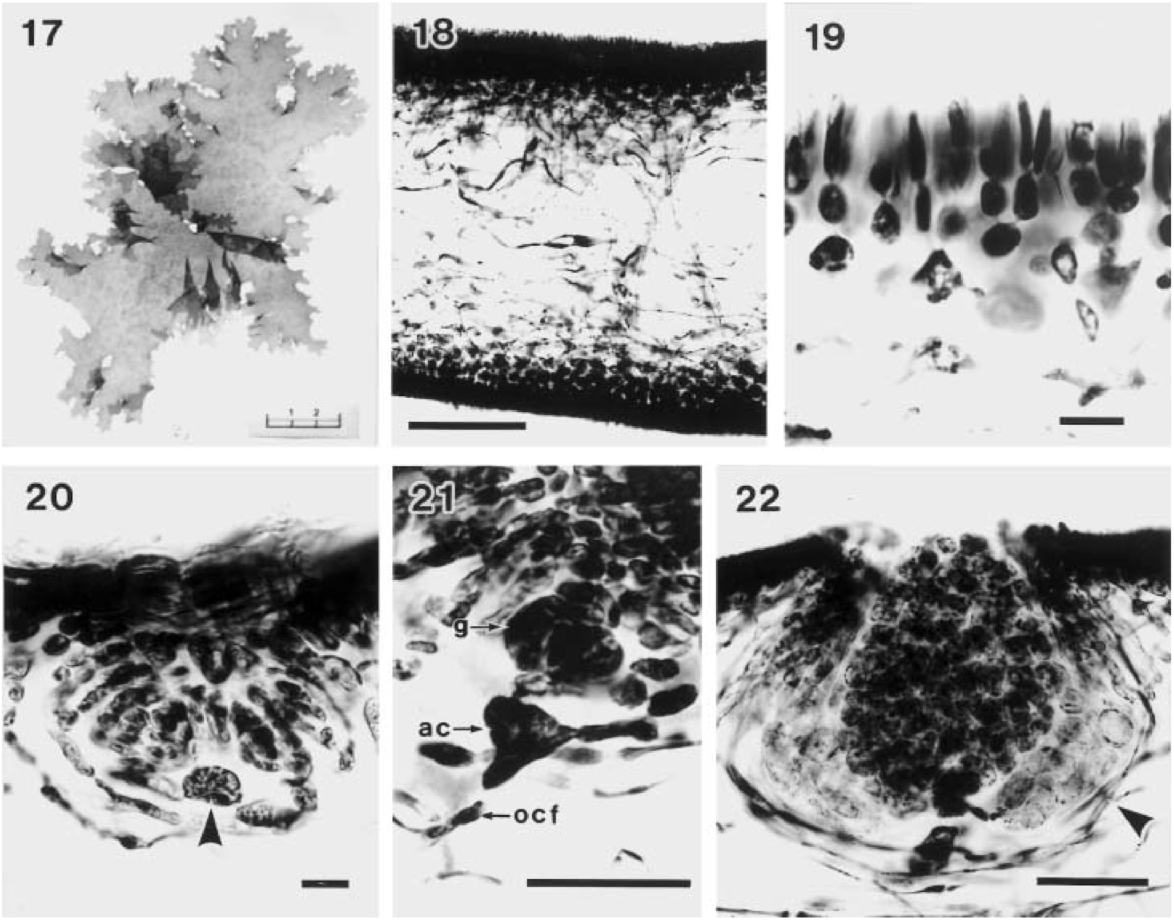
Thalli grow solitarily on dead coral or bedrock in the upper subtidal zone of reef flats. The thalli are bright red or pink in colour and very soft and gelatinous in texture. The margins of broadly elliptical to rounded, maculate blades are usually lightly sinuate or occasionally with deep clefts (Fig. 12). The blades, 220–300 µm thick, consist of a medulla of filaments running mainly perpendicularly from cortex to cortex and a thin cortex, 4–6 cells thick (Fig. 13).

Gametophytes are monoecious. Male and female reproductive structures are formed in respective sori, which are scattered all over the blades except for the basal portions. Auxiliary-cell ampullae are branched to the third order and wide across the top (Fig. 14). Gonimoblasts were very similarly produced as in *H. durvillei* (Fig. 15). Mature cystocarps are spherical, 150–200 µm in diameter, surrounded by a loose network of filaments (Fig. 16).

Halymenia dilatata was established on the basis of material from the Red Sea (Zanardini 1851) and is characterised by basically elliptical to rounded blades with very gelatinous texture and bright red colour as well as maculation on the surfaces (Zanardini 1851, 1858, Balakrishnan 1961, Kawaguchi and Lewmanomont 1999). Overall features of our Malaysian material, including spermatangia and tetrasporangia, agree well with the above-mentioned features of *H. dilatata*. Although Ismail (1995) reported this species from Tioman Island on the east coast of the Malay Peninsula, his material might be confused with *H. maculata*, judging from the strongly dissected margins and the thallus appearing to be neither soft nor gelatinous.

Halymenia maculata J. Agardh 1885: 12
(Figs 17–22)

Distribution: Tropical regions in the Pacific Ocean and the Indian Ocean (Kawaguchi *et al.* 2002 and references therein).



Figs 17–22. *Halymenia maculata* J. Agardh. Transverse sections of Formalin/seawater-preserved specimens stained with cotton blue unless otherwise indicated.
Fig. 17. Herbarium cystocarpic specimen from Pulau Satang Besar (SAP 087573) (scale bar = 3 cm). Fig. 18. Internal structure of a blade (scale bar = 100 µm). Fig. 19. Highly elongated outermost cortical cells ('rabbit-ear' cells) (scale bar = 10 µm). Fig. 20. Auxiliary-cell ampulla: arrowhead shows an auxiliary cell (scale bar = 10 µm). Fig. 21. Early stage of the gonimoblast development. ac, auxiliary cell; g, gonimoblast; ocf, outgoing connecting filament (other outgoing connecting filaments, a cell which produces outgoing connecting filaments, and an incoming connecting filament being out of focus) (scale bar = 50 µm). Fig. 22. Mature cystocarp surrounded by a loose network of filaments (arrowhead) (scale bar = 50 µm).

Specimens examined: Kedah: Pulau Tepor (6°15'55''N, 99°43'10''E; 21.xii.1997; cystocarpic SAP 090432), Langkawi; Teluk Genting (6°10'57''N, 99°43'41''E; 22.xii.1997; tetrasporangial SAP 090433), Pulau Genting, Langkawi. Sarawak: Pulau Satang Besar (1°47'20''N, 110°09'53''E; 23.v.1998; spermatangial SAP 090434 and cystocarpic SAP 087573), Santubong, Kuching; Pulau Talang-Talang Kecil (1°53'50''N, 109°45'59''E; 26.v.1998; cystocarpic SAP 090436), Sematan. Sabah: Pulau Kuraman (5°13'10''N, 115°08'26''E; 31.v.1998; vegetative SAP 090437), Labuan.

Thalli grow solitarily on bedrock in the upper subtidal zone of reef flats. The thalli are dark red or purplish-red in colour and not gelatinous but somewhat carnose in texture. The irregularly shaped foliose blades are up to 10 cm high, and are shallowly or sometimes deeply sinuate with strongly dissected margins (Fig. 17). The clearly maculate blades are 250–350 µm thick. They consist of a medulla of somewhat dense filaments running periclinally or obliquely with occasional anticlinal ones and a cortex which is 7–10 cells thick (Fig. 18), with the outermost ones being conspicuously elongated, often assuming a rabbit-ear appearance (Fig. 19).

Gametophytes are dioecious. Male and female reproductive structures are scattered all over the blades except for the basal portions. Auxiliary cells are formed in narrowly necked or cup-shaped ampullae branched to the third order (Fig. 20). Gonimoblasts were similarly produced as in the former two species (Fig. 21). Mature cystocarps are spherical, 170–220 µm in diameter, surrounded by a loose network of filaments (Fig. 22).

Halymenia maculata was originally described on the basis of material collected from Mauritius (Agardh 1885) and is characterised by shallowly or often deeply sinuate, foliose blades with somewhat carnose texture, dark red or purplish-red colour and clear maculation on the surfaces as well as conspicuously elongated outermost cortical cells (Børgesen 1950, Kawaguchi *et al.* 2002). Our Malaysian material shares these features with the Mauritius specimens (Børgesen 1950) and the Vietnamese ones (Kawaguchi *et al.* 2002), although the latter specimens sometimes have more deeply cleft blades (Kawaguchi *et al.* 2002). Other reproductive features including spermatangia and tetrasporangia of our Malaysian material also agree well with those of Vietnamese specimens (Kawaguchi *et al.* 2002).

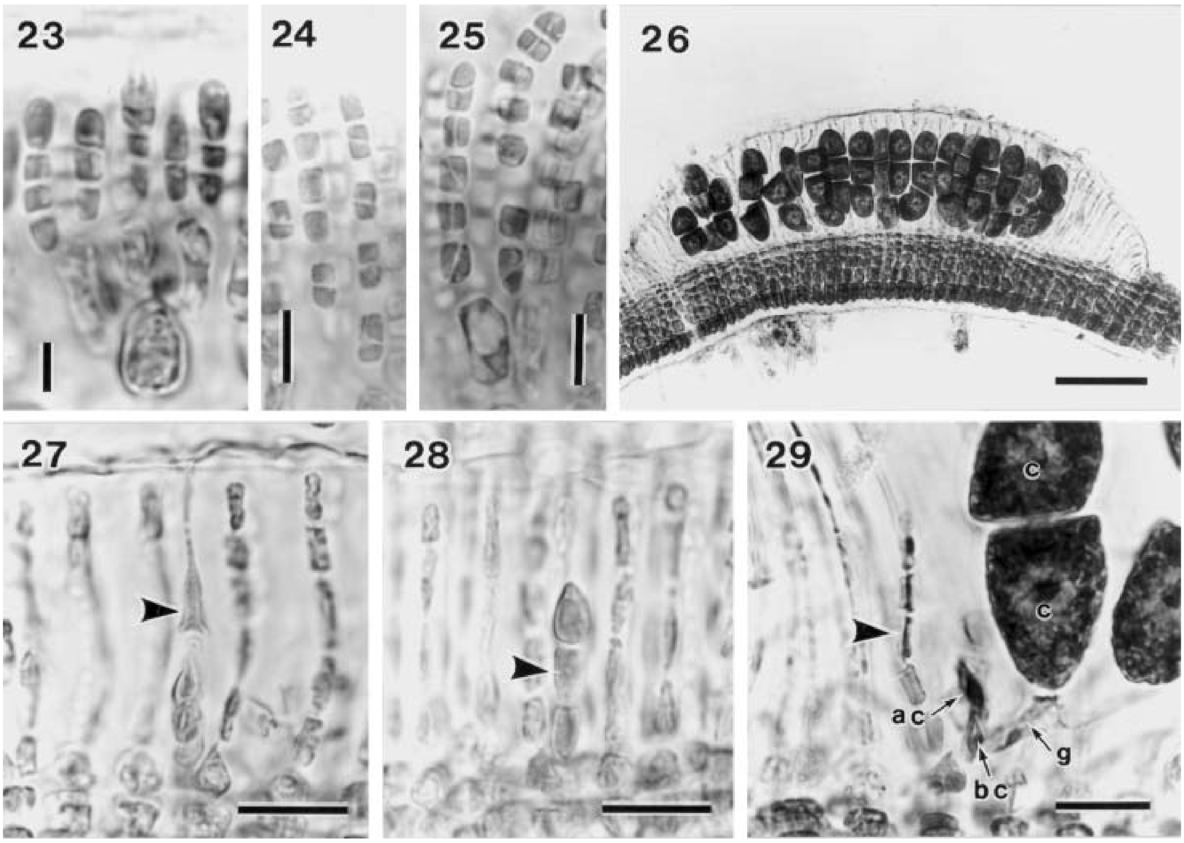
It is worth pointing out that the narrowly necked auxiliary-cell ampullae found in *H. maculata* appear to represent an intermediate form between the *Halymenia*-type and the *Cryptonemia*-type ampullae distinguished by Chiang (1970) and pose a question to the generic distinction based on the two ampullar types. In fact, a similar variation was already reported by Gargiulo *et al.* (1986) from *Halymenia asymmetrica* Gargiulo, De Masi *et* Tripodi from the Mediterranean Sea, which has ovoid ampullae that are similar to the *Cryptonemia*-type ampullae.

Peyssonnelia inamoena Pilger 1911: 311 (Figs 23–29)

Distribution: Tropical to warm temperate regions in the Atlantic Ocean (Pilger 1911, Schneider and Reading 1987, Guimarães and Fujii 1999) and the Pacific Ocean (Womersley 1994, present paper).

Specimens examined: Terengganu: Tanjung Guntong Laut (5 °56'26''N, 102 °43'13''E; 19.v.1999; cystocarpic SAP 091292 and tetrasporangial SAP 091293), Pulau Perhentian Kecil; Tanjung Batu Lepir (5 °53'08''N, 102 °44'22''E; 20.v.1999; spermatangial/cystocarpic SAP 091281 and tetrasporangial SAP 091282), Pulau Perhentian Besar; Teluk Gadung (5 °54'32''N, 102 °46'14''E; 20.v.1999; spermatangial/cystocarpic SAP 091283 and tetrasporangial SAP 091284), Pulau Perhentian Besar; Pasir Panjang Kecil (5 °46'15''N, 103 °02'03''E; 22.v.1999; cystocarpic SAP 091285), Pulau Redang; Tanjung Pasir China (5 °36'36''N, 103 °03'44''E; 23.v.1999; spermatangial/cystocarpic SAP 091286), Pulau Bidong Laut.

Crustose thalli, 1.0–1.5 cm in diameter, grow soli-



Figs 23–29. *Peyssonnelia inamoena* Pilger. Radial vertical sections of Formalin/seawater-preserved specimens stained with cotton blue.
Fig. 23. Young spermatangial filaments (scale bar = 10 μm). Fig. 24. Spermatangial filaments, each cell of which is formed by an intercalary and periclinal division (scale bar = 10 μm). Fig. 25. Spermatangial filaments, each cell of which divides anticlinally or obliquely and bears one-paired spermatangia (scale bar = 10 μm). Fig. 26. Mature cystocarpic nemathecium (scale bar = 100 μm). Fig. 27. Carpogonial branch: arrowhead indicates the carpogonium (scale bar = 20 μm). Fig. 28. Auxiliary cell branch: arrowhead indicates the auxiliary cell (scale bar = 20 μm). Fig. 29. Nemathecial filament (arrowhead) producing an auxiliary cell branch, which is shorter than sterile nemathecial filaments. ac, auxiliary cell; bc, basal cell; c, carposporangium; g, gonimoblast (scale bar = 20 μm).

tarily or gregariously on dead coral, shell or fish-cage nets in the upper subtidal zone of reef flats. They are bright red and 80–190 μm thick excluding nemathecia. Vegetative structures including the parallel arrangement of hypothallial filaments, the perithallial filaments arising from the whole upper surface of each hypothallial cell and closely packed in a firm matrix, unicellular rhizoids, and hypobasal calcification are similar to those reported from the Cameroons (Pilger 1911), North Carolina (Schneider and Reading 1987), southeastern Brazil (Guimarães and Fujii 1999) and southern Australia (Womersley 1994).

Gametophytes are monoecious and produce male and female reproductive structures in separate or the same nemathecia. Spermatangia are produced in both male and female nemathecia. Male nemathecia are slightly elevated and 40 μm high. Initials of spermatangia are borne in a simple chain consisting of 3 or 4 cells on each fertile perithallial filament (Fig. 23). Each cell of this chain undergoes an intercalary and periclinal division, which doubles the length of the chain (Fig. 24). Each cell of the chain then produces two spermatangia by an anticlinal or oblique division, which results in a series of one-paired spermatangia (Fig. 25). This spermatangial development is called the *P. harveyana* type (Maggs and Irvine 1983). Pilger (1911) and Guimarães and Fujii (1999) illustrated such spermatangial filaments; however, each cell of their filaments seems to be just before a final (anticlinal or oblique) division. All perithallial filaments within a male nemathecium produce spermatangia, but only a few perithallial filaments bear spermatangia in a female nemathecium. The mature spermatangia of both nemathecia are 2–3 μm in diameter.

Cystocarpic nemathecia are conspicuously elevated and 110–130 μm high (Fig. 26). Each carpogonial branch consists of 4 cells (Fig. 27). Each auxiliary cell branch is 3- (Fig. 28) to 5-celled, and the suprabasal cell is an auxiliary cell. Gonimoblasts develop from the auxiliary cell (Fig. 29) and form 2–5 catenate carposporangia, which are deeply pigmented, 25–40 μm wide by 25–40 μm high.

Tetrasporangial nemathecia are conspicuously elevated and 75–120 μm high. Tetrasporangia are terminal on perithallial filaments and 28–38 μm wide by 82–100 μm high at maturity.

According to Guimarães and Fujii (1999), Brazilian *P. inamoena* has dioecious gametophytes, although our Malaysian gametophytes are monoecious. Other critical reproductive features including the *P. harveyana*-type spermatangial development and the production of gonimoblasts from the auxiliary cell are similar in the two localities. The occurrence of monoecious or dioecious gametophytes seems to depend on reproductive stages of observed individuals according to the species: when spermatangia are protandrous and ephemeral, they may disappear in fully mature monoecious gametophytes.

Lomentaria gracillima Masuda *et* Kogame, sp. nov. (Figs 30–37)

Diagnosis: *Axes plures e disco basali primario exorientes, pallide brunneoli-ruberi, molliter succulenti, primum erecti vel ascendentes, arcuatescentes aetate provecta, attingentes usque ad 8 mm longi, teres praeter partes tetrasporangiferas, 100–150 μm diametro basaliter, 200–250 μm diametro ad partem mediam, gradatim decrescens versus apicem acutum, ramos ordinis primi unilateraliter dispositos in latere dorsali producentes; ordines tres ad quinque ramorum lateralium facti; textura cellulares ex strato medulloso singulari et stratis corticalibus 2–4 constantes; cellulae glandulosae sphaericae ad ellipsoidales, 5–10 μm diametro. Cystocarpia late ovoidea, 400–450 μm diametro et 420–480 μm in altitudine. Tetrasporangia in partibus compressis ad complanatis (250–500 μm in latitudine) axium ascendentium et ramorum erectorum formata, sporis tetraedrice dispositis, 60–70 μm diametro ad maturitatem.*

Several axes arising from a primary basal disc, pale brownish-red, softly fleshy, first erect or ascending, becoming arcuate with age, reaching up to 8 mm long, terete except for tetrasporangium-bearing portions, 100–150 μm in diameter basally, 200–250 μm in diameter at the middle portion, tapering gradually towards a pointed apex, producing secundly arranged first-order branches on the dorsal side; three to five orders of lateral branches formed; cellular tissue consisting of a single medullary layer and 2–4 cortical layers; gland cells spherical to ellipsoidal, 5–10 μm in diameter. Cystocarps broadly ovoid, 400–450 μm in diameter and 420–480 μm in height. Tetrasporangia formed in compressed to flattened portions (250–500 μm wide) of ascending axes and erect branches, with tetrahedrally arranged spores, 60–70 μm in diameter at maturity.

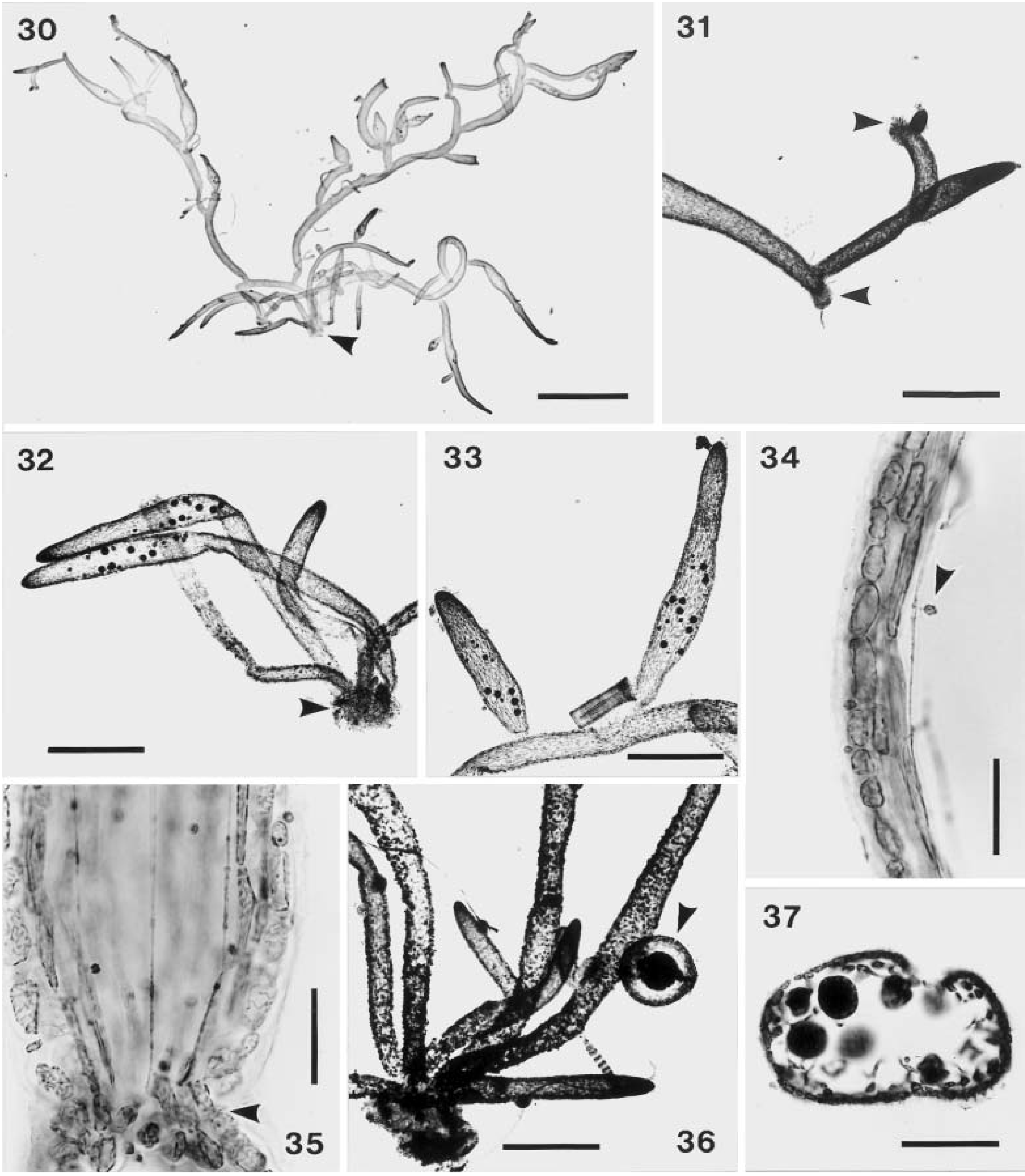
Holotypus: tetrasporangial specimen (SAP 090451, Fig. 30), collected from Pulau Sipadan (4°07'03''N, 118°37'30''E), Sabah, Malaysia, on 27 December 1995.

Etymology: The specific epithet, *gracillima* (the superlative of *gracilis*), alludes to very slender axes and branches of this alga.

Distribution: Tropical regions in the Pacific Ocean.

Other specimens examined: Sabah: Pulau Sipadan [27.xii.1995; tetrasporangial (isotypus SAP 090452; others SAP 090453, 090454) and cystocarpic SAP 090455], Semporna.

Thalli grow solitarily on some brown algae, such as *Hormophysa*, *Sargassum* or *Turbinaria* in the upper subtidal zone of a reef flat. The thalli are pale brownish-red, softly fleshy. Six to twelve axes (including young ones that are detectable with microscopy) arise from a primary discoid holdfast (Fig. 30). These axes are first erect or ascending and become arcuate with age (Fig. 30). Arcuate axes form secondary holdfasts when they are attached to the substratum and



Figs 30–37. *Lomentaria gracillima* Masuda *et* Kogame. Formalin/seawater-preserved specimens stained with cotton blue unless otherwise indicated.
Fig. 30. Whole habit of a tetrasporangial thallus with arcuate and ascending axes mounted in 30 % Karo® on a microscope slide (holotype specimen, SAP 090451): arrowhead indicates the position of the primary discoid attachment; wide (compressed to flattened) portions bear tetrasporangia (scale bar = 2 mm). Fig. 31. Portion of the holotype specimen showing a tip of an arcuate axis: arrowheads indicate discoid attachments (scale bar = 500 µm). Fig. 32. Portion of a tetrasporangial thallus with ascending secondary axes that produce tetrasporangia: arrowhead indicates the primary discoid attachment (mounted in 30 % Karo® on a microscope slide, SAP 090453) (scale bar = 500 µm). Fig. 33. Tetrasporangium-bearing first-order branches (scale bar = 500 µm). Fig. 34. Longitudinal section of a main axis: arrowhead indicates a gland cell formed on an elongated medullary cell (scale bar = 50 µm). Fig. 35. Optical section of a branched portion; arrowhead indicates the region of a diaphragm at the branch base (scale bar = 50 µm). Fig. 36. Cystocarp (arrowhead) formed on one of the axes (mounted in 30 % Karo® on a microscope slide, SAP 090455) (scale bar = 500 µm). Fig. 37. Transverse section of a tetrasporangial sorus (scale bar = 100 µm).

reach up to 8 mm long. Some axes bear attachment discs at the tips, from which 1–3 secondary axes develop (Fig. 31). Some of secondary axes begin to produce reproductive structures (Fig. 32) when they are terete (160–200 µm in diameter by 700–2500 µm in length) and unbranched**.** In tetrasporophytes the soral portion becomes compressed to flattened (250–500 µm wide) as their tetrasporangial production advances. These axes continue to grow apically after the production of reproductive structures and become arcuate with age. The primary and secondary axes are terete except for the previous soral portions, which are compressed to flattened, 100–150 µm in diameter near the primary disc, 200–250 µm in diameter at the middle portion, tapering gradually towards a pointed apex.

The axes produce secundly arranged first-order branches on the dorsal side (Fig. 30). First-order branches begin to form reproductive structures when they are terete (180–200 µm in diameter and 500–800 µm long) and unbranched**.** These branches become compressed to flattened (250–500 µm wide) at the soral portions (Fig. 33) while their tetrasporangial production proceeds. After the production of reproductive structures the first-order branches grow distally (often becoming arcuate branches) and bear secundly arranged second-order branches. This process is repeated one to three times in different thalli or in positions on a single thallus so that up to three to five orders of branches are produced (Fig. 30).

Internally the thallus consists of an outer cellular tissue and an inner mucilage-filled cavity. The cellular tissue consists of a single medullary layer and 2–4 cortical layers (Fig. 34). The medullary layer consists of axially elongated, slender, hyaline cells, which are 5–10 µm wide by 75–200 µm long. The cortex consists interiorly of one layer of ellipsoidal, lightly pigmented cells (10–15 µm thick by 30–65 µm high in longitudinal sections), which become progressively smaller outwards. The outermost cortical cells are ellipsoidal to spherical, 5–12 µm thick by 5–25 µm high in longitudinal sections. Gland cells are borne on the majority of medullary cells (Fig. 34) and some innermost cortical cells. These gland cells are spherical to ellipsoidal, 5–10 µm in diameter. Diaphragms are absent except at branch bases (Fig. 35).

Cystocarps are lateral on axes (Fig. 36) or first-order branches, broadly ovoid and 400–450 µm in diameter by 420–480 µm in height.

Tetrasporangia are formed in sunken sori which are produced in fairly wide regions of ascending axes (Fig. 32) and erect branches (Fig. 33): the subapical or middle portions of the axes; and the proximal to middle portions of the branches. The tetrasporangia are first formed in the ascending axes and then in the first- to third-order laterals with age. Mature tetrasporangia (Fig. 37) are 60–70 µm in diameter, with tetrahedrally arranged spores.

Some ten small-statured species are known in the genus *Lomentaria*, although the generic or specific status of several species needs verification (Wynne 1998 and references therein). Our Malaysian alga deserves comparison with five species with the characteristic secund branching shown in Table I.

Lomentaria amplexans R. Norris, described from Natal, South Africa (Norris 1987), is clearly distinguished from *L. gracillima* by larger and segmented axes producing mostly unbranched branches with hamate tips.

Lomentaria corallicola Børgesen, which was originally described from Iran (Børgesen 1939) and synonymized with *L. rawitscheri* Joly (Bula-Meyer and Norris 2001), is known from scattered localities in the Indian Ocean (Norris 1987, Wynne 1995), the Pacific Ocean (Cribb 1983) and the Atlantic Ocean (Bula-Meyer and Norris 2001). It is distinguished from *L. gracillima* not only by wider axes and the production of a tetrasporangial sorus extending to the whole fertile branch but also by the presence of densely crowded erect branches (Børgesen 1939).

Lomentaria monochlamydea (J. Agardh) Kylin, known from Australian (Millar 1990, Womersley 1996) and Malaysian waters (Masuda *et al.* 2001), differs from *L. gracillima* in wider axes and branches as well as in the production of a tetrasporangial sorus that extends to the whole fertile branch (Millar 1990, Masuda *et al.* 2001).

Lomentaria secunda (Hooker f. *et* Harvey) V. J. Chapman, reported from Australasia (Chapman and Dromgoole 1970, Adams 1994), is distinguished from *L. gracillima* in wider axes, tetrasporangial sori located on the distal portions of fertile branches and larger tetrasporangia (Chapman and Dromgoole 1970).

Lomentaria strumosa Wynne, described from Oman, the northern Arabian Sea (Wynne 1998), is distinguished from *L. gracillima* by larger and wider axes with thicker cell layers, a subapically positioned tetrasporangial sorus on each fertile branch and smaller tetrasporangia (Wynne 1998).

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Table I. A morphological comparison of species of *Lomentaria* that have small-sized thalli with secund branching throughout the thallus or in parts.

	L. amplexans	*L. corallicola*	*L. monochlamydea*	*L. secunda*	*L. strumosa*	*L. gracillima*
Thallus dimension (diameter of axes)	50 mm long (up to 750 µm)	5.0–7.5 mm high (300–500 µm)	Up to 22 mm long (500–2000 µm)	10–20 mm high (250–750 µm)	30–44 mm high and 20 mm long (600–1000 µm)	Up to 8 mm long (200–250 µm)
Thallus texture, consistency, or intensity	Unknown	Unknown	Softly fleshy	Flaccid	Fairly rigid	Softly fleshy
Branching of laterals	Mostly unbranched	Branched to two orders	Branched to three orders	Branched to one order or unbranched[a]	Branched to two orders	Branched to three to five orders
Branches with hamate tips	Present	Absent	Absent	Absent	Absent	Absent
Dimension of ultimate-order branches	Unknown	Unknown	2–6 mm long by 500–700 µm wide	Up to 10 mm long[a]	About 20 mm long[b]	500–800 µm long by 180–200 µm wide[c]
Number of cell layers in axes	3 or 4	3[d]	4 or 5 (5–7 in older parts)	Unknown	6 or 7	3–5
Position of tetrasporangial sorus	Proximal region of erect branch	Whole erect branch	Whole erect branch	Distal region of erect branch	Subapical region of erect branch	Subapical or middle portions of axes, proximal to middle portions of branches
Diameter of tetrasporangia	45 µm	50 µm	30–50 µm	90–100 µm	20–26 µm	60–70 µm
Shape of cystocarps (width by height)	Unknown	Oblique-urceolate (600 µm by 770 µm)	Unknown	Unknown	Unknown	Broadly ovoid (400–450 µm by 420–480 µm)
Substratum	Epiphytic on red algae	On corals	Epilithic or on corals	Unknown	Epilithic	Epiphytic on brown algae
Reference	Norris 1987	Børgesen 1939	Millar 1990, Womersley 1996, Masuda *et al.* 2001	Chapman and Dromgoole 1970	Wynne 1998	Present paper

[a] From the illustration given by Chapman and Dromgoole (1970, fig. 43).
[b] From the illustration of the holotype specimen (Wynne 1998, fig. 8).
[c] Except for tetrasporangial branches that are 250–500 µm wide.
[d] From the illustration given by Børgesen (1939, fig. 31c).

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