

Morphology and systematics of the genus *Halymenia* C. Agardh (Halymeniales, Rhodophyta) in the Philippines

by

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With 14 figures and 2 tables

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Abstract: The vegetative and reproductive morphology and anatomy of *Halymenia* specimens from the Philippines were studied and four species recognised: *H. dilatata* Zanardini, *H. durvillei* Bory de Saint-Vincent, *H. maculata* J. Agardh and *H. porphyraeformis* Parkinson. As many *Halymenia* taxa have previously been reported from the western Pacific and Malayan region, specimens from neighbouring regions and type material of the most relevant taxa were compared with the collections from the Philippines. From these studies, *H. ceylanica* Harvey ex Kützing, *H. durvillei* var. *denudata* Weber-van Bosse, *H. durvillei* var. *edentata* Weber-van Bosse, *H. formosa* Harvey ex Kützing, *H. microcarpa* (Montagne) P. Silva and *H. venusta* Børgesen are considered to be synonyms of *H. durvillei*. *H. porphyraeformis* is reported from the region for the first time, but was found in earlier collections identified as the superficially similar *H. dilatata*.

Key words: *Halymenia*, Halymeniales, Rhodophyta, systematics, Western Pacific

Introduction

In this study the representatives of the genus *Halymenia* have been studied from the Philippines from a morphological-anatomical perspective. The genus is characterised by a lubricous texture, a lax medulla with predominantly anticlinally oriented filaments connecting cortex to cortex, the presence of refractive ganglionic cells, and somewhat

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flattened and expanded auxiliary cell ampullae with branched secondary filaments (Balakrishnan 1961; Abbott 1967; Chiang 1970; Codomier 1974; Maggs & Guiry 1982; Guimarães & Fuji 1998). Traditionally *Halymenia* has been classified in the family Halymeniaceae, one of several families belonging to the large order Cryptonemiales. The definitions of the Cryptonemiales has, however, been seriously refined in the past two decades and a suite of new, smaller and more homogenous orders, have been proposed by removing clearly heterogenous elements (Pueschel & Cole 1982; Kraft & Robins 1985; Silva & Johansen 1986; Maggs & Pueschel 1989; Saunders & Kraft 1994). The order Halymeniales is a new name for the Cryptonemiales, one of Kylin's (1956) core orders, restricted to two families, the Halymeniaceae and Sebdeniaceae (Saunders & Kraft 1996; Kraft & Saunders 2000). The Sebdeniaceae encloses a single genus *Sebdenia* (J. Agardh) Berthold, while the Halymeniaceae contains a total of 21 genera (Kylin 1956; Chiang 1970; Womersley & J.A. Lewis 1994; Lee et al. 1997) of which the largest genera in terms of species are *Halymenia*, *Cryptonemia* and *Grateloupia*. Species concepts within these genera are often ill-defined and in need of review. This study aims to describe and illustrate the representatives of the genus *Halymenia* in the Philippines (and up to a lesser extent in the Indo-Malayan region). As a large number of *Halymenia* taxa have been reported from the western Pacific, type collections of taxa reported from the region have also been examined and compared.

Material and methods

Specimens of *Halymenia* were collected by Coppejans (HEC-numbers) in April 1998 and by Leliaert, Liao, Dargent & De Smedt (PH-numbers) in August 1998 during two separate field trips in the Philippines and are deposited in GENT. Several earlier collections from Indonesia were also studied: the Siboga-expedition housed in L (Weber 1902; Weber-van Bosse 1921), and the Snellius II-expedition partly housed in GENT (Coppejans & Prud'homme van Reine, 1992). Specimens in GENT from Papua New Guinea were also examined (Millar et al. 1999; Coppejans & Millar 2000). Herbarium abbreviations follow Holmgren et al. (1990).

Collected plants were immediately prepared as herbarium specimens with a small amount preserved in 4% Formalin/seawater of each specimen. Sections of the laminae were made by hand and stained in a mixture of 1 g cotton blue powder, 35 ml Karo®, 60 ml distilled water and 5 ml acetic acid to which a few crystals of phenol were added. Resin-embedded material was used for transverse and longitudinal sections of the stipes using Technovit 7100 as described by De Clerck & Coppejans (1999). Sections were cut on a Reichert-Jung Autocut 2040 microtome and stained with toluidine blue. Line-drawings were prepared using a camera lucida mounted on a Zeiss Diaplan microscope. AGFA APX25 was used in making photographs.

Specimens examined:

Halymenia durvillei

INDIA. Gujarat, Dwarka: (Børgesen, 20/1/1928, C FB 5394 [holotype *H. venusta*], C FB 5442 [isotype *H. venusta*])

INDONESIA. Borneo-Bank, Sabankatan Reef: (Weber-van Bosse, 1899, L 941.312-310, L 941.97-492 [holotype *H. durvillei* var. *denudata*]); Gissen-Reef: (Weber-van

Bosse, 27/8/1899, L 941.27-186); Komodo Island: (Snellius II, 26/10/1984, 10942E); Sumba (NE Coast): (Snellius II, 15/9/1984, 10610E); SW Sulawesi, Lanyukang Island (W): (3/5/1989, L 992.274-135); Sulawesi, Sanana-Rif: (Weber-van Bosse, 14/9/1899, L 941.27-209); Sulawesi, Parepare: (Weber-van Bosse, 10/1888, L 941.97-494 [holotype *H. durvillei* var. *denudata*]); Waigeo, Woenok Bay: (Weber-van Bosse, 13/8/1899, L 941.27-187)

PAPUA NEW GUINEA. Madang, Manam: (Coppejans, 16/7/1988, HEC 7821); Madang, Ruo Island: (Coppejans & Prud'homme van Reine, 19/7/1990, HEC 13253B); Port Moresby, Loloata: (Coppejans & De Clerck, 31/7/1994, HEC 10362); Tissot of Patot: (Weber-van Bosse, L 941.97-493)

PHILIPPINES. Luzon, Ilocos Norte, Burgos, Bobon: (Cordero, 2/1973, US 55593); Luzon, La Union, San Fernando, Poro Pt.: (Escudero, 12/3/1984, T13559, PUH); Luzon, Pangasinan, San Fabian, Alacan: (Cordero, 9/1979, US 091466); Luzon, Zambales, Candelaria: (Cordero, 11/1979, US 091465); Luzon, Bataan, Morong, Panibatuhan: (Santiago, 18/10/1969, T 11196, PUH); Luzon, Cavite: (Bartlett 14587, 7/7/1935, MICH); Luzon, Tayabas (now Quezon), Mauban, Halopag: (Pastrana 18, 16/9/1935, MICH); Luzon, Batangas, Wawa: (Santos 117, 14/7/1935, MICH); Luzon, Sorsogon, Bulusan, Dancalan: (Coppejans, 21/4/1998, HEC 12287); Luzon, Sorsogon, Gubat: (Leliaert et al., 17/8/1998, PH 326, PH 340); Catanduanes, Baras, Danao, Minabalay: (Trono, 3/11/1968, T 1263, PUH); Occidental Mindoro, Lubang Island: (Villaflores 26, 11-17/9/1935, MICH); Oriental Mindoro, Puerto Galera Bay: (Bartlett 14019, 1935, MICH); Samar, Marabut, Calauayan: (5/1973, L 383784); Samar (E), Borongan, Punta Maria: (5/1973, L 383807); Samar, Calbayog City, Tinaplacan: (Rosaroso, 4/1995, CEBU); Palawan, Tukuran Island: (Velsquez 5654, 24/4/1964, CEBU); Palawan, Cuyo Islands, West Putik Island: (Meñez et al., 20/5/1978, US 013836); Panay, Iloilo, Barotac Viejo, San Francisco: (Bronzal, 15/2/1984, VEBU); Guimaras, Taklong Island: (Castro 307, 26/7/1983, T 16309, PUH); Biliran, Almeria, Agta: (Dacles, 21/1/1994, CEBU); Negros Oriental, Amlan: (Pages 63, 31/12/1959, CEBU); Cebu, Malapascua Island: (Pages 32, 30/11/1956, CEBU); Cebu, Daanbantayan, Tapilon: (Arceo, 29/8/1992, CEBU); Bohol, Ubay, Cuya: (Young, 13/4/1993, CEBU); Mindanao, Misamis Oriental, El Salvador: (Rivera, 18/10/1978, T 13107, PUH); Mindanao, Lanao del Norte, Magoong: (Rosagaron, 10/7/1974, T 12936, PUH); Mindanao, Zamboanga City: (Leliaert et al., 22/8/1998, PH 416, PH 420, PH 429, PH 432, PH 541); Tawi-Tawi, Bongao, Pasiagan: (Aliaza, 15/5/1990, T 18445, PUH); Philippines: (Montagne, 1844, Cuming 2221 [PC MA 8966, holotype *M. microcarpa*])

SRI LANKA. Beruwela: (Coppejans, 24/1/1997, HEC 11804); Matassan, Poelau Barang: (Weber-van Bosse, 24/5/1899, L 941.27-183); Weligama: (Coppejans, 5/1/1996, HEC 11552); (Harvey, 1866, TCD 39 [isotype *H. ceylanica*])

TONGA. (Harvey, 1855, L 941.61-8 [holotype *H. formosa*])

Halymenia dilatata

PHILIPPINES. Luzon, Sorsogon, Bulusan: (Leliaert et al., 16/8/1998, PH 288, PH 303); Luzon, Sorsogon, Gubat: (Leliaert et al., 17/8/1998, PH 337, PH 342, PH

343); Cebu, north side of Sillon Island: (Young, 10/3/1994, CEBU); Cebu, Bantayan Island: (Young, 5/2/1994, CEBU); Cebu, Mactan Island, Punta Engaño: (Young, 19/12/1993, CEBU); Cebu, Liloan: (Paloma et Cortez, 20/7/1980, CEBU); Cebu, Carcar, Tuyum: (Rosaroso, 26/10/1961, CEBU); Mindanao, Surigao del Norte, Nonoc Island, Dinayugan: (Largo, 3/4/1984, CEBU); Mindanao, Zamboanga City: (Leliaert et al., 25/8/1998, PH 538, PH 539).

RED SEA. (Portier, *Musea Civico di Storia Naturale di Venezia*, s.n. [lectotype *H. dilatata*])

Halymenia maculata

INDONESIA. Ambon: (Weber-van Bosse, L 941.97-498); Jedan Island, Aru: (Weber-van Bosse, L 941.97-483); Flores, Maumere: (Weber-van Bosse, 12/1888, L 941.97-496); Saleyen Reef: (Weber-van Bosse, L 941.97-497); Sulawesi (SW), Lac Lae Island (S): (2/6/1989, L 992.274-354)

MAURITIUS. (Melville, 1882, LD 22216 [lectotype *H. maculata*])

PAPUA NEW GUINEA. Bogia Bay: (Coppejans, 21/7/1988, HEC 7884); Hansa Bay, Barol Point: (Coppejans, 23/7/1980, HEC 4557; 1/7/1988, HEC 7649); Madang, D'Lole Island: (Coppejans, 4/8/1988, HEC 8063); Madang, Kranket Island: (Coppejans, 13/7/1990, HEC 13131B); Madang, Wongat Island: (Coppejans, 21/6/1988, HEC 7536); Port Moresby area, Motupore Island (S): (Coppejans, 20/7/1994, HEC 10174)

PHILIPPINES. Luzon, Sorsogon, Bulusan: (Leliaert et al., 16/8/1998, PH 290); Luzon, Sorsogon, Gubat: (Leliaert et al., 17/8/1998, PH 327, PH 339); Mindanao, Zamboanga City: (Leliaert et al., 22/8/1998, PH 419, PH 421, PH 446)

VIETNAM. Nhatrang, Cau Da Wharf: (17/3/1953, L 961.176-439)

Halymenia porphyraeformis

INDIA. Gujarat, Okha: (Børgesen, 23/1/1928, C FB 5490 [holotype *H. porphyraeformis*])

INDONESIA. Balikpapan: (Weber-van Bosse, 1899, L 941.97-484); Jedan Island, Aru: (Weber-van Bosse, 1899, L 941.97-500); Sulawesi (SW), Lac Lae Island (S): (Weber-van Bosse, 2/6/1989, L 992.274-122); Sulawesi (SW), Kayagan Island: (9/1991, L 993.114-286)

PAPUA NEW GUINEA. Hansa Bay, Barol Point Reef: (Coppejans, 23/7/1980, HEC 4561)

PHILIPPINES. Bohol, Panglao Island, Danis: (Leliaert et al., 10/8/1998, PH 100); Luzon, Sorsogon, Bulusan, Dapdap: (Coppejans, 22/4/1998, HEC 12326); Luzon, Sorsogon, Gubat: (Leliaert et al., 17/8/1998, PH 335); Mindanao, Santa Cruz: (Leliaert et al., 24/8/1998, PH 532); Mindanao, Zamboanga City: (Leliaert et al., 21/8/1998, PH 380, PH 384, PH 412; 22/8/1998, PH 418; 25/8/1998, PH 540)

Results

Halymenia durvillei Bory de Saint-Vincent, 1828: 180-181, Pl. 15 (as *H. durvillaei*). Kützting (1866: 33, Pl. 91: Figs g, h, as *H. formosa*; 33, Pl. 93: Figs a,b, as *H. ceylanica*); Weber-van Bosse (1921: 232-237, Pl. 8: Figs 1,2, incl. varieties and formas); Børgesen (1932: 124-125, Fig. 11, Pl. 5, as *H. venusta*); Cribb (1983: 54-55, Pl. 12, Fig. 1); Calumpang & Meñez (1997: 169, Fig. 170); Trono (1997: 185, Fig. 118); Abbott (1999: 146, Figs 34F-G, as *H. formosa*); Coppejans & Millar (2000: 320)

Lectotype: Port Praslin, New Ireland, Papua New Guinea (leg. Dumont d'Urville, 1825, PC TA33701).

Synonyms:

Mesogloia microcarpa Montagne, 1844: 660.

Holotype: Phillipines (Leg. Cuming, Cuming 2221 [= PC MA 8966])

Halymenia ceylanica Harvey ex Kützting, 1866: 33, Pl. 93, Figs a,b.

Holotype: Sri Lanka (Leg. Harvey, 1853, MEL 503874).

Halymenia formosa Harvey ex Kützting, 1866: 33, Pl. 91, Figs g,h.

Holotype: Tonga (Leg. Harvey, 1855, L 941.61-8).

Sebdenia ceylanica (Harvey ex Kützting) Heydrich, 1892: 477-480.

Halymenia microcarpa (Montagne) P. Silva, in Silva et al. 1987: 31.

Halymenia durvillei Bory de Saint-Vincent var. *ceylanica* (Harvey ex Kützting) Weber-van Bosse, 1921: 235.

Halymenia durvillei Bory de Saint-Vincent var. *formosa* (Harvey ex Kützting) Weber-van Bosse, 1921: 235.

Halymenia durvillei Bory de Saint-Vincent var. *denudata* Weber-van Bosse, 1921: 236.

Holotype: Indonesia, Borneo Bank, Sabankatan Reef (Leg. Weber-van Bosse, x. 1888, L 941.97-492).

Halymenia durvillei Bory de Saint-Vincent var. *edentata* Weber-van Bosse, 1921: 236, Pl. 8, Fig. 2. Holotype: Indonesia, Celebes, Paré-Paré, (Leg. Weber-van Bosse, x.1888, L 941.97-494).

Halymenia venusta Børgesen, 1932: 124-125, Fig. 11, Pl. V.

Holotype: India, Gujarat, Dwarka, (Leg. Børgesen, 21.i.1928, C FB5394).

Note: According to Silva et al. (1996) the epithet *durvillaei* is correctable to *durvillei* in accordance with Rec. 60C.1(c) enforced by Art. 60.11. of the ICBN (Greuter et al. 2000).

Description: (Figs 1-6)

Thallus epilithic, erect, up to 42 cm long, flattened, generally abundantly branched up to 7 orders, axes either flat or contorted and up to 5.4 cm wide, gradually tapering towards the apices; branching mainly marginal, but secondary axes often arising as proliferations on the surface of the primary axes; colour even dark pink to red; substance supple, cartilaginous with slippery surface; margins rarely smooth, generally

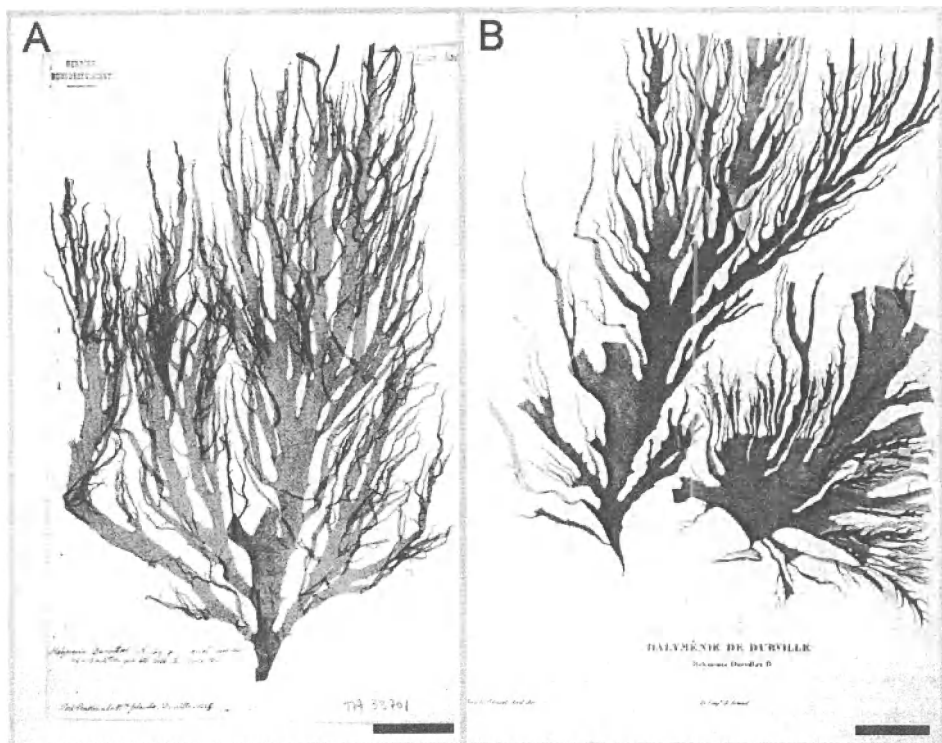


Fig. 1. Type of *Halymenia durvillei*. A. Lectotype of *H. durvillei* (PC, TA 33701); B. Original illustration of the lectotype specimen and an isolectotype (PC, TA 33700) by Bory de Saint-Vincent (1828: Pl. 15). Scale bars = 5 cm.

dentate or laciniate; stipe unbranched, (0,5-) 5,5 (-14) mm long and (1-) 3 (-6) mm in diameter, bearing mostly one or sometimes a few principal axes; thallus surface smooth in young plants, becoming covered with spiny proliferations in older thalli; blade (370-) 710 (-1625) μm thick; cortex (50-) 80 (-100) μm with 6-8 cells forming anticlinal rows, differentiated into an outer cortex [2-3 (-4) cell layers] and inner cortex [(3-) 4-5 (-6) cell layers], outer cortex cells subspherical to elongated (3-4 times as long as wide), (8-) 13 (-19) μm long in cross section; inner cortical cells rounded to stellate, (11-) 16 (-25) μm in diameter; medulla lax, (185-) 530 (-1250) μm thick, medullary filaments mainly anticlinally arranged, (4-) 9 (-16) μm in diameter; refractive ganglionic cells relatively abundant, irregularly shaped, arms branched and connected with each other under the inner cortex, diameter (25-) 40 (-65) μm , (6-) 8 (-9) arms (Fig. 6); stipe composed of a distinct cortex and medulla with a compact layer of spherical cells (20-30 μm in diameter) separating cortex from medulla, the cortex consisting of more or less anticlinal rows of relatively small irregular cells (12-20 μm in diameter), the medulla lax with mainly longitudinal and some anticlinal filaments in a matrix (Fig. 6).

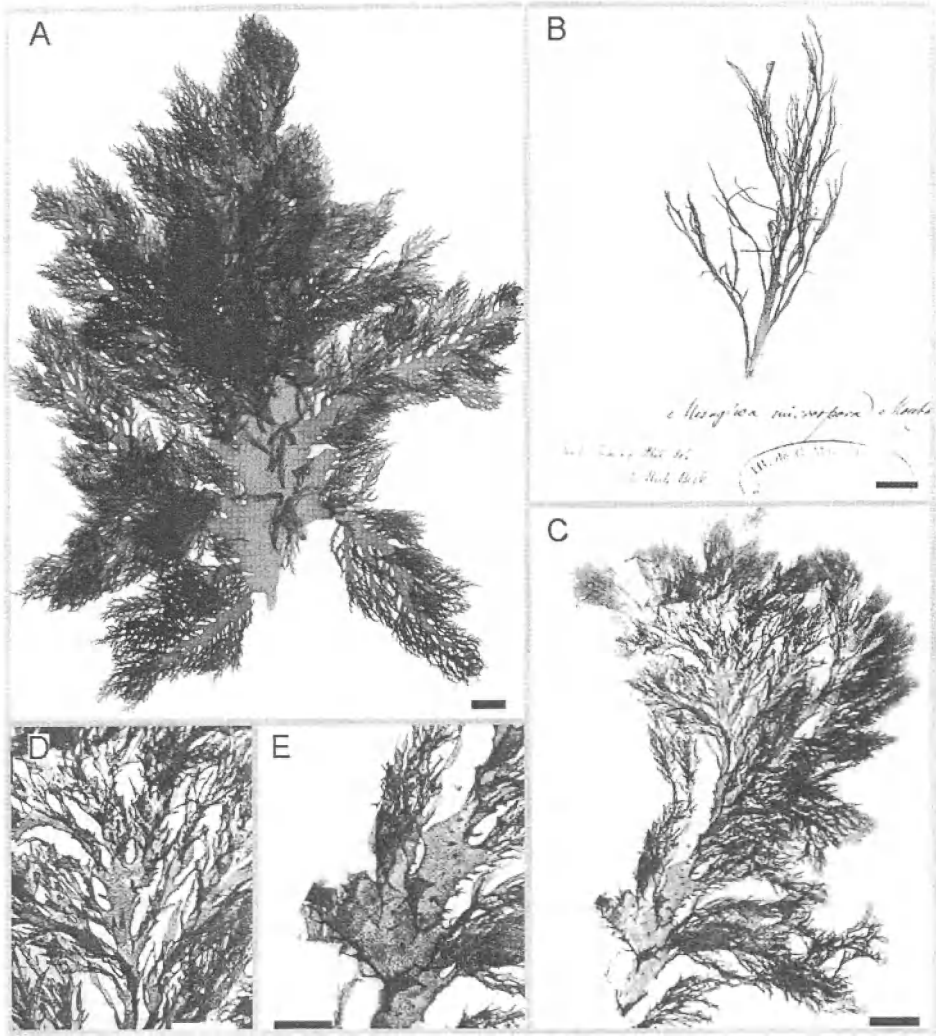


Fig. 2. Type specimens of species, now in synonymy with *Halymenia durvillei*. A. Holotype of *H. venusta* (C FB 5394). Scale bar = 1 cm. B. Holotype of *H. microcarpa* (PC MA 8966). Scale bar = 1 cm. C. Isotype of *H. ceylanica* (TCD 39). D. Detail of branching of C. Scale bar = 5 cm. E. Detail surface with spines of C. Scale bar = 5 cm.

Tetrasporangia scattered over the thallus, cut off from cells below the surface cells, decussate, approx. 17 μm long and 14 μm wide. Spermatangial sori scattered over the thallus surface, 1-2 spermatangia cut off from each fertile surface cell; carpogonial ampullae formed in the inner cortex, carpogonial branches 2-celled, surrounded by a few secondary ampullary filaments; auxiliary cell ampullae formed in the inner

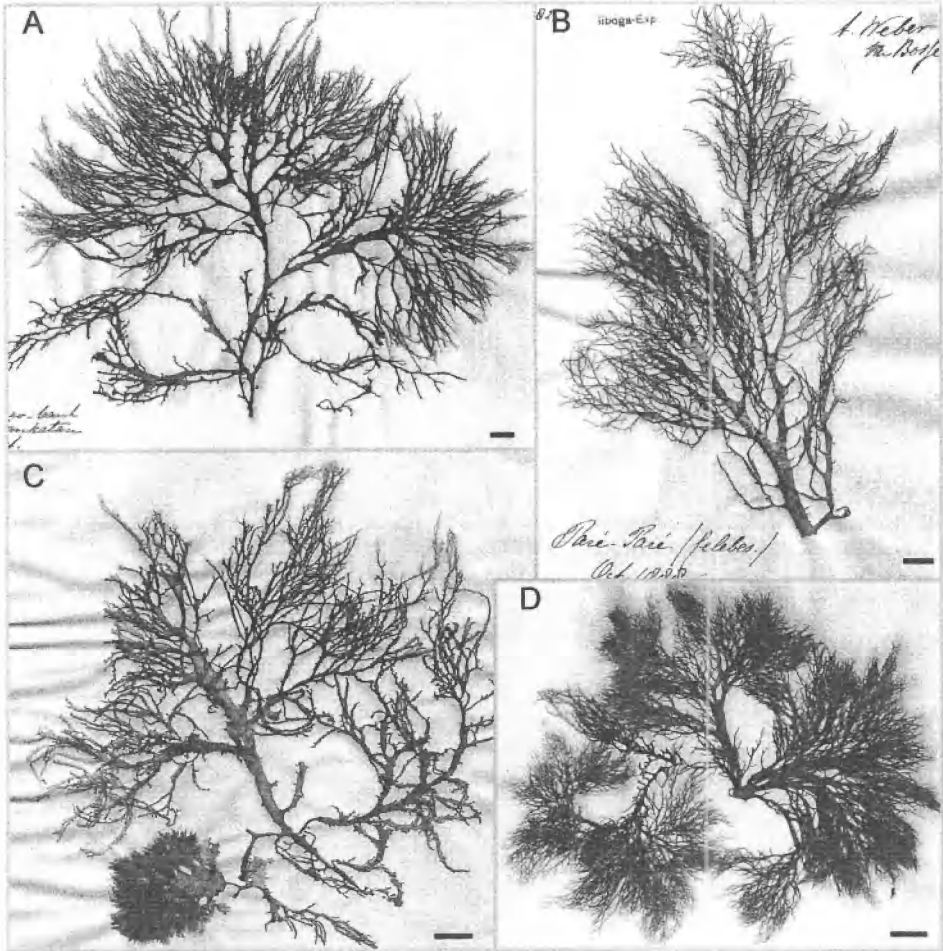


Fig. 3. *Halymenia* specimens of the Weber-van Bosse collection (L). A. *H. durvillei* var. *ceylanica* (L 941.27-183); B. Holotype of *H. durvillei* var. *edentata* (L 941.97-494); C. Holotype of *H. durvillei* var. *denudata* (L 941.97-492); D. Holotype of *H. formosa* (L 941.61-8). Scale bars = 1 cm

cortex, basal cells of the primary ampullary filaments small and elongated from which 1 or 2 secondary ampullary filaments originate that are simple or branched up to third order, auxiliary cell the basal cell of a secondary ampullary filament, approx. 11 μm in diameter; carposporophyte consisting of a few sterile filaments surrounding the gonimoblast. Carpospores irregularly rounded, approx. 12 μm in diameter, released through an ostiole.

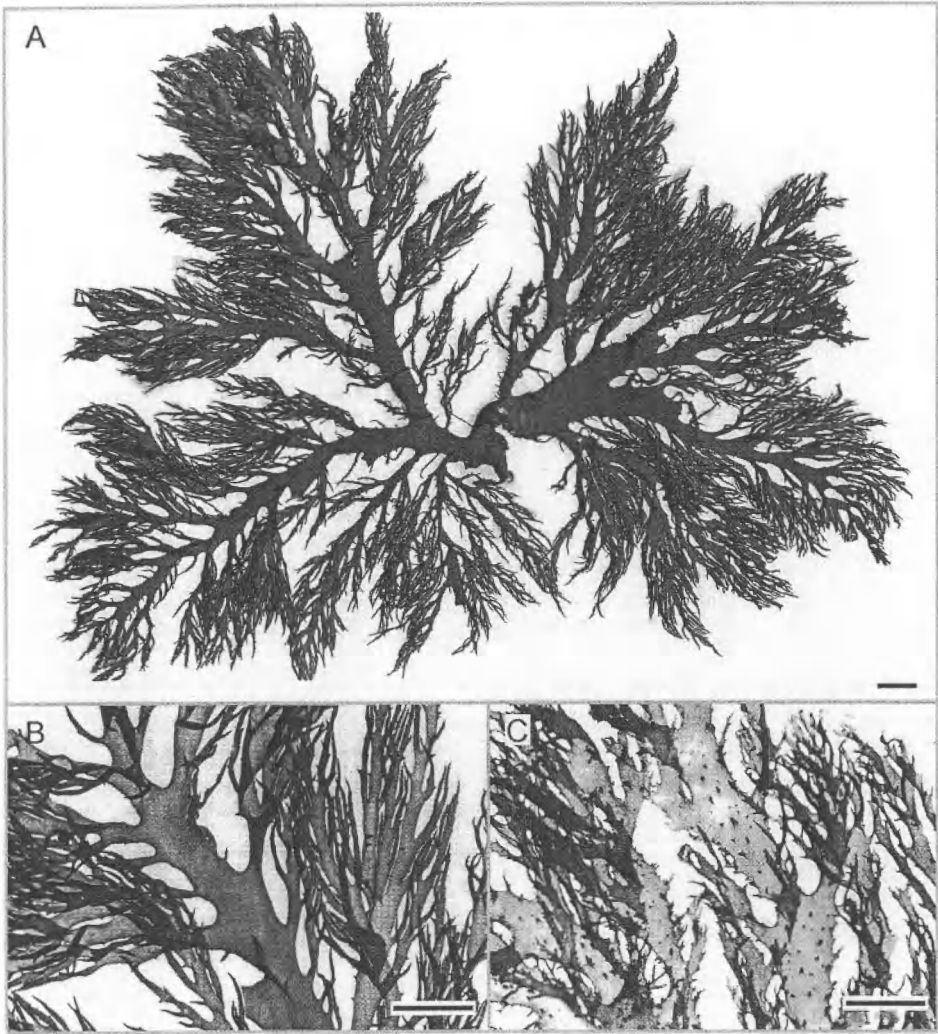


Fig. 4. Philippine specimens of *Halymenia durvillei*: A. Habit (PH 432); B. Detail showing smooth surface (PH 432); C. Detail showing surface with spines (HEC 12287). Scale bars = 1 cm

Remarks:

H. durvillei is a very common species in the Indian and West-Pacific Ocean, characterised by its branched thallus, multiple surface proliferations, supple cartilaginous structure and evenly coloured thallus surface. Despite its distinctive morphology, the taxonomic history of *H. durvillei* is long and confusing, which can probably be attributed to the rather variable external morphology (degree of branching, thallus width, and degree of dentation). The species was originally described and illustrated from New Ireland, Papua New Guinea (Bory de Saint-Vincent, 1828: 180-181,

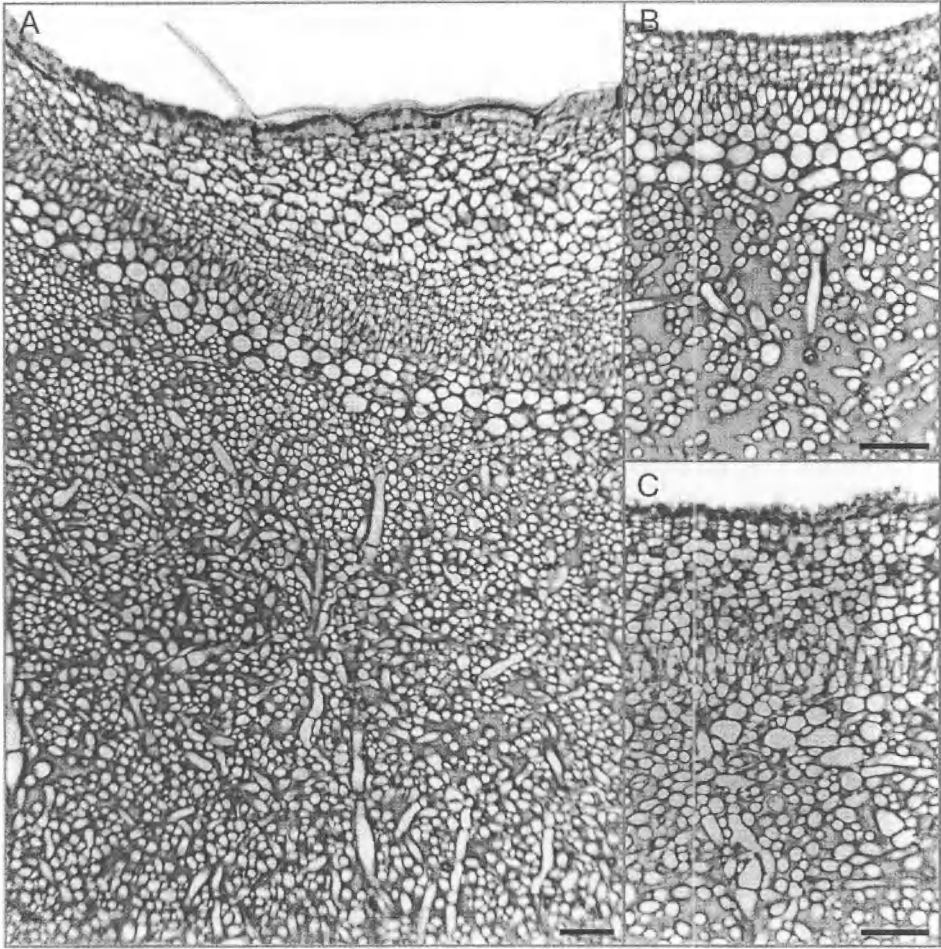


Fig. 5. Anatomy of the stipe of *Halymenia durvillei*. A. Overall view of the cross-section of a stipe; B. Detail of the cross- and C. longitudinal section of a stipe showing a cortex with radially arranged rows of cells, transition zone with spherical cells and a medulla with mainly longitudinally oriented filaments. Scale bars = 50 μm

Pl. 15) (Figs 1A,B). Montagne (1844) subsequently described *Mesogloia microcarpa* based on a specimen collected by Cuming in the Philippines. This species was transferred to *Halymenia* by Silva (in Silva et al. 1987). The holotype is the apical, narrow part of a thallus (Fig. 2B) which is morphologically consistent with *H. durvillei*. Grunow (1874) originally proposed the synonymy of *H. ceylanica* Harvey ex Kützing with *M. microcarpa*. *H. ceylanica* was part of Harvey's Ceylon exsiccata (1857a: n°39), formally described by Kützing (1866). Heydrich (1892) treated it as a *Sebdenia*, but investigation of the isotype (Figs 2C-E), as well as some fertile

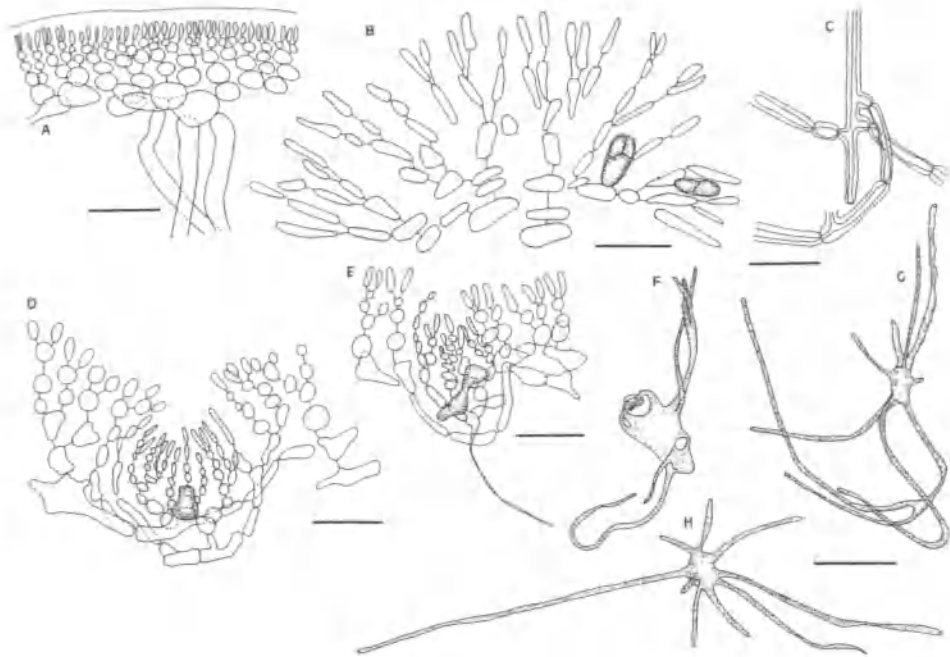


Fig. 6. Anatomy of the thallus of *Halymenia durvillei*: A. Cross-section of the mid-region of a thallus showing a 4-5 cell-layered outer cortex, 2(-3) cell-layered inner cortex and anticlinally oriented medullary filaments (PH 326). Scale bar = 50 μ m. B. Decussate tetrasporocysts cut off from intercalary cortical cells (L 941.27-183). Scale bar = 25 μ m. C. Primary and secondary pit-connections in medullary filaments (PH 541). Scale bar = 50 μ m. D, E. Auxiliary cell-ampullae with involucrel auxiliary cell-filaments (PH 416). Scale bar = 25 μ m. F, G, H. Refractive ganglionic cells irregularly shaped, arms branched (f: TCD 39, g: PH 541; h: L 383784). Scale bar = 50 μ m.

specimens from close to the type locality (HEC 11804 and HEC 11552) reject this possibility. The presence of carpogonial and auxiliary ampullae, the presence of a 2-celled carpogonial branch, the overall medullary structure and the absence of gland cells preclude a placement in the genus *Sebdenia*. *H. formosa* Harvey ex Kützing, another specimen collected by Harvey, should also be considered synonymous with *H. durvillei*. It was distributed in Harvey's Friendly Island exsiccata (1857b: n°55), and formally published by Kützing (1866) (Fig. 3D). Weber-van Bosse (1921) noticed the similarities between *H. durvillei*, *H. ceylanica* and *H. formosa*, and reduced the latter two to varieties of *H. durvillei* as *H. durvillei* var. *ceylanica* and *H. durvillei* var. *formosa*. Weber-van Bosse also described two new varieties *H. durvillei* var. *edentata* (Fig. 3B) and *H. durvillei* var. *denudata* (Fig. 3C).

Børgesen (1932) described an additional species, *H. venusta* from Dwarka, India (Fig. 2A), which is also consistent in morphology with *H. durvillei*. Lawson (1980) considered that all records of *H. formosa* from the East African coast belonged to *H.*

Table 1. Comparison of measurements of the Philippine specimens with type-material of *H. durvillei*-like species

	<i>H. durvillei</i> Philippines	<i>H. durvillei</i> var. <i>denudata</i> ISOTYPE L 941.312-310	<i>H. durvillei</i> var. <i>edentata</i> HOLOTYPE L 941.97-494	<i>H. ceylanica</i> ISOTYPE TCD 39	<i>H. formosa</i> HOLOTYPE L 941.61-8	<i>H. microcarpa</i> HOLOTYPE PC MA 8966	<i>H. venusta</i> HOLOTYPE FB 5394
BLADE							
length (mm)	(180-)301(-420)	170	190	230	169	92	300
width main axis (mm)	(12-)21.8(-54)	3	5	7	24	2.5	20
width secondary axis (mm)	(4-)8.7(-15)	3	2	4	10.5	1	8
thickness (µm)	(163-)447,3(-610)			515	432	242	
habit	branched up to 7th order, secondary branches arising from surface and margin, axes <i>contort</i> or straight	branching up to 6th order	branching up to 6th order	branching up to 4th order	branching palmate	branching up to 6th order	branching up to 4th order
structure surface	soft to firmly gelatinous smooth or besel with protractions, spines, bladelets	gelatinous smooth	gelatinous smooth	gelatinous smooth with some bladelets	gelatinous spines, proliferations	gelatinous smooth	gelatinous smooth with some bladelets arising from the surface
margin	smooth	smooth	smooth	smooth	smooth	smooth	smooth
colour	pink to brown	pink	pink	pinkish brown	pink	pink	pink
STIPE		not observed	not observed	not observed		not observed	not observed
diameter (mm)	(2-)3,4(-6)				1		
length (mm)	(0.5-)5,4(-14)				4		
CORTEX							
thickness OutCo (µm)	(15-)24(-38)	63	25	30	28	43	17.5
thickness InnCo (µm)	(42-)81(-75)	38	75	45	42	15	35
total thickness Co (µm)	(61-)85,3(-100)	100	100	75	70	58	53
cell-layers OutCo	2-3(-5)	5	2	2-3	2	3	2
cell-layers InnCo	(3-)4-5(-8)	3	5	3	3-4	2	3
shape surface-cells	subspherical to elongated	elongated	elongated	elongated	subspherical	elongated	subspherical
length surface-cells (µm)	(7.9-)12,2(-15,8)	16	15	10	13.5	17.5	10
diameter InnCo-cells (µm)	(11,2)16,5(25)	14.4	16	22	19	9.5	20
density (#surf.cells/100µm)		14	30		21		
MEDULLA							
thickness (µm)	(248-)494,9(-1250)			320	320	130	
diameter med.fil.	(4-)15,9(-15,6)	9.6	7.2	11	10	10	7.5
REFRACTIVE GLANGLIONIC CELLS							
diameter (µm)	(23-)39,4(-64)	58	27	54	34	25	49
# arms	(6-)7-9(-9)	5-6	6	7	5-6	4	7
shape	irregular (star- to cophioid shaped, arms branched or not, connected under InnCo or not)	irregular	irregular	arms branched, starshaped	irregular, few, connected under InnCo	irregular	irregular

OutCo= outer cortex, InnCo= inner cortex, # = number

venusta, but failed to point out the differences between both taxa. In this study, type material and several collections from the entire Indo-Pacific were studied and no differences that warrant recognition on the species level could be detected among the many specimens (Table 1). Hence it is concluded that only a single species of branched *Halymenia*, *H. durvillei*, is present in the study area. The recognition of several varieties and formas as suggested by Weber-van Bosse (1921) seems needless to us since all possible growth forms fall within the morphological range of recently collected specimens and continuous intergrades between the most extreme growth forms are frequently found (sometimes even within a single specimen).

Halymenia durvillei seems to be very similar to *H. floresia* (Clemente y Rubio) C. Agardh. The latter species is originally described from the Mediterranean Sea and has subsequently been reported from most tropical and numerous warm temperate regions (including Indian Ocean, Pacific Ocean, and Caribbean Sea). Examination of the type collection (MA) and numerous additional collections of *H. floresia* from the Mediterranean Sea (GENT) reveals that *H. floresia* is characterised by a more regularly branched thallus, the near absence of surface proliferations, and a thinner cortex. The branching pattern of *H. floresia* is typically pinnate with up to 3-4 orders of branching. In comparison, the branching pattern of *H. durvillei* is more irregular with often more than 5 orders of branching. The thallus surface of *H. floresia* is smooth; only occasionally a single tooth (or surface leaflet) is present. In the majority of *H. durvillei* specimens the thallus surface is beset with prominent acute teeth. Some specimens, presumably young ones, however, are characterised by a smooth thallus surface. The cortex anatomy also differs markedly between *H. floresia* and *H. durvillei*, up to 3-4 layers thick versus more than 6 layers thick respectively. *H. floresia* has repeatedly been reported from the Indo-Pacific region (see J.A. Lewis 1984; Silva et al. 1987; Silva et al. 1996). During the present study, however, no specimens were encountered with a typical *H. floresia* morphology as observed in the Mediterranean collections. *H. floresia* subsp. *harveyana* (J. Agardh) Womersley & J.A. Lewis (1994) is described from southern Australia. This subspecies resembles *H. floresia* somewhat in external morphology and anatomy, but is more profusely branched and has a thicker thallus. The main difference with genuine *H. floresia* is situated in the reproductive anatomy of which bisporangia appear to be the only means of reproduction (Womersley & J.A. Lewis 1994). The relationship with *H. floresia* subsp. *floresia*, however, needs further study.

Halymenia dilatata Zanardini, 1851: 35

Zanardini (1858: 280, Pl. 5: Fig. 1); Okamura (1921: 109-110, Pl. CLXXVI: Figs 1-4; Pl. CLXXVII, Figs 3, 4); Balakrishnan (1961: 197-202, Figs 20-27); Norris & Aken (1985: 56, Figs 1, 2)

Lectotype: Red Sea (leg. Portier, Museo Civico di Storia Naturale, Venezia, s.n.).

Synonym: *Sebdenia dilatata* (Zanardini) De Toni, 1900: 531

Description: (Figs 7-8)

Thallus epilithic, erect, foliose, lamina irregular in outline, up to 80 cm long and 50 cm wide; surface of the lamina smooth, with small orbicular proliferations; structure supple, cartilaginous; colour dark pink to reddish with darker spots; margins smooth or minutely dentate; stipe bearing a single lamina, unbranched; lamina (285-) 340 (-400) μm thick; cortex (35-) 40 (-50) μm thick, composed of (4-) 6 (-7) cell-layers in anticlinal rows, differentiated into an outer cortex (2-3 (-4) cell-layers) and an inner cortex (2-3 cell-layers); surface cells subspherical in cross-section (< 3x as long as wide), (6.5-) 8.5 (-11) μm long; inner cortical cells irregularly stellate and somewhat tangentially flattened, (9.5-) 12.5 (-15) μm in diameter; medulla (200-) 230 (-300) μm thick, relatively lax, medullary filaments nearly all anticlinally oriented, (3-) 4 (-6) μm in diameter; refractive ganglionic cells common but not abundant, (15-) 40 (-60) μm in diameter, mostly with 6 arms. Tetrasporangia scattered over the thallus, cut off from cells subtending the surface cells, decussate, approx. 18 μm long and 15 μm wide. Spermatangial sori scattered over the thallus surface, 1-2 spermatangia cut off from each fertile surface cell. Carpogonial ampullae formed in the inner cortex, carpogonial branches 2-celled, surrounded by a few secondary ampullary filaments; auxiliary cell ampullae formed in the inner cortex, basal cells of the primary ampullary filaments small and elongated from which 1 or 2 secondary ampullary filaments originate that are simple or branched up to the third order, auxiliary cell the basal cell of a secondary ampullary filament, approx. 17 μm in diameter; carposporophyte consisting of a few sterile filaments surrounding the gonimoblast. Carpospores irregularly rounded, approx. 14 μm in diameter, released through an ostiole.

Remarks:

The specimens from the Philippines (Figs 7B,C) agree in all aspects with the lectotype of *H. dilatata* (Fig. 7A). Characteristics which distinguish the species from other soft gelatinous to cartilaginous foliose species are the discoidal holdfast bearing a relatively small stipe, the brownish spots on the brightly coloured thallus surface, and the minute teeth which often form a fringed margin (Fig. 7D). Examination of a Weber-van Bosse specimen (1921) from Indonesia, identified as *H. ulvoidea* Zanardini [non *H. ulvoidea* (Sonder) Kützing (= *Gelinaria ulvoidea* Sonder)], reveals it to be extremely similar to our *H. dilatata* specimens. Cribb (1961) reported on 2 specimens collected from Thursday Island, Queensland, which he identified as *H. ulvoidea* referring to the Siboga-material of Weber-van Bosse. He questioned, however, the conspecificity of the western Pacific specimens with the Mediterranean *H. ulvoidea*. The latter was reduced to a variety of *H. floresia* by Codomier (1974). It should be noted, however, that *H. ulvoidea* was described as a foliose plant and Codomier illustrates it as a foliose variety of *H. floresia*. Further research is necessary to clarify the status of the former. The specimens reported by both Weber-van Bosse and Cribb differ clearly from the Mediterranean *H. floresia* by their foliose habit rather than the typically branched thallus. Assigning them conclusively, however, to *H. dilatata* is difficult because of the absence of wet material or slide preparations clearly showing the anatomical features.

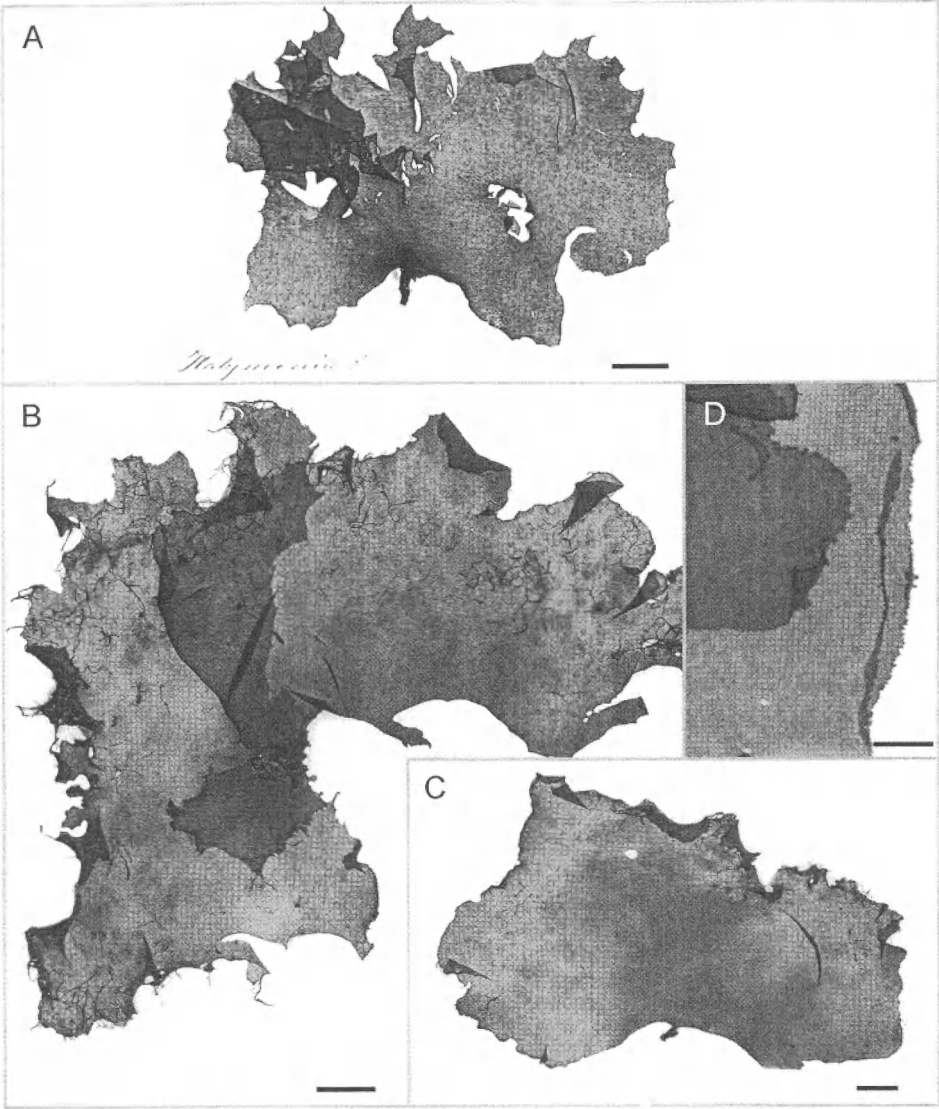


Fig. 7. Habits of *Halymenia dilatata*. A. Lectotype of *H. dilatata* (Red Sea, Zanardini 1851); B, C Habits Philippine specimens (B: PH 538; C: PH 539); D. Detail of the fringed margin (PH 288). Scale bars = 1 cm.



Fig. 8. Anatomy of the thallus *Halymenia dilatata* (PH 337): A. Cross-section of the mid-region of a thallus showing a 4 cell-layered outer cortex, 2 cell-layered inner cortex and anticlinally oriented medullary filaments; B. Auxiliary cell-ampullae with connecting filament reaching the auxiliary cell, auxiliary cell-filaments branched up to 4th order; C, D. Refractive ganglionic cells with 6 arms; E. Anomalous refractive ganglionic cell with 8 arms of which one branched. Scale bars = 50 µm.

***Halymenia maculata* J. Agardh, 1885: 12**

Børghesen (1950: 9-11, Figs 2, 3); Dawson (1954: 432, Fig. 44); Trono (1997: 187, Fig. 119)

Lectotype: Mauritius (Leg. Melville, 1882, LD 22216).

Description: (Figs 9-11)

Thallus epilithic, erect, foliose, circular to irregularly lobed, up to 21 cm long and 38 cm wide; surface mottled, often with proliferations, spines or small bladelets; texture cartilaginous with slippery surface; colour dark pink to reddish brown; margins irregularly to regularly lobed (like jig-saw pieces) or denticulate; stipe firm, 0.5-14 mm long and 1-4 mm in diameter mostly bearing a single blade; blade (270-) 330 (-450) µm thick; cortex (50-) 82 (-100) µm thick, composed of 5-7 cell-layers forming anticlinal rows differentiated into an outer cortex [2-3 (-4) cell layers] and inner cortex [(2-) 3-4 (-5) cell layers], surface cells (7.5-) 17 (-35) µm long and elongated on cross-section of the thallus (> 4x as long as wide); inner cortical cells rounded to

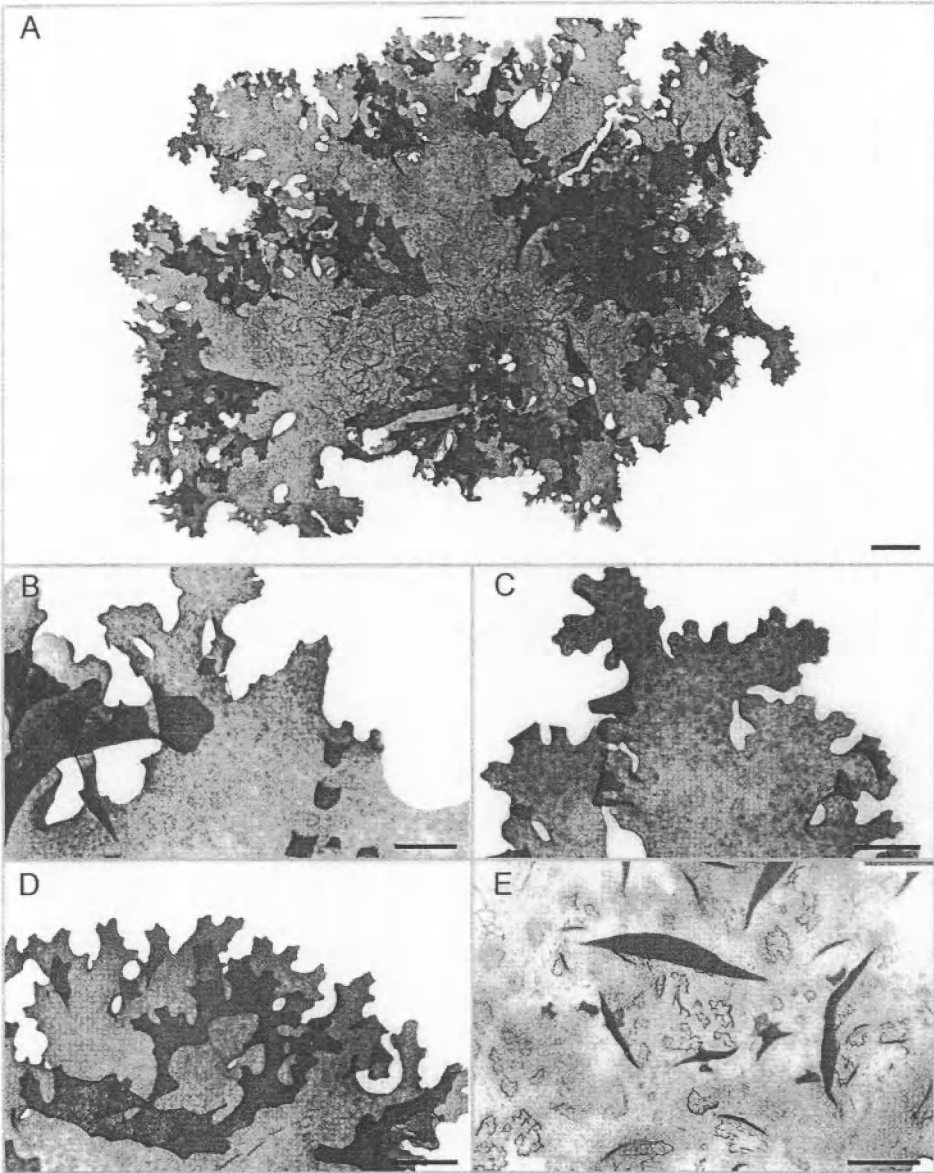
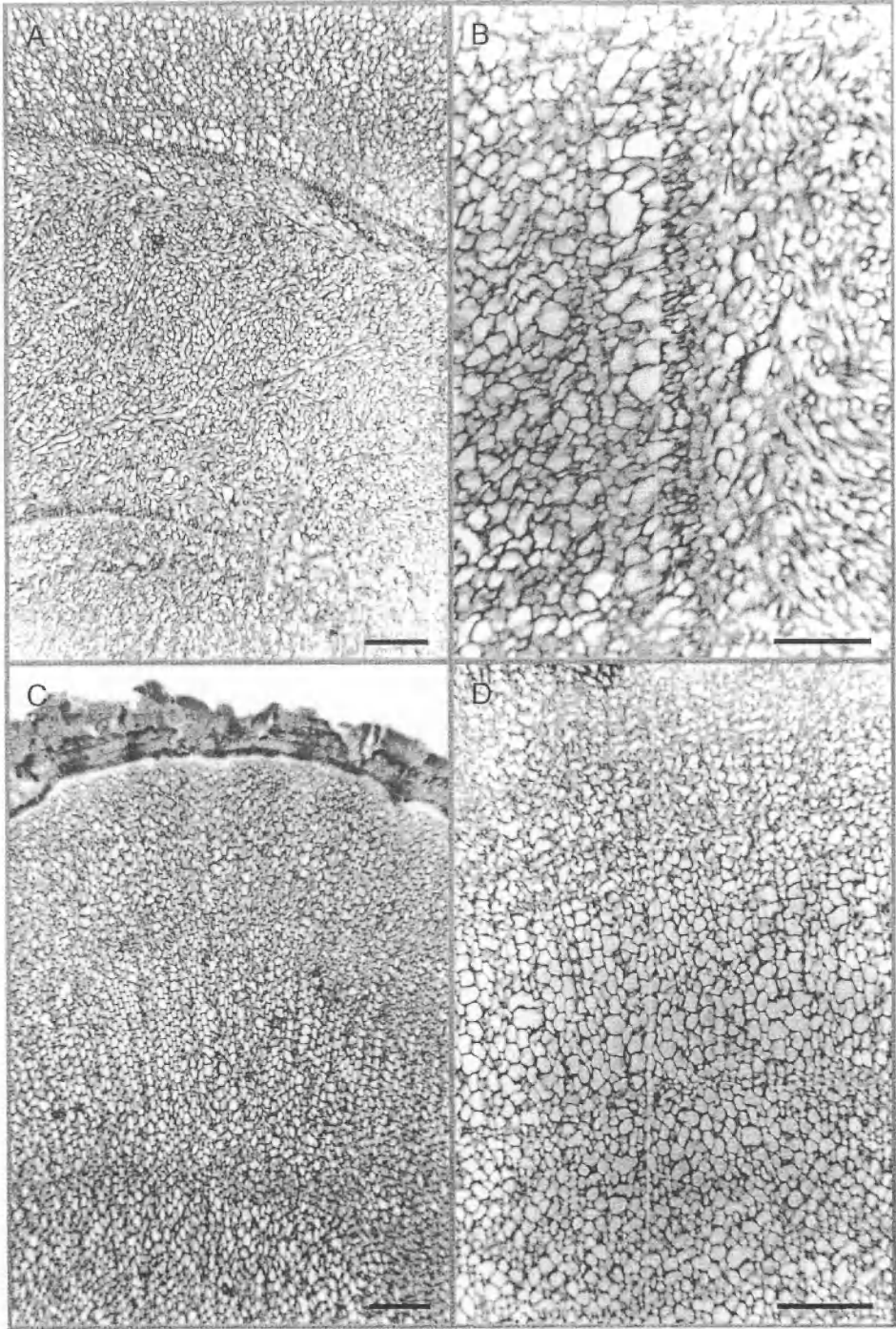


Fig. 9. Habit of *Halymenia maculata*. A. Philippine specimen (PH 339). Scale bar = 1 cm. B. Detail of surface with laminal proliferations (PH 422). Scale bar = 0.5 cm. C. Detail of spotted surface (PH 339). Scale bar = 0.5 cm. D. Detail of jig-saw-like margins (PH 396). Scale bar = 0.5 cm. E. Detail of surface proliferations (PH 419). Scale bar = 0.5 cm.



stellate, (11-) 20 (-33) μm in diameter; medulla (95-) 164 (-300) μm thick, medullary filaments sparse, mostly anticlinally oriented, (3-) 7 (-11.5) μm in diameter; refractive ganglionic cells irregularly shaped, connected with their branches under the inner cortex, (19-) 26 (-37) μm in diameter, (5-) 7 (-9) arms; stipe in cross section with a distinct cortex and medulla, cortex consisting of several zones of anticlinal rows of cells (14-30 μm in diameter) in which "growth-zones" of smaller cells (4-10 μm in diameter) are detectable, medulla dense with mainly longitudinal and some anticlinal filaments without an extensive matrix. Tetrasporangia scattered over the thallus, cut off from cells subtending the surface cells, decussate, approx. 27 μm long and 19 μm wide. Spermatangial sori scattered over the thallus surface, 1-2 spermatangia cut off from each fertile surface cell. Carpogonial ampullae formed in the inner cortex, carpogonial branches 2-celled, surrounded by a few secondary ampullary filaments; auxiliary cell ampullae formed in the inner cortex, basal cells of the primary ampullary filaments small and elongated from which 1 or 2 secondary ampullary filaments originate that are simple or branched up to the third order, auxiliary cell the basal cell of a secondary ampullary filament, approx. 14 μm in diameter; carposporophyte consisting of a few sterile filaments surrounding the gonimoblast. Carpospores irregularly rounded, 12-14 μm in diameter, released through an ostiole.

Remarks:

The main characteristics of *H. maculata* are the firm texture, jigsaw-like margins and rather rough surface due to the multiple proliferations, small spines or bumps (Fig. 9). Another typical character involves the radially elongated surface cells (>4x as long as wide) which always occur in pairs on a cortical cell (Fig. 10 a). This feature was referred to by Abbott (1996; 1998; 1999) as "rabbit-ears". The elongate shape of the outer cortical cells is, however, not restricted to *H. maculata*. *H. stipitata* Abbott (1998; 1999) is characterised by identical cortical cells, but differs from *H. maculata* in the nearly woody stipe, the smaller habit (only reaching 5-7 cm in height) and the less dissected margins. Some specimens from the Philippines and Papua New Guinea (PH 421, HEC 7649, HEC 8063, HEC 13131B), are morphologically very similar to *H. maculata*, but the stipes are noticeably firmer. Despite the stipe morphology which would relate these specimens to *H. stipitata*, the overall habit and heavily dissected margins point towards *H. maculata*. Further study is needed to clarify the presence of *H. stipitata* in the Indo-Malayan region. Another similar species is *H. jelinekii* Grunow (1867, Pl. 9, Fig. 2) described from the Nicobar Islands. This differs from *H. maculata* in its smaller habit (2 cm long, 2.5-3 cm wide), the elliptical shape of the lamina and the lobed margins beset with several branching hairy proliferations. *H. maculata* is larger (25 cm) with firm irregular lobes and small proliferations (Wynne, 1993).

Fig. 10. Anatomy of the stipe of *Halymenia maculata*. A. Overall view of the cross-section of a stipe (HEC 7649); B. Detail of the transition zone with spherical cells between medulla and cortex (HEC 7649); C. Cortex with growth zones in radially arranged rows of cells (HEC 7649); D. Detail of growth zones separated by 2-3 cell-layered zone of smaller cells (HEC 7536). Scale bars = 75 μm .

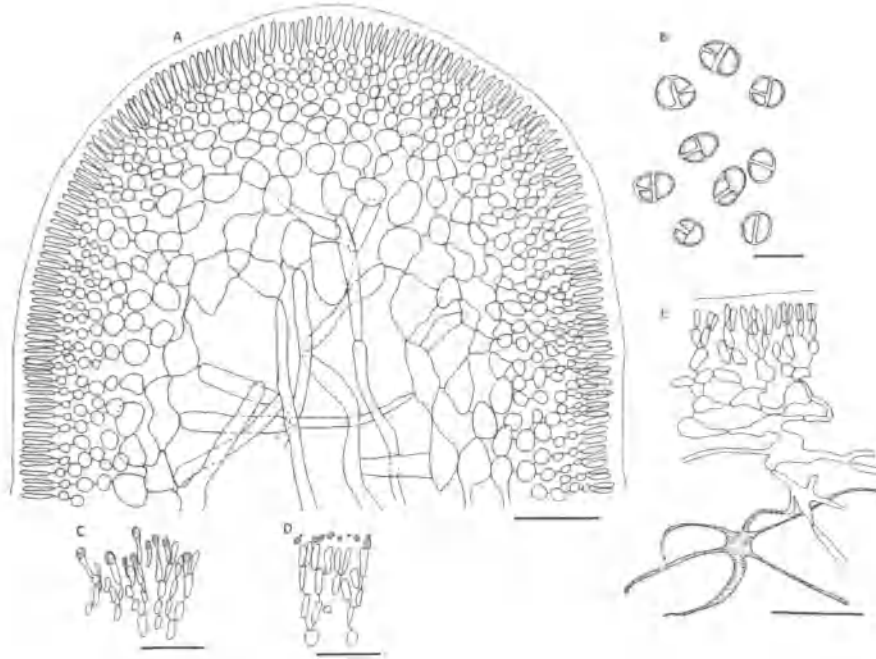


Fig. 11. Anatomy of the thallus of *Halymenia maculata*: A. Cross-section of the marginal region of a thallus showing a 4-5 cell-layered outer cortex, a 3-4 cell-layered inner cortex and medullary filaments (HEC 4557). Scale bar = 50 μ m. B. Decussate tetrasporocysts (HEC 7649). Scale bar = 25 μ m. C,D. Surface cells with enlarged distal ends forming spermatocysts (PH 419). Scale bar = 25 μ m. E. Cross-section of the mid-region of a thallus showing a 4 cell-layered outer cortex, a 3 cell-layered inner cortex and a refractive ganglionic cell connected to an inner cortex-cell (PH 446). Scale bar = 25 μ m.

H. dilatata differs from *H. maculata* by the thinner cortex (up to ca. 50 μ m thick), the minutely dentate margins, and the relatively smooth surface with only small proliferations. In *H. maculata* the cortex is up to 100 μ m thick and the surface is stronger mottled and beset with proliferations and outgrowths of various kinds. The margins in *H. maculata* may range from irregularly lobed to denticulate, but are never minutely dentate as in *H. dilatata*. *H. porphyraeformis* differs from *H. dilatata* in the smooth sinusoidally undulated margins and the absence of proliferations on the surface.

Halymenia porphyraeformis Parkinson, 1980: 17 ('as *H. porphyriaeformis*') Børgesen (1932: 120-122, Figs 8, 9, Pl. 2, as *H. porphyroides*); Balakrishnan (1961: 184-191, Figs 1-10, Pl. 6: Fig. 1, as *H. porphyroides*); Coppejans & Milar (2000: 321)

Holotype: India, Gujarat, Okha (Leg. Børgesen, 23.i.1928, C FB 5490).

Synonyms: *Halymenia porphyroides* Børgesen, 1932: 120-122, Figs 8, 9, Pl. III.

Note: We refer to Parkinson (1980) and Silva et al. (1996) for a detailed discussion of the nomenclature involving *H. porphyroides* Børgeesen and *H. porphyraeformis* Parkinson.

Description: (Figs 12-14)

Thallus epilithic, erect, foliose, blade irregularly circular to elliptical, up to 80 cm long and 50 cm wide; surface mostly smooth, rarely with orbicular proliferations; texture soft, very supple; colour pink, spotted with lighter patches; margins undulated, sinusoidal, forming secondary blades as a result of damage in older specimens; stipe unbranched, (0.5-) 2 (-3) mm long and (1-)1.5 (-2) mm wide, bearing a single blade; blade (65-) 260 (-410) μm thick; cortex (15-) 40 (-85) μm , composed of 4-6 cell-layers forming anticlinal rows, differentiated in an outer cortex (2-3 cell layers) and inner cortex (2-3 cell layers); surface cells subspherical to elongate ($< 3x$ as long as wide), (6-) 8.5(-10,5) μm long; inner cortical cells irregularly stellate, (9.5) 14.5 (-17.5) μm in diameter; medulla (40-) 170 (-310) μm thick, lax, all medullary filaments anticlinally arranged, (2-) 4.5 (-8.5) μm in diameter; refractive ganglionic cells asteroid, (21-) 27 (-40) μm in diameter, with (5-) 6 (-8) arms; stipe in cross section with a distinct cortex and medulla separated by a compact layer of spherical cells, cortex consisting of several zones of anticlinal rows of relatively smaller cells, medulla dense with mainly longitudinal and some anticlinal filaments without an extensive matrix. Tetrasporangia scattered over the thallus, cut off from cells below the surface cells, decussate, approx. 18 μm long and 12 μm wide. Spermatangial sori scattered over the thallus surface, 1-2 spermatangia cut off from each fertile surface cell. Carpogonial ampullae formed in the inner cortex, carpogonial branches 2-celled, surrounded by a few secondary ampullary filaments; auxiliary cell ampullae formed in inner cortex, basal cells of the primary ampullary filaments small and elongated from which 1 or 2 secondary ampullary filaments originate that are simple or branched up to the third order, auxiliary cell the basal cell of a secondary ampullary filament, approx. 16 μm in diameter; carposporophyte consisting of few sterile filaments surrounding the gonimoblast. Carpospores irregularly rounded, 12-14 μm in diameter, released through an ostiole.

Remarks:

The main characters defining *H. porphyraeformis* are its very supple cartilaginous structure, extremely slippery touch, orbicular to elliptical shape, smooth surface and sinusoidally undulated margins (Figs 12A,B). Despite these distinctive characters, the species appears to have been misidentified as *H. dilatata* Zanardini in the Philippines (Trono, 1997; Calumpong & Meñez, 1997). This latter species is, however, quite distinct in its firmer structure, rough surface with numerous proliferations and minutely dentate to fringed margins. *H. porphyraeformis* has not previously been reported for the area, though it seems to be quite common (collected from 6 of the 22 sites visited in the Philippines).

The western Pacific specimens match the holotype of *H. porphyraeformis* (C FB 5490) in all characters but colour. The holotype is even pink, whereas the specimens from the Philippines and Papua New Guinea (Coppejans & Millar, 2000) are slightly mottled (Figs 12A-F).

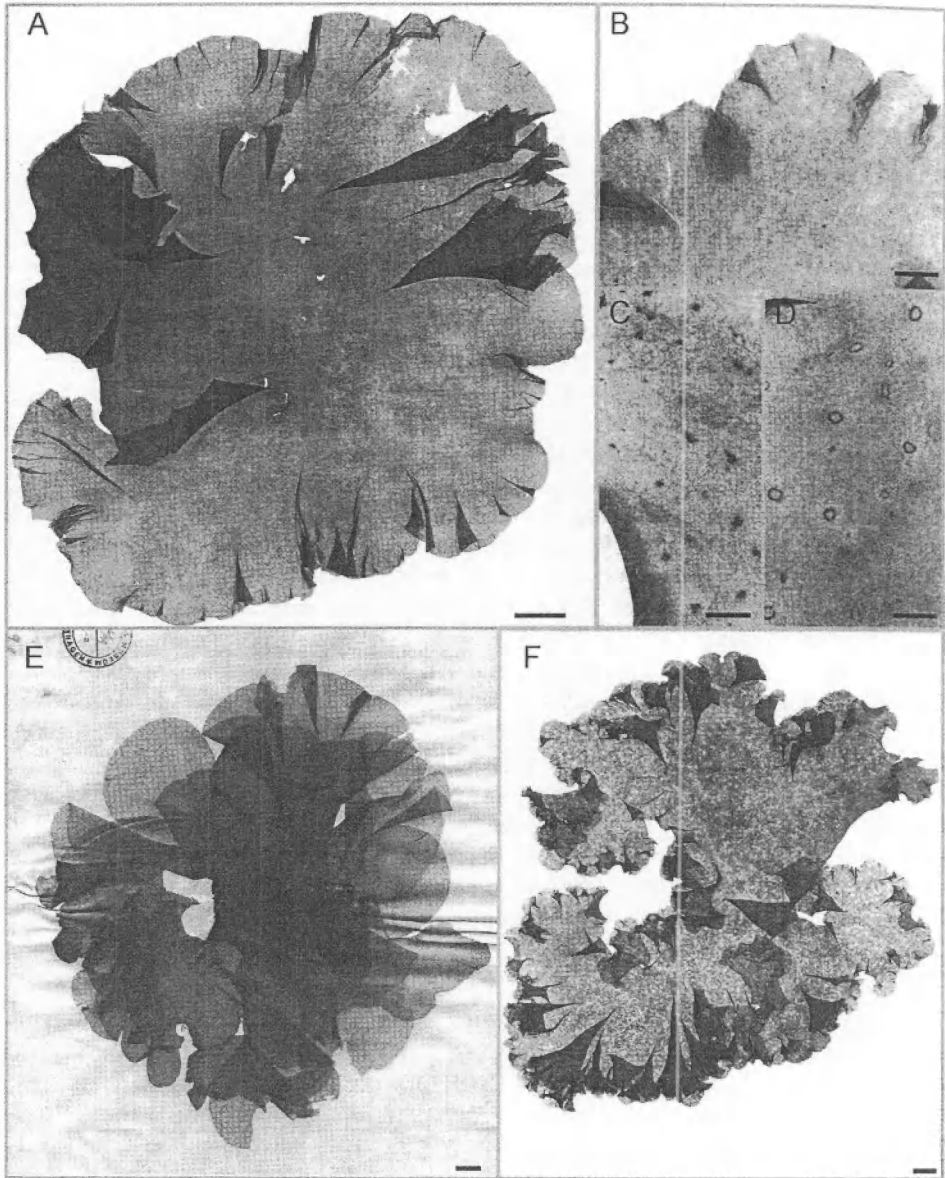


Fig. 12. Habit of *Halymenia porphyraeformis*. A. Philippine specimen (PH 540). Scale bar = 2 cm. B. Detail of the sinusoidally undulating margin (PH 335). Scale bar = 0.5 cm. C. Proliferations on surface of older specimen (PH 532). Scale bar = 0.5 cm. D. Circular proliferations on surface of older specimen (PH 532). Scale bar = 0.5 cm. E. Holotype of *H. porphyraeformis* (C FB 5490). Scale bar = 1 cm. F. Papua-New Guinean specimen (HEC 4561). Scale bar = 1 cm.

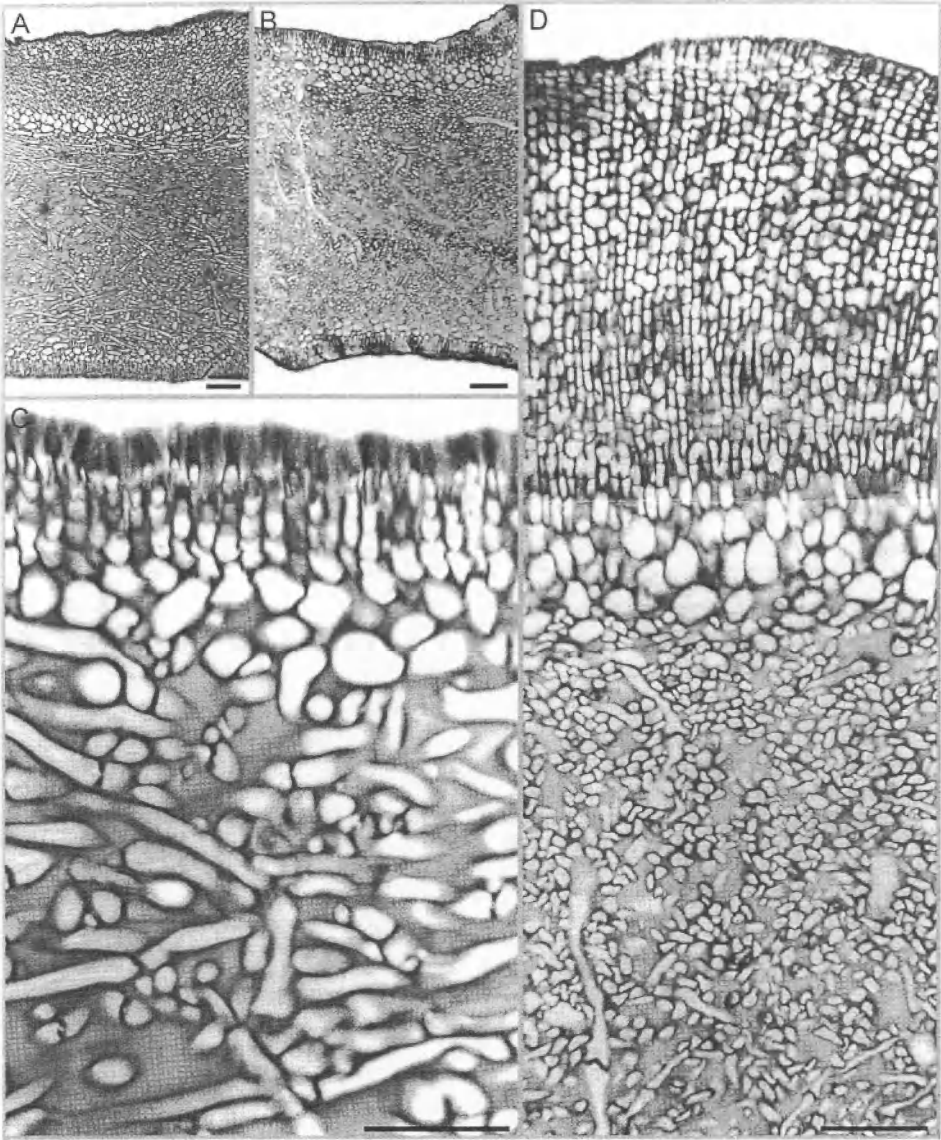


Fig. 13. Stipe anatomy of *Halymenia porphyraeformis* (PH 540). A. Overall view of a longitudinal- and B. cross-section of the stipe; C. Detail of a longitudinal- and D. cross-section of the stipe showing radially arranged rows of cortical cells, a transition zone with spherical cells and a medulla with mainly longitudinally oriented filaments. Scale bars = 100 μ m

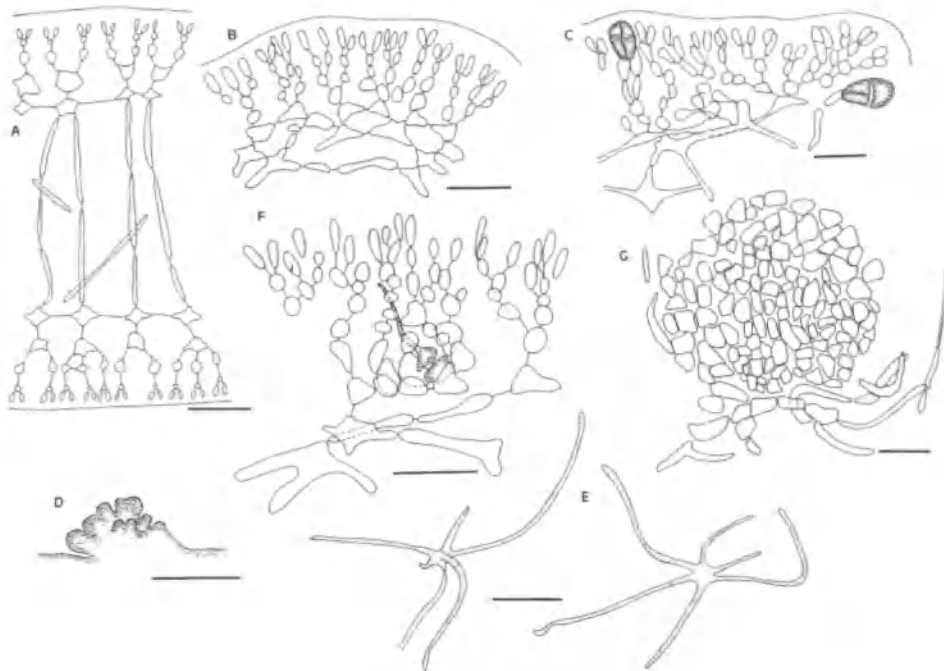


Fig. 14. Anatomy of the thallus of *Halymenia porphyraeformis*: A. Schematic cross-section of the mid-region of a thallus showing 3 cell-layered outer cortex, 2 cell-layered inner cortex and anticlinal medullary filaments connecting inner cortex to inner cortex (PH 335). Scale bar = 50 μ m. B. Cross-section of the cortex of a thallus with a 4 cell-layered outer cortex and 3 cell-layered inner cortex (PH 375). Scale bar = 20 μ m. C. Decussate tetrasporocysts cut off from cells below the thallus surface (PH 532). Scale bar = 20 μ m. D. Surface proliferation on older specimen (PH 532). Scale bar = 400 μ m. E. Refractive ganglionic cells with 6 arms (PH 532). Scale bar = 40 μ m. F. Carpogonial cell-ampulla with 2-celled carpogonial branch (PH 375). Scale bar = 20 μ m. G. Gonimoblast forming carpospores with involucrel filaments (PH 412). Scale bar = 20 μ m.

Key to the species

- 1.a. Thallus branched, blade surface smooth or with pointed proliferations or bladelets, not mottled; inner cortex > 3 cell layers and > 25 μ m thick; length of surface cells in cross section of the thallus > 8 μ m; medulla > 200 μ m thick..... *H. durvillei*
- 1.b. Thallus foliose, blade surface smooth or with rounded proliferations or mottled; inner cortex \leq 3 cell layers and \leq 25 μ m thick; medulla \leq 200 μ m thick..... 2
 - 2.a. Surface cells elongated on cross section (> 4 \times as long as wide); surface mottled, often with proliferations, spines or small bladelets; margins regularly lobed (like jig-saw pieces) or denticulate; thallus stiff, cartilaginous..... *H. maculata*
 - 2.b. Surface cells spherical to subspherical (< 3 \times as long as wide); surface smooth or with small proliferations; margins smooth or with minute teeth; thallus supple..... 3
- 3.a. Margins smooth, sinusoidally undulated; more or less orbiculate..... *H. porphyraeformis*
- 3.b. Margins smooth or with minute teeth; blade irregular in outline..... *H. dilatata*

Discussion

A total of 9 species (including synonyms) of *Halymenia* have been reported from the Malayan region (Table 2). Some of these taxa are only poorly known. *H. japonica* reported from the Philippines by Domantay (1968), is probably a nomen nudum as no original description has ever been found (Silva et al. 1987). Seven other taxa of *Halymenia* have been reported for the Philippines: *H. dilatata* Zanardini, *H. durvillei* Bory de Saint-Vincent, *H. formosa* Harvey ex Kützing, *H. microcarpa* Montagne, *H. floresia* (Clemente y Rubio) C. Agardh, *H. floresia* subsp. *harveyana* (J. Agardh) Womersley & J.A. Lewis, and *H. maculata* J. Agardh (Silva et al. 1987). Of these taxa, *H. formosa* and *H. microcarpa* are considered to be synonymous with *H. durvillei*.

The presence of *H. floresia*, originally described from the Mediterranean Sea, is in need of critical re-examination. The type specimen in MA and specimens from the Mediterranean Sea housed in GENT, L and PC, are generally branched up to 2-3(-4) orders, have an evenly coloured pink surface without surface proliferations. Specimens attributed to *H. floresia* from Papua New Guinea (Coppejans & Millar 2000) and to *H. floresia* subsp. *harveyana* from Australia (Womersley & J.A. Lewis 1994) are more profusely branched. Furthermore, the specimens from Papua New Guinea were characterised by a spotted surface, a character not observed among Mediterranean (pers. obs.) and Australian populations of *H. floresia*. The conspecificity of Mediterranean and Indo-Pacific populations of *H. floresia* remains to be determined. Some specimens from the post-congress excursion for the 16th International Seaweed Symposium in Cebu (April 1998) in Bulusan (Kraft et al. 1999) were identified as *H. floresia*, but after careful examination proved to belong to *Grateloupia acuminata* Holmes (HEC 12276, HEC 12324, HEC 12325), others belong to the genus *Cryptonemia* (most probably an undescribed species) (HEC 12287b, HEC 12337). The occurrence of legitimate *H. floresia* remains to be confirmed.

Weber-van Bosse (1921, 1926) reported 11 species from Indonesia, several of which have already been transferred to other genera or reduced to synonymy. *H. agardhii* De Toni, *H. tubulosa* Weber-van Bosse and *H. arachnophylloidea* Weber-van Bosse are now considered synonyms of *Sebdenia flabellata* (J. Agardh) Parkinson (Millar 1990). *H. elongata* C. Agardh was reported from the Philippines by (Kraft et al. 1999), but re-examination of the specimens showed that they were genuine *S. flabellata*.

H. kallymenioides Harvey was also reported from Indonesia by Weber-van Bosse (1921), but Scott et al. (1982), who transferred the species to *Cryptonemia kallymenioides* (Harvey) Kraft, doubted its presence outside Australia. Examination of the Siboga collection confirmed that the specimens do not belong to *C. kallymenioides*, but certain identification was not possible, because of the fragmentary nature of the specimens and the absence of wet preserved material. Weber-van Bosse (1921) also reported several *H. durvillei* specimens under different species and varieties, all of which are treated here under *H. durvillei*. The minor differences in gross thallus morphology and branching pattern observed by several authors (Grunow 1867; Grunow 1874; Cribb 1983) were not thought to be sufficient to warrant

Table 2: Distributional data of the genus *Halymenia* in Malayan and tropical Pacific region (synonyms are reported under the currently accepted names and further explained in the discussion)

	Philippines	Indonesia	Papua New Guinea	Taiwan	Fiji
<i>H. amoena</i> Bory de Saint-Vincent		+			
<i>H. clavaeformis</i> Suhr		+			
<i>H. dilatata</i> Zanardini	+	+	+		
<i>H. durvillei</i> Bory de Saint-Vincent	+	+	+	+	+
<i>H. floresia</i> (Clemente y Rubio) C. Agardh	+	+	+		+
subsp. <i>harveyana</i> (J. Agardh) Womersley & Lewis	+		+		
var. <i>ulvoidea</i> (Zanardini) Codomier		+			
<i>H. japonica</i>	+				
<i>H. jensenii</i> Weber-van Bosse		+			
<i>H. maculata</i> J. Agardh	+	+	+		
<i>H. porphyraeformis</i> Parkinson	+		+		
References	Silva et al. (1987), Trono (1997), this study	Weber-van Bosse (1921), Verheij & Prud'homme van Reine (1993)	Millar et al. (1999), Coppejans & Millar (2000)	J.E. Lewis & Norris (1987)	N'Yeurt et al. (1996)

recognition at the species level. The decision by Weber-van Bosse (1921) to recognise several varieties and formas within *H. durvillei* seems needless to us since all possible growth forms fall within the morphological range of recently collected specimens and continuous intergrades between the most extreme growth forms are frequently found (sometimes even within a single specimen).

H. porphyraeformis, previously misidentified as *H. dilatata*, is reported for the Philippines for the first time. The two species have similar foliose habits, but differ in shape and characters of the margins. *H. dilatata* is characterised by irregular sheet-like thalli with a minutely dentate or fringed margin; *H. porphyraeformis* thalli are regularly sinusoidally lobed and the margins are smooth. Weber-van Bosse (1921) and Cribb (1961) reported *H. floresia* var. *ulvoidea* from Indonesia and Queensland respectively, but the specimens are more like *H. dilatata* than the foliose forms of *H. floresia*.

The status of a number of other taxa is yet to be determined. *H. tenuispina* Kützing (1867), described from Java, Indonesia, and *H. polyclada* A. Gepp & E. Gepp (1905), described from Christmas Island, resemble *H. durvillei*, but type material has not been examined. *H. amoena* Bory de Saint-Vincent (1834), described from Cape Comorin (India), was reported from Indonesia by Weber-van Bosse (1921). *H. amoena* was cited by de Jong & Soler-Onís (1998) as *Sebdenia amoena* (Bory de Saint-Vincent) Soler-Onís, an invalid combination. Reasons for this intended new combination were not given. The Weber-van Bosse specimen seems to represent a genuine *Halymenia* species (absence of stellate medullary cells, and presence of a 2-celled carpogonial branch). Unfortunately the type specimen of *H. amoena*, normally

housed in PC, could not be found. In this respect a correct identification of the Weber-van Bosse specimen remains difficult. Weber-van Bosse (1926) also described *H. jensenii* from the Kei Islands, Indonesia. The type specimen is a small (4 cm tall) red, sterile blade, of uncertain affinities. The vegetative anatomy, a laxly branched medulla with predominantly transversely orientated filaments and deeply staining ganglionic cells would not exclude a placement in the genus *Halymenia*.

So far stipe anatomy has not featured prominently in the taxonomy of the Halymeniaceae. Scott et al. (1982) studied the stipe anatomy of some prominently stalked Australian Halymeniaceae. From these data it appears that the anatomy of the stipe could reveal several characters which could be used in species characterisation or generic delimitation. This study initiates the use of the stipe anatomy in the genus *Halymenia*. Stipes of *H. porphyraeformis* and *H. durvillei* were found to be similar in having a distinctive firm cortex, in which growth zones were visible, and a medulla with mainly longitudinally orientated filaments embedded in a matrix. In contrast, *H. maculata* differed with the medulla lacking a matrix. Though somewhat preliminary, these observations suggest that stipe anatomy may be a characteristic useful in distinguishing species.

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References

- ABBOTT, I.A. (1967): Studies in some foliose red algae of the Pacific Coast. I. Cryptonemiaceae. - *J. Phycol.* **3**: 139-149.
- ABBOTT, I.A. (1996): New species and notes on marine algae from Hawai'i. *Pacific Science* **50**: 142-156.
- ABBOTT, I.A. (1998): Some new species and new combinations of marine red algae from the Central Pacific. - *Phycol. Res.* **46**: 97-109.
- ABBOTT, I.A. (1999). Marine red algae of the Hawaiian Islands. Bishop's Museum Press, Honolulu.
- AGARDH, J.G. (1885): Till algernes systematik. Nya bidrag. (Fjerde afdeiningen.) -Lunds Univers. Årsskr. Afdel. Math. Naturv. **21**: 8
- BALAKRISHNAN, M.S. (1961): Studies on Indian Cryptonemiales - III *Halymenia* C.A.Ag. - *J. Madras Univ.* **31**: 183-217.
- BØRGENSEN, F. (1932): Some Indian Rhodophyceae, especially from the shores of the Presidency of Bombay. II. - *Bull. Misc. Inform. Kew* **1932**: 113-134.

- BØRGENSEN, F. (1950): Some marine algae from Mauritius. Additions to parts previously published. II. - Biol. Medell. Kongel. Danske Vidensk. Selsk. **18(11)**: 44 pp.
- BORY DE SAINT-VINCENT, J.B.G.M. (1826-1829): Cryptogamie. In: DUPERREY, L.I. (ed.): Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825. Paris. 301 pp. Atlas. Histoire Naturelle, Botanique. Pls. 1-13, 13bis, 14-38. [Pp. 1-96 (1827), 97-200 (1828), 201-301 (1829); Atlas (1826).]
- BORY DE SAINT-VINCENT, J.B.G.M. (1834): Hydrophytes, Hydrophytae. In: BÉLANGER, C. (ed.): Voyage aux Indes-Orientales ... pendant les années 1825, 1826, 1827, 1828 et 1829: Botanique, Cryptogamie. 159-178.
- CALUMPONG, H.P. & E.G. MEÑEZ (1997): Field guide to the common mangroves, seagrasses and algae of the Philippines. Bookmark, Inc., Makati.
- CHIANG Y.-M. (1970): Morphological studies of red algae of the family Cryptonemiaceae. - Univ. Calif. Publ. Bot. **58**. 95 pp.
- CODOMIER L. (1974): Recherches sur la structures et le développement des *Halymenia* C. Ag. (Rhodophycées, Cryptonémiales) des côtes de France et de la Méditerranée. - Vie & Milieu, Sér. A, Biol. Mar. **24**: 1-24.
- COPPEJANS, E. & A.J.K. MILLAR (2000): Marine Red Algae from the North Coast of Papua New Guinea. - Bot. Mar. **43**: 315-346.
- COPPEJANS, E. & W.F. PRUD'HOMME VAN REINE (1992): The oceanographic Snellius-II expedition. Botanical results. List of stations and collected plants. - Meded. Zitt. Kon. Acad. Overz. Wet. **37**: 153-194.
- CRIBB, A.B. (1961): Some marine algae from Thursday Island and Surrounding Areas. - Univ. Queensl. Dept. Biol. Pap. **4**: 51-59.
- CRIBB, A.B. (1983): Marine algae of the southern Great Barrier Reef. Part I. Rhodophyta. Australian Coral Reef Society, Brisbane. Handbook no. 2. 173 pp.
- DAWSON, E.Y. (1954): Marine plants in the vicinity of the Institute Océanographique de Nha Trang, Viêt Nam. - Pacific Sci. **8**: 372-469.
- DE CLERCK, O. & E. COPPEJANS (1999): Two new species of Dictyota (Dictyotales, Phaeophyta) from the Indo-Malayan region. Phycologia **38**: 184-194.
- DE JONG, Y.S.D.M. (1998): Systematic, Phylogenetic and Biogeographic Studies of Atlantic Seaweeds. PhD thesis at the Rijksuniversiteit Leiden. 203 pp.
- DE TONI, J. B. (1900): Sylloge Algarum. Vol. IV. Florideae. Sectio II. Padova. pp. 387-774 + 775-776.
- DOMANTAY, J.S. (1968): Aquatic Biological Resources of the Philippines. - Acta Manilana, **A 1**: 24-58.
- GEPP A. & E.S. GEPP (1905): Some cryptogams from Christmas Island. - J. Bot. **43**: 337-344.
- GREUTER, W. et al. (eds.) (2000): International Code of Botanical Nomenclature (Saint Louis Code) adopted by the Sixteenth International Botanical Congress St. Louis, Missouri, July - August 1999. Koeltz, Königstein.
- GRUNOW, A. (1867): Algae. In: FENZL, E. (ed.): Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859... Botanischer Theil. Erster Band. Sporenpflanzen. Wien. pp [1]-104, Pls. I, Ia, II-XI.
- GRUNOW, A. (1874): Algen der Fidschi-, Tonga- und Samoa-Inseln, gesammelt von Dr. E. Graeffe. - J. Mus. Godeffroy **3**: 23-50.
- GUIMARÃES, S.M.P.B. & M.T. FUJI (1998): Two species of foliose *Halymenia* (Halymeniaceae, Rhodophyceae) from Brazil. - Bot. Mar. **41**: 495-504.

- HARVEY, W.H. (1857a): Ceylon algae. Nos. 1—30, 31—47, 49—86, 88—106. [Exsiccata with printed names.]
- HARVEY, W.H. (1857b): Friendly Island algae. Nos. 1—15, 15*, 16—50, 50*, 51—124. [Exsiccata with printed names.]
- HEYDRICH, F. (1892): Beiträge zur Kenntnis der Algenflora von Kaiser-Wilhelms-Land (Deutsch-Neu-Guinea). - Ber. Deutsch. Bot. Ges. **10**: 458-485.
- HOLMGREN, P.K., N.H. HOLMGREN & L.C. BARNETT (1990): Index Herbariorum Part I: The Herbaria of the world. New York Botanical Garden, New York.
- KRAFT, G.T., L.M. LIAO, A.J.K. MILLAR, E.G.G. COPPEJANS, M.H. HOMMERSAND & D.W. FRESHWATER (1999): Marine benthic red algae (Rhodophyta) from Bulusan, Sorsogon Province, Southern Luzon, Philippines. -Philipp. Scient. **36**: 1-50.
- KRAFT, G.T. & P.A. ROBINS (1985): Is the order Cryptonemiales defensible? -Phycologia **24**: 67-77.
- KRAFT, G.T. & G.W. SAUNDERS (2000): Bringing order to red algal families: taxonomists ask jurists 'Who's in charge here?' (Commentary). - Phycologia **39**: 358-361.
- KÜTZING, F.T. (1866): Tabulae phycologicae Vol. 16. Nordhausen.
- KÜTZING, F.T. (1867): Tabulae phycologicae Vol. 17. Nordhausen.
- KYLIN, H. (1956): Die Gattungen der Rhodophyceen. Gleerups, Lund.
- LAWSON G.W. (1980): A check-list of East African seaweeds (Djibouti to Zanzibar), Department of Biological Sciences, University of Lagos, Nigeria. Lagos
- LEE, H.B., J.A. LEWIS, G.T. KRAFT & I.K. LEE (1997): *Sinkoreana* gen. nov. (Halymeniaceae, Rhodophyta) from Korea, Japan and southern Australia. -Phycologia **36**: 103-113.
- LEWIS, J.A. (1984): Checklist and bibliography of benthic marine macroalgae recorded from northern Australia. I. Rhodophyta. Department of Defence, Report, Melbourne, Australia.
- LEWIS, J.E. & J.N. NORRIS (1987): A history and annotated account of the benthic marine algae of Taiwan. - Smithsonian Contr. Mar. Sci. **29**: 38.
- MAGGS, C.A. & M.D. GUIRÝ (1982): Morphology, phenology and photoperiodism in *Halymenia latifolia* Kütz. (Rhodophyta) from Ireland. - Bot. Mar. **25**: 589-599.
- MAGGS, C.A. & C.M. PUESCHEL (1989): Morphology and development of *Ahnfeltia plicata* (Rhodophyta): proposal of Ahnfeltiales ord. nov. - J. Phycol. **25**: 333-351.
- MILLAR A.J.K. (1990): Marine red algae of the Coffs Harbour Region, northern New South Wales. - Austr. Syst. Bot. **3**: 293-593.
- MILLAR, A.J.K., O. DE CLERCK, E. COPPEJANS & L.M. LIAO (1999): Annotated and illustrated survey of the marine macroalgae from Motupore Island and vicinity (Port Moresby area, Papua New Guinea). III. Rhodophyta. - Aust. Syst. Bot. **12**: 549-591.
- MONTAGNE, C.D.M. (1844): Plantae cellulares quas in insulis philippinensibus a cl. Cuming collectae recensuit, observationibus non nullis descriptionibusque illustravit C. Montagne, D.M. - London J. Bot. **3**: 658-662.
- NORRIS, R.E. & M.E. AKEN (1985): Marine benthic algae new to South Africa. - S. Afr. J. Bot. **51**: 55-65.
- N'YEURT, A.R., G.R. SOUTH & D.W. KEATS. (1996): A revised checklist of the benthic marine algae of the Fiji Islands, South Pacific (including the Island of Rotuma). - Micronesica **29**: 49-98.
- OKAMURA, K. (1921): Icones of Japanese algae. Vol. 4. Tokyo. pp. 63-149, Pls. CLXLVI-CLXXXV.
- PARKINSON, P.G. (1980): *Halymenia*. III. Pettifogging Press, Auckland.

- PUESCHEL, C.M. & K.M. COLE (1982): Rhodophycean pit-plugs : an ultrastructural survey with taxonomical implications. - *Amer. J. Bot.* **69**: 703-720.
- SAUNDERS, G.W. & G.T. KRAFT (1994): Small-subunit rRNA gene sequences from representatives of selected families of the Gigartinales and Rhodymeniales (Rhodophyta). I. Evidence for the Plocamiales ord.nov. - *Canad. J. Bot.* **72**: 1250-1263.
- SAUNDERS, G.W. & G.T. KRAFT (1996): Small subunit rRNA gene sequences from representatives of selected families of the Gigartinales and Rhodymeniales (Rhodophyta). 2. Recognition of the Halymeniales ord. nov. - *Canad. J. Bot.* **74**: 694-707.
- SCOTT, F.J., R. WETHERBEE & G.T. KRAFT (1982): The morphology and development of some prominently stalked southern Australian Halymeniaceae (Cryptonemiales, Rhodophyta). I. *Cryptonemia kallymenioides* (Harvey) Kraft comb. nov. and *C. undulata* Sonder. - *J. Phycol.* **18**: 245-257.
- SILVA, P.C., P.W. BASSON & M.L. MOE (1996): Catalogue of the Benthic Marine Algae of the Indian Ocean. - *Univ. Calif. Publ. Bot.* **79**: 1259 pp.
- SILVA, P.C. & H.W. JOHANSEN (1986): A reappraisal of the Order Corallinales (Rhodophyceae). - *Brit. Phycol. J.* **21**: 245-254.
- SILVA, P.C., E.G. MEÑEZ & R.L. MOE (1987): Catalog of the Benthic Marine Algae of the Philippines. - *Smithsonian Contrib. Mar. Sci.* **27**: 179 pp.
- TRONO, G.C. (1997): Field guide and atlas of the seaweed resources of the Philippines. Bookmark, Inc., Makati.
- VERHEIJ, E. & W.F. PRUD'HOMME VAN REINE (1993): Seaweeds of the Spermonde Archipelago, SW Sulawesi, Indonesia. - *Blumea* **37**: 385-510.
- WEBER, M. (1902): Siboga Expeditie. Introduction et description de l'expédition. Brill, Leiden.
- WEBER-VAN BOSSE, A. (1921): Liste des Algues du Siboga II. Rhodophyceae Première Partie: Protofloridae, Nemalionales, Cryptonemionales. Brill, Leiden.
- WEBER-VAN BOSSE, A. (1926): Algues de l'expédition danoise aux îles Kei. - *Vidensk. Meddel. Dansk Naturhist. Foren. København* **81**: 57-155.
- WOMERSLEY, H.B.S. & J.A. LEWIS (1994): Halymeniaceae. In: WOMERSLEY, H.B.S.: The marine benthic flora of Southern Australia Part IIIA. Australian Biological Resources Study, Canberra. 167-218 pp.
- WYNNE, M.J. (1993): Benthic marine algae from the Maldives, Indian Ocean, collected during the R/V Te Vega Expedition. - *Contrib. Univ. Michigan Herb.* **19**: 5-30.
- ZANARDINI, J. (1851): Algae novae vel minus cognitae in mari rubro a Portiero collectae. - *Flora* **3**: 33-38.
- ZANARDINI, J. (1858): Plantarum in mari Rubro hucusque collectarum enumeratio (juvante A. Figari). - *Mem. Reale Ist. Veneto Sc.* **7**: 209-309.

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